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Valentin Bault

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Valentin Bault. Evolution de la biodiversité des trilobites du Dévonien d'Afrique du Nord : richesse taxonomique, disparité morphologique et impact de l'environnement. Planète et Univers [physics]. Université Lille, 2021. Français. NNT : . tel-04418961

HAL Id: tel-04418961

<https://hal.science/tel-04418961>

Submitted on 26 Jan 2024

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Université de Lille

UMR CNRS 8198 – Evo-Eco – Paléo

Ecole doctorale – 104

Sciences de la Matière, du Rayonnement et de l'Environnement

Thèse en vue de l'obtention du titre de Docteur de l'Université de Lille

Spécialité : Géosciences, Ecologie, Paléontologie et Océanographie

par

Valentin Bault

**Evolution de la biodiversité des trilobites du Dévonien d'Afrique du Nord :
richesse taxonomique, disparité morphologique et impact de
l'environnement**

Thèse dirigée par

Catherine Crônier

Soutenue le 6 décembre 2021

Membres du jury:

Gregory D. Edgecombe	Professeur	Natural History Museum, UK	<i>Rapporteur</i>
Sophie Montuire	Directeur d'études	EPHE-Univ. Bourgogne, France	<i>Rapporteuse</i>
Sylvain Gerber	Maître de conférences	MNHN, France	<i>Examineur</i>
Christian Klug	Professeur	Univ. Zurich, Suisse	<i>Examineur</i>
Thomas Servais	Directeur de recherche	CNRS-Univ. Lille, France	<i>Président</i>
Claude Monnet	Ingénieur de recherche	Univ. Lille, France	<i>Invité</i>
Catherine Crônier	Professeure	Univ. Lille, France	<i>Directrice de thèse</i>

Université de Lille
CNRS-UMR 8198 Évo-Éco-Paléo
Bâtiment SN5
Avenue Paul Langevin
Cité Scientifique
59655 Villeneuve d'Ascq cedex
France

RÉSUMÉ :

L'effet des changements environnementaux sur la biodiversité actuelle est une préoccupation majeure. Comprendre l'impact de ces changements sur la biodiversité passée est une des clés pour pouvoir appréhender les bouleversements actuels et futurs. Les trilobites, ont connu de nombreux changements favorables à leur diversification ainsi que de nombreuses crises les amenant proche de l'extinction. Leurs fossiles abondent en Afrique du Nord, ce qui en fait une région idéale pour les étudier. L'objectif de cette thèse a été d'estimer les variations de la biodiversité des trilobites de cette région et d'en identifier leurs origines et conséquences à partir de bases de données compilant l'ensemble des occurrences issues de la littérature. Le premier aspect de la biodiversité étudié a été celui de la richesse taxonomique. A l'aide de différents indices de diversité, on a évalué les grandes tendances globales puis les variations régionales. Alors que la diversité générique était faible au début du Dévonien, une régression marine a ensuite conduit à une importante diversification, visible à l'échelle globale : la diversification Praguienne. Les trilobites atteignirent un pic de diversité à l'Emsien, mais par la suite, une succession de changements abrupts du niveau marin associés à de l'anoxie les ont affectés sévèrement. Entre l'Eifelien et le Givétien, les trilobites ont perdu plus de 90% de leur diversité générique. Celle-ci devient encore plus faible au Frasnien et deux ordres disparurent. Après l'extinction de masse du Kellwasser à la limite Frasnien-Famennien, une légère récupération eut lieu impliquant uniquement les ordres Proetida et Phacopida. Le deuxième aspect a été d'étudier la disparité morphologique avec l'aide de points homologues et d'analyses Procruste. Cette étude de la variabilité morphologique a montré les mêmes tendances que celle de la diversité avec un nombre important d'innovations au Dévonien inférieur. Parmi les nouveautés on a noté le développement d'épines. Si les premiers événements biotiques n'ont conduit qu'à une faible perte de morphologies, la plupart des formes ont disparu au Givétien. Les formes les plus touchées sont celles apparues au Praguien et à l'Emsien alors que les formes héritées du Silurien vont se maintenir tout au long du Dévonien. La versatilité de ces formes vis-à-vis des changements d'environnements ou de mode de vie les a aidés à survivre, les ordres caractérisés par ces morphologies ont pu ainsi résister aux différentes crises écologiques. La transition Frasnien-Famennien a marqué le développement des trilobites à vision réduite en réponses aux événements environnementaux. La diversité et la disparité des trilobites d'Afrique du Nord sont donc relativement couplées. Une attention particulière a été donnée aux phacopidés, une famille emblématique du Dévonien qui y atteindra son apogée avant de disparaître à la fin de la période. Les variations géographiques ont aussi joué un rôle important dans la biodiversité des trilobites avec d'importants échanges fauniques qui ont caractérisé les environnements homogènes du Dévonien inférieur. A contrario, les disparités géographiques et les événements tectoniques du Dévonien moyen et supérieur ont empêché les migrations et les échanges fauniques et ont accéléré le déclin des trilobites. En conclusion, cette étude régionale a montré que les changements environnementaux ont eu des effets importants sur la biodiversité mais que ces effets ont pu être positifs ou négatifs. Un même type de changement peut aboutir à des conséquences différentes en termes de diversité et de disparité car plusieurs phénomènes peuvent intervenir en même temps et l'estimation de leur impact mutuel reste primordial.

Mots-clés : Trilobites, Dévonien, Afrique du Nord, Extinction, Changements environnementaux, Diversité, Disparité morphologique

ABSTRACT:

The effect of environmental changes on current biodiversity is a major concern. Understanding the impact of these changes on past biodiversity is one of the keys to interpret current and future upheavals. The trilobites have undergone many changes favourable to their diversification as well as many crises leading them close to extinction. Their fossils abound in North Africa, which make it an ideal region to study them. The objective of this thesis was to estimate the variations in the biodiversity of trilobites in this region and to identify their origins and consequences from databases compiling all the occurrences of the literature. The first aspect of biodiversity studied was the taxonomic richness. Using different diversity indices, we assessed the major global trends and then regional variations. While generic diversity was low at the beginning of the Devonian, a subsequent marine regression led to an important diversification, observable at a global : the Pragian diversification. Trilobites reached a peak of diversity in the Emsian, but subsequently a succession of abrupt sea level changes associated with anoxia events severely affected them. Between the Eifelian and the Givetian, trilobites have lost more than 90% of their generic diversity. Generic diversity still decreased in the Frasnien and two orders disappeared. After the Kellwasser mass extinction at the Frasnian-Famennian boundary, a slight recovery occurred involving only the Proetida and Phacopida orders. The second aspect was to study the morphological disparity by using landmarks. This study of morphological variability showed the same trends as that of diversity with a significant number of innovations in the Lower Devonian. Among the novelties, there was the development of spines. While the first biotic events only led to a slight loss of morphology, most forms disappeared in the Givetian. The most affected shapes are those that appeared in the Pragian and Emsian, while the forms inherited from the Silurian persisted throughout the Devonian. The versatility of these forms toward environmental or lifestyle changes helped them to survive, as the orders characterized by these morphologies were thus able to withstand various ecological crises. The Frasnien-Famennien transition marked the development of reduced vision trilobites in response to environmental events. The diversity and disparity of North African trilobites are therefore relatively coupled. Particular attention was given to phacopids, an emblematic Devonian family which reached its peak there before disappearing at the end of the period. Geographic variations also played an important role in the biodiversity of trilobites with important faunal exchanges that characterized the homogeneous environments of the Early Devonian. Conversely, the geographic disparities and tectonic events of the Middle and Late Devonian prevented migration and wildlife exchanges and accelerated the decline of trilobites. In conclusion, this regional study showed that environmental changes had significant effects on biodiversity but that these effects could be positive or negative. The same type of change can lead to different consequences in terms of diversity and disparity because several phenomena occurred at the same time and it is essential to estimate their combined effect.

Keywords: Trilobites, Devonian, North Africa, extinction, environmental changes, diversity, morphological disparity

REMERCIEMENTS :

Je souhaite remercier en premier lieu Catherine Crônier pour m'avoir encadré lors de cette thèse, en m'apportant toute l'aide nécessaire et en me poussant sans-cesse à m'améliorer. Je tiens aussi à remercier Claude Monnet pour toute son aide et ses réponses à mes questions, jusqu'aux repas ! Un grand merci également à tous les membres de l'équipe Pal et à notre directeur de laboratoire Xavier Vekemans, pour leur disponibilité et leur soutien dès que j'en avais besoin.

Je souhaite exprimer mes remerciements envers Christian Klug pour son aide et pour m'avoir donné l'opportunité unique d'aller sur le terrain au Maroc. Merci à lui, à Céline Poux, à Pascal Neige et à Borja Cas-Miñana pour leur aide précieuse lors des comités de thèse. J'en profite pour remercier les membres du jury dont Christian Klug fait aussi parti : Gregory D. Edgecombe, Sylvain Gerber, Sophie Montuire et Thomas Servais.

Merci à tous les doctorants cotoyés au cours de ma thèse : Léa, David, Navid, Houcine, Zhen, Berlin, Shucan, Vahram, Hayk, Elliott, Veronica, Juan et Mathias. Grâce à eux j'ai pu m'améliorer en paléontologie, en langues étrangères et en basket ! Merci également aux Argentins et notamment JuanJo, Diego et Arnaud, pour leur accueil et leur collaboration. Je n'oublie pas les doctorants qui m'ont accueilli à Córdoba et les Zurichois qui m'ont accompagné sur le terrain dans le Tafilalt.

Je remercie mes financeurs, la région Hauts-de-France et l'Université de Lille, et également le projet ECOS-Sud pour m'avoir permis un séjour en Argentine.

Je remercie également mes amis : les Chuiffettes, les Vauclusiens et à tous les autres pour m'avoir encouragé et supporté tout au long de ma thèse. Un grand merci également à ma famille, particulièrement à ma mère et mon frère, pour qui je travaille sur des « sortes de crevettes ».

Enfin, je tiens à exprimer ma gratitude aux diverses personnes qui ont relu mon anglais afin d'améliorer la qualité de mes manuscrits.

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INTRODUCTION

1. Evolution en temps profond

Depuis l'apparition de la vie il y a plus de 3,5 milliards d'années (Nutman et al., 2016 ; Dodd et al., 2017), la biodiversité a beaucoup changé. Les changements sont de différentes natures avec des variations de forme, d'abondance, d'écologie, de métabolisme et bien d'autres (Bambach et al., 2002 ; McNamara, 2008 ; Alroy, 2010 ; Klug et al., 2010). Comprendre ces modifications et expliquer la disparition de certaines espèces au cours des temps géologiques est devenue une préoccupation scientifique et sociétale majeure (Bellard et al., 2012 ; Jones et Cheung, 2015 ; Briggs, 2017 ; Worm et Lotze, 2021). L'étude de ces changements de biodiversité peut être abordée selon deux échelles évolutives complémentaires : la macroévolution et la microévolution (Erwin, 2010 ; Li et al., 2018). La microévolution concerne tout ce qui se passe à l'échelle intra-spécifique, notamment les changements génétiques au sein des populations (Hendry et Kinnison, 2001) alors que la macroévolution se réfère aux changements supra-spécifiques (Hautmann, 2020). Ainsi, si les biologistes tentent de comprendre les extinctions actuelles et leurs conséquences potentielles, les paléontologues contribuent à cet effort en analysant l'évolution de la biodiversité dans le temps profond. Un objectif essentiel en macroévolution est de mieux connaître les événements de la biodiversité telles que les phases d'extinction et de radiation (Sepkoski, 1984 ; Jablonski, 1994 ; Kirchner et Weil, 2000 ; Bambach et al., 2004 ; Erwin, 2008). Ces événements sont souvent consécutifs à des changements paléoenvironnementaux et leurs études permettent notamment de comprendre les modalités (mode et rythme) d'évolution (Eldredge et Gould, 1972). C'est dans ce cadre d'évolution de la biodiversité en temps profonds que s'inscrit cette thèse.

1.1. Evolution et paléobiodiversité

L'étude de la biodiversité passée - la paléobiodiversité - et son évolution au cours du temps se base surtout sur le registre fossile (Benton et Harper, 2021). L'enregistrement des données fossiles a fortement augmenté depuis l'explosion cambrienne avec le développement d'organismes biominéralisés plus facilement préservables (Briggs, 2015). La préservation des fossiles n'est d'ailleurs pas homogène ni dans le temps, ni dans l'espace (Holland, 2016). De plus, de nombreux organismes sont composés majoritairement - voire complètement - de tissus

mous et restent difficilement conservés au cours des temps géologiques (Briggs, 1995 ; Klompmaker et al., 2017 ; Purnell et al., 2018). Ils sont surtout connus grâce aux sites à conservation exceptionnelle, les Lagerstätten, dont l'un des plus connus est celui de Burgess (Morris 1979 ; Gaines 2014). Ce problème de préservation s'ajoute à d'autres biais d'échantillonnages comme l'effort d'échantillonnage (Tarver et al., 2007). Ces biais compliquent le travail des paléontologues, l'étude de la paléobiodiversité se basant sur l'abondance et les caractéristiques des fossiles.

Les savants ont cherché à comprendre ce qu'étaient ces fossiles et pourquoi il y avait de tels changements de forme dès l'Antiquité. Les doctrines telles que l'établissement des modalités évolutives, l'identification des processus mis en jeu et l'évaluation de l'impact de l'environnement se sont basées sur les études de la forme des organismes (Simpson, 1953 ; Eldredge et Gould, 1972 ; Hunter, 1998 ; Gayon, 2000 ; Gerber et al., 2008). Les premières véritables théories de l'évolution n'ont été établies qu'au XIX^{ème} siècle par Jean-Baptiste Lamarck puis Charles Darwin. Charles Darwin met en avant la sélection naturelle comme mécanisme de l'évolution (Darwin, 1859 ; Greenberger, 2005). Il explique que l'élimination des individus les moins adaptés à la survie permet aux espèces de se perfectionner. Au XX^{ème} siècle, la théorie a évolué avec le courant Néo-Darwiniste emmené notamment par Ernst Mayr, Theodosius Dobzhansky et George G. Simpson. Ces scientifiques ont établi la Théorie Synthétique de l'Evolution (TSE, Huxley, 1942), attribuant les changements évolutifs aux mutations génétiques aléatoires adoptées ou non par la sélection naturelle. La sélection naturelle est donc le moteur de l'évolution, l'adaptation à l'environnement est le seul critère d'évolution à partir de mutations (Gould, 1984). Les espèces doivent alors évoluer en permanence pour survivre dans un environnement sans cesse changeant : c'est la théorie de la Reine Rouge (Van Valen, 1973). La question de l'impact de l'environnement sur la biodiversité est donc primordiale. Cependant, lors des dernières décennies, les avancées réalisées en biologie et en paléontologie ont montré que la Théorie Synthétique de l'Evolution était trop simpliste (Alberch, 1982 ; Smith, 1992 ; Lenski et Mittler, 1993). Les Néo-Darwinistes ont situé l'évolution au niveau des populations et ont négligé les mécanismes au niveau de l'individu et en particulier au niveau de l'ontogénèse (Depew et Weber, 1989). Cette phase développementale a pourtant un rôle majeur dans les mécanismes de l'évolution (Alberch, 1980 ; Minelli, 2003 ; Klingenberg, 2010) et a été intégrée dans la théorie actuelle connue sous le nom d' « Evo-Dévo ». L'environnement reste cependant un acteur majeur de l'évolution même si selon certaines théories, la sélection des mutations reste très limitée : c'est le neutralisme (Kimura 1983). La sélection naturelle agit donc en fait plutôt comme un filtre à

partir d'une évolution dirigée par les contraintes développementales et la dérive génétique. L'évolution se fait donc au niveau de l'individu, mais se manifeste à différents niveaux taxonomiques.

Les variations spatiale et temporelle de l'environnement sont donc en partie source de divergence écologique, amenant à des espèces différentes avec des morphologies et des écologies différentes (Erwin, 1993, 2015 ; Dumont et al., 2012). La spéciation est notamment une composante primordiale des changements de paléobiodiversité, les espèces étant des lignées de métapopulations évoluant séparément (De Queiroz, 2007). Il est donc important de quantifier les morphologies (i.e., la disparité morphologique) et la biodiversité au cours du temps pour comprendre les adaptations et ainsi interpréter les processus de diversification.

1.2. Paléobiodiversité, crises biotiques et phases de récupération post-crise

Bien que les écosystèmes précambriens sont de mieux en mieux identifiés (Buatois et Mángano, 2016 ; Darroch et al., 2018), les études de paléobiodiversité se focalisent surtout sur le Phanérozoïque (Raup et Sepkoski, 1982 ; Alroy et al., 2008 ; Fan et al., 2020). La diversité a rapidement augmenté au Cambrien avant de fluctuer pendant les 500 millions d'années qui suivirent. Les clades phanérozoïques connaissent généralement un pic de diversité assez tôt dans leur histoire évolutive (Hughes et al., 2013). Ce type de clade est appelé « *Bottom Heavy Clade* » (Gould et al., 1987). En plus des changements quantitatifs, le paysage biologique a changé avec le renouvellement des faunes et des flores au cours du temps (Sepkoski, 1981 ; Alroy, 2010 ; Capel et al., 2021). La biodiversité est notamment dirigée par les changements environnementaux aussi bien à long qu'à court terme (Roberts et Mannion, 2019).

Au cours du Phanérozoïque, des phases d'extinctions brutales sont venues perturber la biodiversité avec la disparition de nombreux clades (Raup et Sepkoski, 1982 ; Bambach, 2006) et une modification considérable de la biosphère (Jablonski, 2005). Ces crises biotiques sont causées par des perturbations plus ou moins brutales de l'environnement à grande échelle (Hallam, 1998 ; Bond et Grasby, 2017). Parmi les causes des extinctions de masse on retrouve le volcanisme (Wignall, 2001 ; Bergquist, 2017), la chute d'astéroïdes (Schulte, 2010), les changements climatiques (Song et al., 2021), les variations eustatiques associées à des événements anoxiques (House, 2002), les paramètres orbitaux (De Vleeschouwer et al., 2017), tous ces facteurs pouvant être étroitement liés. Cinq extinctions ont notamment eu un impact considérable sur la paléobiodiversité : ce sont les cinq extinctions de masses (Raup et Sepkoski, 1982). Elles ont eu lieu à la fin de l'Ordovicien, à la fin du Dévonien, à la limite Permien-Trias,

à la limite Trias-Jurassique et à la limite Crétacé-Paléogène (Fig. 1) et ont toutes conduit à la disparition de plus de 75% des espèces (Jablonski, 1994), la plus sévère étant celle survenant à la fin du Permien (Erwin, 1990). D'autres crises ayant eu un moindre impact ont aussi eu lieu au cours du Phanérozoïque (Walliser, 1996 ; House, 2002 ; Bambach, 2006). Outre les extinctions brutales que constituent les crises biologiques, la biodiversité est en renouvellement sans-cesse avec des apparitions et des disparitions continuent d'espèces (Hartvigsen, 2013). Ce bruit de fond est majoritairement dû à des facteurs biotiques tels que la compétition et la prédation (Hartvigsen, 2013). Les taux d'apparitions augmentent en périodes de faible diversité, après les extinctions, et au contraire, les taux d'extinctions augmentent en périodes de forte diversité (Alroy, 2008). Les extinctions ayant conduit à la disparition de nombreux taxons, les survivants peuvent coloniser de nouvelles niches laissées vacantes et ainsi se diversifier : c'est l'hypothèse de l'éco-espace vide, ou « *empty ecospace* » (Erwin, 1993, 2001). Ces nouvelles opportunités peuvent conduire à la diversification écologique et morphologique des taxons, c'est une radiation adaptative (Erwin, 2015 ; Jablonski, 2017 ; Stroud et Losos, 2016). Ce phénomène est en partie le moteur des récupérations post-crisis, périodes plus ou moins longues où la biodiversité redémarre (Jablonski, 1994, 2005). Cependant, certains clades ayant échappé à une extinction ne connaissent pas de récupération et restent longtemps appauvris avant de disparaître, ce sont les « *Dead Walking Clade* » (Jablonski, 2002 ; Barnes et al., 2021).

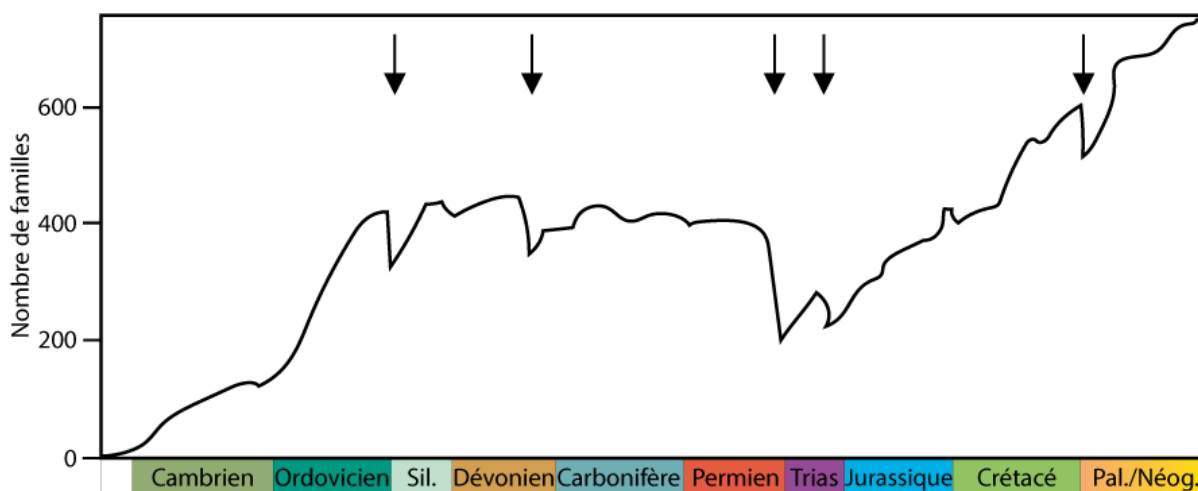


Figure 1 : Evolution de la diversité des organismes marins au cours du Phanérozoïque et position des cinq extinctions de masse (modifié d'après Raup et Sepkoski, 1982). Abréviations : Sil. : Silurien ; Pal. : Paléogène ; Néog. : Néogène

1.3. Macroévolution et disparité

Lors des dernières décennies, de nombreuses études ont montré l'intérêt d'analyser la disparité morphologique des clades (Roy & Foote, 1997 ; Neige, 2003 ; Adams et al., 2004, 2009), la macroévolution reposant principalement sur l'étude de la forme des organismes. En quantifiant la diversité de formes dans différents contextes, cette métrique est largement complémentaire de la diversité taxonomique, longtemps considérée comme la métrique standard de l'étude de la biodiversité et de ses fluctuations (Sepkoski, 1978 ; Hallam et Wignall, 1997). L'approche morphologique n'est pas nécessairement corrélée avec l'approche taxonomique. Leur confrontation dans le temps (Roy et Foote, 1997) et dans l'espace (Neige, 2003) est une source importante de compréhension des fluctuations de la biodiversité à grande échelle, en termes de patrons et de processus.

La disparité morphologique s'est accrue dès le Paléozoïque inférieur et a continué à s'étendre ensuite (Foote, 1993 ; Deline et al., 2018). En effet, les clades se diversifient morphologiquement généralement assez rapidement au cours de leur histoire évolutive (Hughes et al., 2013), bien qu'une augmentation tardive de disparité morphologique puisse se produire (Hopkins et Smith, 2015). Disparité morphologique et diversité peuvent être couplées bien que ce ne soit pas automatique (Foote, 1993). Ainsi, au-delà de l'aspect quantitatif, les crises biologiques impliquent des modifications morphologiques avec des changements de taille (Harries et Knorr, 2009), de la perte de morphologies (Korn et al., 2013 ; Puttick et al., 2020 ; Cole et Hopkins, 2021) et des innovations (Friedman, 2010 ; Schoenemann, 2018 ; Lowery et Fraas, 2019) en lien avec les changements environnementaux. Une perte de morphologie peut mettre en évidence la sélectivité des extinctions, ce qui n'est pas systématiquement le cas (Peters, 2008 ; Janevski et Baumiller, 2009 ; Korn et al., 2013 ; Payne et al., 2016 ; Cole et Hopkins, 2021). Les innovations peuvent être la conséquence d'une adaptation à un nouveau biotope suite aux changements environnementaux (Schoenemann, 2018 ; Feist, 2019).

1.4. Paléobiodiversité et paléobiogéographie

La diversité des organismes évolue au cours du temps mais aussi dans l'espace. Une composante importante de son estimation est donc la biogéographie, qui est l'étude de la distribution géographique des êtres vivants. Elle a pour objectif d'identifier les facteurs biotiques et abiotiques responsables de la répartition des espèces. La biogéographie est en fait subdivisée en deux aspects : la biogéographie écologique qui analyse l'interaction fonctionnelle des organismes avec l'environnement et la biogéographie historique qui étudie l'héritage historique (Cecca et Zaragüeta, 2015). Des provinces biogéographiques (Udvardy, 1975 ;

Costello et al., 2017) ou paléobiogéographiques (Boucot et al., 1969 ; Dowding et Ebach, 2019) ont ainsi pu être identifiées. Les espèces ne réagissent pas toutes de la même façon face aux hétérogénéités environnementales de la planète, certaines étant cosmopolites avec un fort pouvoir de migration et de dispersion tandis que d'autres sont plus endémiques, restreintes à un environnement particulier (Fattorini, 2017 ; Eller et al., 2017). Les changements environnementaux impactent différemment les espèces suivant leur faculté de dispersion (Pacifci et al., 2015 ; Button et al., 2017).

1.5. Modèle d'étude

Ce travail a pour objectif de contribuer à la compréhension des facteurs de régulation biotiques et abiotiques de la diversité. Il s'agit de comprendre comment s'articulent les diversités taxonomique et morphologique au cours des temps géologiques. Le but étant de comprendre comment certains changements écologiques ont pu avoir des conséquences positives sur la diversité alors que d'autres ont au contraire eu des répercussions néfastes. De plus, un même type de changement environnemental a-t-il toujours eu les mêmes conséquences ? Si non, comment l'expliquer ? Quels sont les effets des changements environnementaux sur la biosphère ? Comment la biodiversité redémarre-t-elle après une extinction ? Pour répondre à ces questions, le modèle du passé choisi doit être restreint dans le temps et l'espace. Il doit aussi se baser sur un support permettant de quantifier ces changements. C'est dans ce contexte que les **trilobites du Dévonien d'Afrique du Nord** ont été choisis comme modèle d'étude.

2. Le Dévonien, période clé de l'histoire de la vie

2.1. La période Dévonienne

Afin d'analyser quantitativement la biodiversité passée et ses réponses face aux changements environnementaux, il est nécessaire de travailler sur une échelle contrainte temporellement. Le Dévonien est l'une de ces périodes clés qui a été grandement étudiée. C'est la quatrième période géologique du Paléozoïque après le Cambrien, l'Ordovicien et le Silurien. Il s'étend de -419 à -359 millions d'années et est subdivisé en trois époques (tableau 1). Le Dévonien représente une période clé de l'histoire de la vie pour l'Ere Paléozoïque puisqu'il comporte l'une des cinq grandes crises biologiques du Phanérozoïque : la crise Frasnien–Famennien. C'est une période

caractérisée par de profonds changements environnementaux, climatiques et écologiques qui se répercutent sur la biosphère. C'est une période idéale pour étudier l'impact de l'environnement sur la biodiversité ainsi que la capacité de réaction des organismes.

System / Epoch	Series / Epoch	Stage / Age	numerical age (Ma)	
Devonian	Upper	Famennian	358.9 ±0.4	
		Frasnian	372.2 ±1.6	
	Middle	Givetian	382.7 ±1.6	
		Eifelian	387.7 ±0.8	
	Lower	Emsian	393.3 ±1.2	
		Pragian	407.6 ±2.6	
		Lochkovian	410.8 ±2.8	
				419.2 ±3.2

Tableau 1 : Divisions stratigraphiques internationales du Dévonien (modifié d'après [Cohen et al., 2013](#) ; v. 03/2020).

2.2. Contexte paléogéographique et paléoenvironnemental

Au Dévonien inférieur, il existe trois principaux continents : le Gondwana, la Laurentia, la Siberia-Kazakstania (Fig. 2). La plupart des surfaces continentales sont situées dans l'hémisphère sud et entourées par un immense océan : la Panthalassa ([Scotese et al., 2021](#)). Entre ces continents se situent deux océans plus petits : l'Océan Rhéique et la Paléothétys. Le Gondwana tend à remonter vers le nord au Dévonien ([Scotese et al., 2021](#)). L'orogénèse Calédonienne à l'origine de la Laurentia s'est terminée au Silurien mais témoigne de la dynamique d'unification des continents, afin de former le futur supercontinent la Pangée au Carbonifère ([Stampfli et al., 2013](#) ; [Scotese et al., 2021](#)). Toutefois, le continent Cathaysia (Chine du Sud et Chine du Nord) se sépare du Gondwana au Dévonien inférieur ([Scotese et al., 2021](#)). Au Dévonien supérieur, l'océan Rhéique qui sépare la Laurentia et le Gondwana se ferme ([Scotese et al., 2021](#)). L'orogénèse Varisque se met alors en place en Europe et en Afrique du Nord ([Franke et al., 2017, 2021](#)) et l'orogénèse Acadienne en Amérique du Nord ([Hatcher, 2010](#)). De son côté, la Paléothétys s'agrandit et des zones de rifting affectent la Laurussia et la Siberia produisant une forte activité volcanique ([Golonka, 2020](#)).

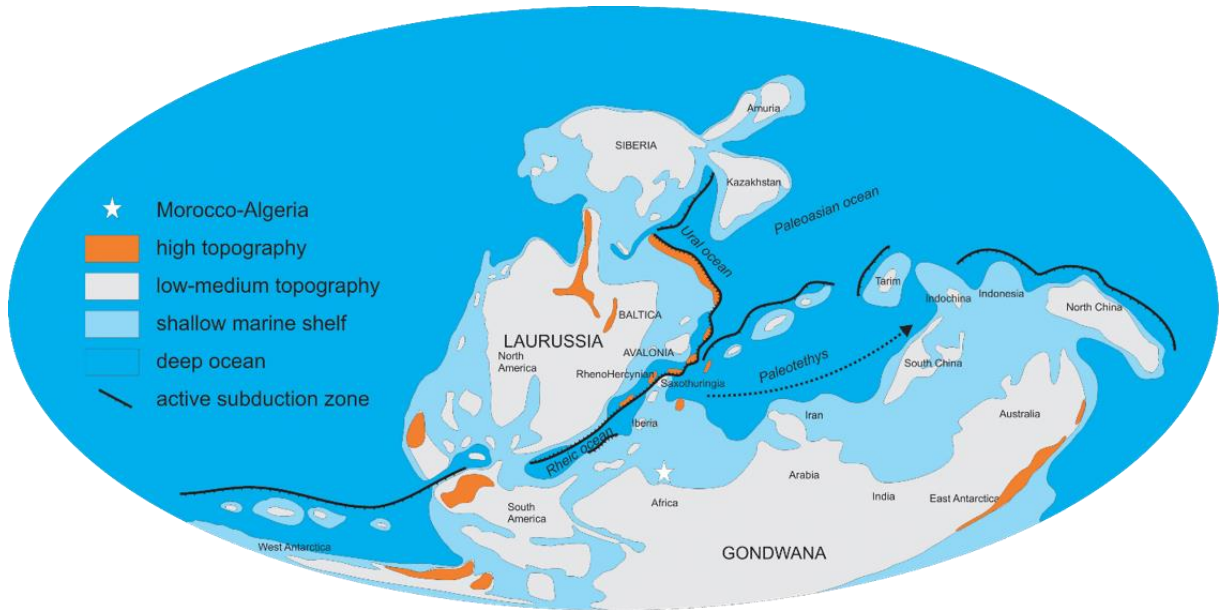


Figure 2 : Paléogéographie du Dévonien Moyen et position du Maroc et de l'Algérie (modifié d'après *Golonka et Gaweda, 2012*).

Les progrès de la science permettent de reconstituer de mieux en mieux les variations environnementales passées. Un des moyens pour arriver à ces reconstitutions est l'utilisation de proxys isotopiques comme le $\delta^{13}\text{C}$, indicateur du cycle du carbone, le $\delta^{18}\text{O}$, indicateur des paléotempératures, et le rapport $^{87}\text{Sr}/^{86}\text{Sr}$, indicateur de l'expansion crustale et/ou de l'altération des silicates continentaux (*Jones et al., 1994 ; Capo et al., 1998 ; Joachimski et al., 2009*). D'autres paramètres environnementaux sont reconstitués à partir des données stratigraphiques et biologiques entre autres. Cela a notamment permis d'obtenir pour le Paléozoïque des données concernant l'indice de fragmentation continentale (*Zaffos et al., 2017*), la pression partielle en CO_2 ($p\text{CO}_2$, *Foster et al., 2017*), la paléotempérature marine et atmosphérique (*Scotese et al., 2021*) ou encore le niveau marin (*Haq et Schutter, 2008*). *Cocks (2007)* a contribué à mieux connaître les environnements passés en identifiant les périodes de glaciations et *Hay et al. (2006)* en estimant la masse sédimentaire des continents et océans.

Avec toutes ces informations compilées, le climat et la paléogéographie du Dévonien ont pu ainsi être reconstruits. Le climat était chaud au Lochkovien et le niveau marin était élevé. Mais, dès le Praguien, une phase régressive commença, associée à une baisse des températures (Fig. 3). Cette tendance continua à l'Emsien où les températures atteignirent des valeurs relativement basses, malgré un bref réchauffement à l'Emsien inférieur (*Scotese et al., 2021*). Entre l'Emsien et le Givétien, le climat était le plus froid du Dévonien avec des températures moyennes de $18,7^\circ\text{C}$ (*Scotese et al., 2021*), ce refroidissement restant néanmoins modéré (*Boucot et al., 2013*). Le climat commença à se réchauffer au Givétien tandis qu'une phase transgressive à

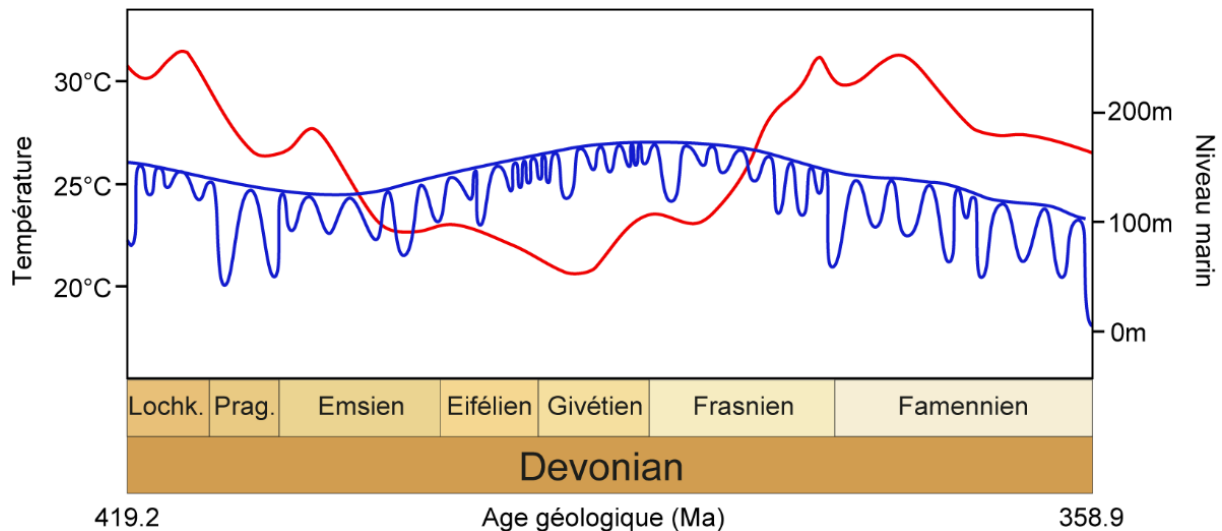


Figure 3 : Variations du niveau marin d'après [Haq et Schutter \(2008\)](#) et paléotempérature d'après [Joachimski et al. \(2009\)](#) au cours du Dévonien. Age d'après [Cohen et al. \(2013, v. 03/2020\)](#).

long-terme se mit en place ([Haq et Schutter, 2008](#)). L'augmentation des températures conduisit au développement de nombreux récifs ([Copper et Scotese, 2003](#) ; [Joachimski et al., 2009](#)). Au Dévonien supérieur, les températures étaient élevées tout comme le niveau marin, notamment au Frasnien ([Johnson et al., 1985](#) ; [Haq et Schutter, 2008](#) ; [Joachimski et al., 2009](#)). Cette époque a également été marquée par un volcanisme effusif intense, en lien avec la tectonique Eovarisque, qui a été un acteur de la crise du Frasnien–Famennien ([Racki, 2020](#)). L'eau de mer est devenue alors anormalement riche en $^{87}\text{Sr}/^{86}\text{Sr}$ ([Zhang et al., 2020](#)). Une importante et rapide transgression suivie d'une régression globale accompagna ces changements ([Johnson et al., 1985](#) ; [Bond et Wignall, 2008](#)). A la fin du Famennien, le niveau marin et les températures diminuèrent, menant jusqu'à une potentielle glaciation ([Joachimski et al., 2009](#) ; [Kaiser et al., 2015](#)). Tout au long du Dévonien, la pression partielle en CO_2 atmosphérique diminua ([Witkowski et al., 2018](#)). Cette baisse était probablement due au développement de la végétation continentale augmentant l'altération des silicates et donc l'apport de nutriments, et à l'augmentation de l'enfouissement du carbone résultant de l'augmentation de la productivité primaire ([Algeo et Scheckler, 1998](#) ; [Simon et al., 2007](#)). La tectonique et le volcanisme en résultant ont également pu amener à l'altération des silicates et donc au refroidissement du climat ([Macdonald et al., 2019](#) ; [Racki, 2020](#)).

2.3. Evolution de la biodiversité Siluro-Dévonienne

L'étude des proxies environnementaux liés à l'évolution paléogéographique et celle du registre fossile ont montré que la première extinction de masse causée par les changements climatiques à la fin de l'Ordovicien (Bond et Grasby, 2020 ; Liao et Sun, 2020) a eu des conséquences cataclysmiques avec la disparition de 85% des espèces (Sheehan, 2001). Cependant, après une telle extinction, les océans n'ont pas été dépeuplés pour autant et de nombreux clades siluriens ont remplacé ceux qui n'ont pas survécu à la crise (Jin et Copper, 2010 ; Melchin et al., 2011 ; Copper et Jin, 2012). Malgré quelques crises écologiques mineures provoquées par des changements environnementaux (Calner, 2008), le Silurien est réputé comme une période relativement stable. En revanche, la période suivante, le Dévonien, est caractérisé par des changements majeurs à la fois en termes de biodiversité et d'environnement. En effet, il y a eu des phases importantes de diversification, dont le développement de certains clades qui changeront le visage de la Terre et des océans à tout jamais, mais aussi des extinctions majeures. Une régression majeure à la transition Lochkovien–Praguien a permis la mise en place de vastes mers épicontinentales peu profondes ayant favorisé la prolifération de faunes benthiques au Dévonien inférieur (Chlupáč, 1994 ; Morzadec, 2001). Le Dévonien étant une période plus chaude que les précédentes (Tinn et al. 2020), le développement de vastes récifs a été facilité au Dévonien moyen et au Frasnien (Copper et Scotese, 2003 ; Copper, 2011). Cependant, les faunes benthiques ne sont pas les seules à connaître une diversification significative à cette époque puisque les océans ont connu à cette période la Révolution Nectonique Dévonienne (The Devonian Nekton Revolution, Klug et al., 2010). Alors que la plupart des espèces étaient benthiques, démersales ou planctoniques auparavant, de nombreux clades nectoniques se sont développés dont les poissons et les céphalopodes. Toutes les espèces nectoniques ne se sont pas diversifiées en même temps puisque les Dacryoconaridés (tentaculites) ou les Ostréostracés (poissons sans mâchoire) se sont développés dès le Praguien alors que les Nauliloïdes, les Ammonoïdes, les Placodermes (poissons à mâchoire) et les Elasmobranches (poissons cartilagineux) se sont diversifiés dans la seconde moitié du Dévonien (Klug et al., 2010). Sur terre aussi, la vie connaît une diversification importante avec le développement des plantes. Si les traces des premières plantes terrestres remontent à l'Ordovicien (Servais et al., 2019), elles ont colonisé de manière importante les continents au Dévonien grâce notamment au développement des plantes vasculaires (Capel et al., 2021).

Le Dévonien n'est cependant pas seulement une période de prolifération de la vie, puisqu'à partir du Dévonien moyen, de nombreux clades vont connaître une perte de diversité à cause

d'événements environnementaux répétés (Walliser, 1996 ; House, 2002 ; Becker et al., 2016).

Ces événements brutaux correspondent généralement à une phase transgressive rapide associée

chrono.	conodont zonations		amm.	anox.	events/ crises	chrono.	conodont zonations		amm.	anox.	events/ crises
	old	new					old	new			
GIVETIAN	middle	m.	<i>ansatus</i>	D	Taghanic Cr.	F	<i>sulcata</i>	<i>sulcata</i>	I-A		Upper Middle Lower Hangen- berg Cr.
		varcus	<i>rhenuanus- varcus</i>	C	Upper <i>pumilio</i>		upp.	<i>kockeli</i>	F		
	lower	low.	<i>timorensis</i>	MD II B	Lower <i>pumilio</i>		m.	<i>ckl</i>	E		
		upp.	<i>hemiansatus</i>	A			low.	<i>praesulcata</i>	UD VI C B		
EIFELIAN	upper	387.7	<i>ensensis</i>	F ₂	Upper Kačák Lower	upper	<i>expansa</i>	<i>costatus</i>	UD V C B		Dasberg Cr.
		low.	<i>ensensis</i>	F ₁	Stony Hollow		m.	<i>aculeatus</i>	A ₁		
	<i>kockelianus</i>	<i>eifilius kockelianus</i>	MD I E	Bakoven	low.		<i>stabilis</i>	C			
	low.	<i>australis</i>	A		upp.		<i>manca</i>	UD IV B ₂			
lower	393.3	<i>costatus</i>	<i>costatus</i>	D		middle	<i>postera</i>	<i>styriacus</i>	B ₁		Upper Lower Annulata
		<i>partitus</i>	<i>partitus</i>	C	Choteč		upp.	<i>granulosus</i>	A		
	<i>marginifera</i>	<i>marginifera</i>	B		low.		<i>trachytera</i>	UD C ₂ III C ₁			
	<i>marginifera</i>	<i>marginifera</i>	A		upm.		<i>velifer</i>	B			
EMSIAN	upper	<i>patulus</i>	<i>patulus</i>	D _{2b}		lower	<i>rhomboidea</i>	<i>gracilis</i>	F		Upper Lower Condroz
		<i>serotinus</i>	<i>cooperi</i>	LD D _{2a}			low.	<i>rhomboidea</i>	E		
		<i>serotinus</i>	<i>serotinus</i>	D ₁			upm.	<i>pectinata</i>	D		
		<i>latiostatus/</i>	<i>latiostatus</i>	C	Daleje		upp.	<i>prima</i>	UD II B		
	<i>inversus</i>	<i>inversus</i>	B		m.		<i>termini</i>	A			
	<i>inversus</i>	<i>inversus</i>	A	Upper Zlichov	low.		<i>crepida</i>				
	<i>nothoperbonus</i>	<i>nothoperbonus</i>	C ₂		upp.		<i>minuta</i>				
	<i>gronbergi</i>	<i>gronbergi</i>	LD C ₁ III B	Chebbi	m.		<i>clarkei</i>				
PRAGIAN	upper	407.6	<i>dehiscens</i>	D	(basal Zlichov) atopus	middle	<i>linguiformis</i>	<i>ubiquitus</i>	L		Upper Lower Kellwasser
		low.	<i>dehiscens</i>	C ₁			upp.	<i>linguiformis</i>	K		
	<i>pireneae</i>	<i>kitabicus</i>	B		low.		<i>winchelli</i>	J			
	<i>kindlei</i>	<i>profunda</i>	A		low.		<i>feisti</i>	I	semichatovae		
LOCHKOVIAN	upper	410.8	<i>pesavis</i>	LD II		lower	<i>jamieae</i>	<i>plana</i>	H		Upper Rhinstreet Lower
		low.	<i>pesavis</i>	A			upp.	<i>proversa</i>	G ₂		
	<i>delta</i>	<i>kutscheri</i>	LD I		low.		<i>housei</i>	I			
	<i>delta</i>	<i>trigonius</i>			6		<i>primus</i>	G ₁			
GIVETIAN	middle	419.2	<i>eurekaensis</i>			upper	<i>transitans</i>	<i>transitans</i>	D		Middlesex
			<i>woschmidti</i>	<i>irregularis</i>				4	<i>transitans</i>	C	
	<i>woschmidti</i>	<i>hesperius</i>			upp.		<i>rugosa</i>	B			
	<i>woschmidti</i>	<i>hesperius</i>			m.		<i>rotundiloba</i>	A			

Figure 4 : Succession des événements globaux et des crises au Dévonien (Becker et al., 2016).

à des événements d'anoxie/dysoxie au niveau du fond marin (Fig. 4). Ils peuvent se produire en plusieurs pulses. Le premier d'entre eux est l'évènement Basal Choteč au début de l'Eifélien, suivi de l'évènement Kačak à la fin de l'Eifélien, et de l'évènement Taghanic à la fin du Givétien moyen. Ces événements ont conduit à divers changements fauniques et extinctions à l'échelle planétaire. Ils ont principalement affecté les faunes benthiques mais l'évènement Taghanic a également été létal pour les organismes nectoniques comme les ammonoïdes (Walliser, 1996). Le début du Dévonien supérieur n'est pas non plus épargné par des événements qui vont affecter la biodiversité. L'évènement Frasnien est dû à un approfondissement marin à la base du Frasnien et a principalement affecté les faunes récifales (Walliser, 1996). A la transition Frasnien–Famennien, l'évènement Kellwasser, une crise majeure en deux phases distinctes a eu un impact conséquent sur la biodiversité dévonienne tel que Raup et Sepkoski (1982) l'ont considérée comme l'une des cinq crises majeures ayant frappé la Terre au Paléozoïque. D'autres événements mineurs ont été reportés au Dévonien supérieur (le Condroz, l'Annulata et le Dasberg) mais sans réellement bouleverser les écosystèmes. En revanche, la transition entre le Dévonien et le Carbonifère est marquée par une nouvelle crise biologique de grande ampleur, c'est l'évènement Hangenberg (Kaiser et al., 2015).

3. Les trilobites, groupe majeur du Paléozoïque

3.1. Taxonomie et écologie des trilobites

Pour comprendre l'impact des changements globaux sur la biodiversité au Dévonien, il est nécessaire de travailler sur un clade bien représenté dans le registre fossile. Les trilobites, groupe emblématique du Paléozoïque offrent cette perspective de comprendre ces variations de diversité et de forme. Ces animaux sont apparus lors de l'explosion cambrienne parmi de nombreuses autres faunes (Foote, 1991 ; Shu, 2008 ; Paterson et al., 2019) et disparaissent au Permien (Lerosey-Aubril et Feist, 2012). Ce sont des arthropodes (Harrington et al., 1959 ; Fortey, 2001). Les arthropodes sont un clade majeur dans l'histoire de la biodiversité et ont l'avantage d'abonder dans le registre fossile (Edgecombe et Legg 2013). Comme tous les arthropodes, les trilobites sont segmentés. Ils sont composés, comme leur nom l'indique, de trois lobes longitudinaux. Leur corps est aussi décomposé en trois tagmes : céphalon, thorax et pygidium (Harrington et al. 1959 ; Fig. 5). Ces segments sont recouverts d'un exosquelette de calcite faiblement magnésienne qui protège leurs parties molles (Wilmot et Fallick, 1989;

Whittington et al., 1997). La croissance discontinue des trilobites impose des mues successives lors du processus d'exuviation (Daley et Drage, 2016).

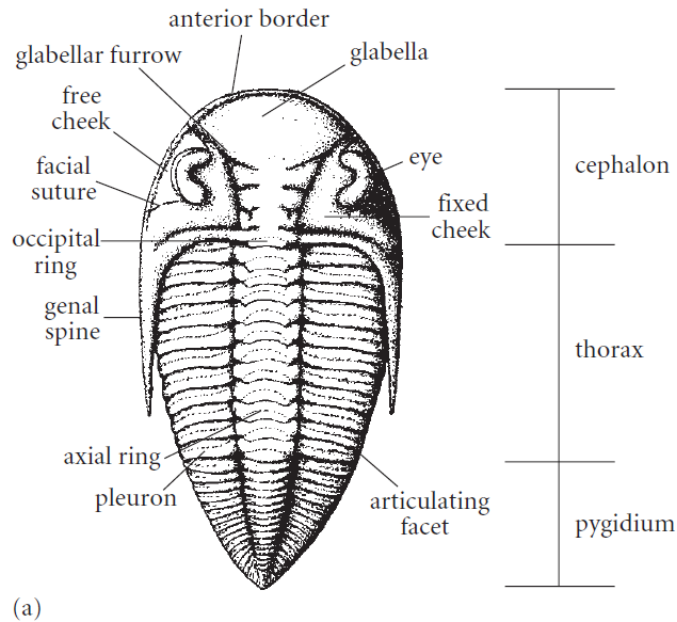


Figure 5 : Principaux traits de la morphologie des trilobites (d'après Benton et Harper, 2009).

La taxonomie de la classe des Trilobites a beaucoup évolué au cours du temps et reste encore aujourd'hui source de débat et d'incertitudes (Paterson, 2020). La dernière classification complète est celle de Adrain (2011) mais depuis d'autres analyses à plus haut niveau taxonomique ont apporté des modifications. Un nouvel ordre a été extrait des Asaphida : les Trinucleida (Bignon et al., 2020). *A contrario*, Aulacopleurida, qui avait été érigé au rang d'ordre par Adrain (2011), serait plutôt une super-famille de Proetida (Lamsdell et Selden, 2014). Au total, à ce jour, il y a onze ordres de trilobites, tous apparus au Paléozoïque inférieur (Fig. 6). Les ordres les plus anciens apparus au Cambrien sont les ordres Redlichida, Olenida, Eodiscida et Corynexochida. Six ordres sont présents au Dévonien et seul l'ordre Proetida a survécu jusqu'au Permien (Lerosey-Aubril et Feist, 2012).

Les trilobites ont connu un succès évolutif notamment grâce à leur faculté à s'adapter et à proliférer dans de nombreuses niches écologiques. En effet, ces arthropodes ont intégré le benthos comme le pélagos lors de leur histoire. Parmi les trilobites benthiques, certains ont adopté un mode de vie épibenthique tandis que d'autres ont opté pour un mode de vie plutôt endobenthique (Whittington et al., 1997). Au niveau de la nutrition Fortey et Owens (1999) ont identifié différentes stratégies alimentaires, regroupées en quatre catégories. Certains étaient prédateurs et/ou charognards, d'autres étaient plutôt détritivores, d'autres filtreurs et enfin, certains trilobites étaient suspensivores. Seules les trois premières habitudes alimentaires

étaient encore présentes au Dévonien. [Fortey et Owens \(1999\)](#) notèrent d'ailleurs que le régime alimentaire pouvait changer au cours de l'ontogénèse, le stade larvaire impliquant probablement

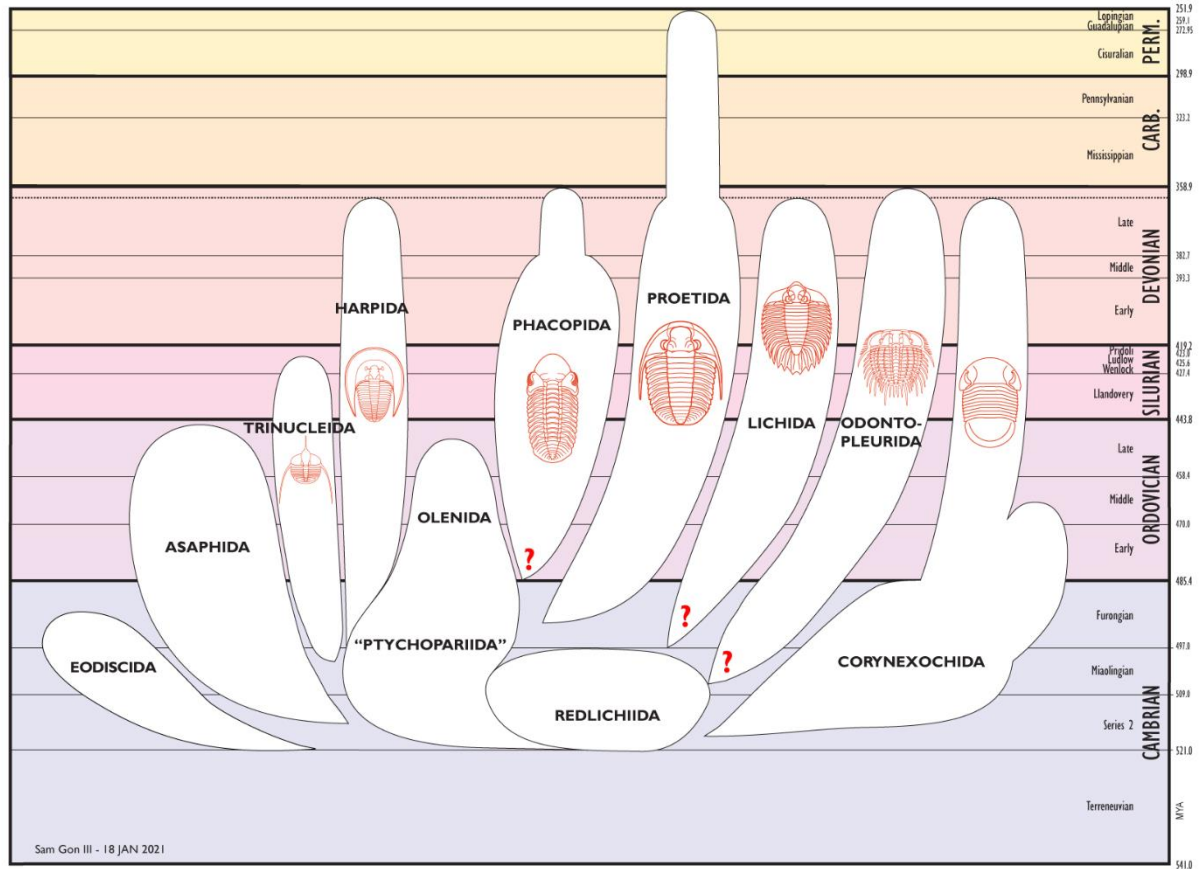


Figure 6 : Représentation schématique de l'histoire évolutive des ordres de trilobites au cours du Paléozoïque. Modifié de [Gon, S.M.](#) (<https://www.trilobites.info>).

un mode de nutrition différent à l'instar de nombreux arthropodes actuels ([Fryer, 1988](#)). Les trilobites ont également montré une facilité d'adaptation à coloniser le milieu marin à différentes profondeurs. En effet, ils étaient benthiques ou nectoniques et on les retrouvait dans des environnements peu profonds jusqu'au-delà de la zone d'action des vagues de tempête, dans des environnements de pente et de bassin ([Thomas, 1979](#) ; [Adrain et al., 2004](#)). Les trilobites sont également trouvés dans des dépôts sédimentaires de différentes natures lithologiques : ils pouvaient aussi bien apprécier les environnements silicoclastiques que les environnements carbonatés ([Hopkins, 2014](#)). Certains trilobites se développaient même dans les environnements récifaux ([Ludvigsen, 1987](#)). Par contre, au niveau des familles ou sous-familles, la nature des sédiments a une importance, comme par exemple les astéropyginés qui proliféraient dans les environnements clastiques ([Morzadec, 1992](#)).

La diversité des milieux colonisés, des comportements se traduit également par une diversité de taille et de forme. Ainsi, les trilobites étaient diversifiés au niveau de la taille. La plus grande espèce de trilobite connue est *Isotelus rex* [Rudkin et al., 2003](#) qui vivait à l'Ordovicien et mesurait plus de 70 cm ([Rudkin et al., 2003](#)) alors que les plus petits n'excédaient pas 1 mm ([Clarkson et Ahlberg, 2002](#)). Deux périodes particulières sont notamment connues pour la présence de formes géantes, favorisées par un climat avantageux pour le développement des trilobites : ce sont l'Ordovicien et le Dévonien inférieur ([Klug et al., 2014](#)).

Au cours de leur histoire évolutive, de nombreux cas de réduction des yeux pouvant aller jusqu'à la cécité ont été répertoriés, et tout particulièrement dans des lignées indépendantes du Dévonien supérieur ([Feist et Clarkson, 1989](#) ; [Feist, 1995](#) ; [Crônier et Feist, 2000](#) ; [Crônier et Courville, 2003](#) ; [Lerosey-Aubril et Feist, 2012](#) ; [Schoenemann, 2018](#) ; [Feist, 2019](#)). Cette évolution a été interprétée comme une adaptation à une vie marine à plus grande profondeur dans une période de haut niveau marin ; cependant, une réduction des yeux peut également correspondre à un mode de vie endobenthique ([Clarkson, 1967](#) ; [Feist et al., 2009](#)). Ces changements polyphylétiques soulignent que des changements de vision constituent une adaptation à des changements environnementaux. Les trilobites ont aussi développé des épines au cours de leur histoire évolutive. Ces épines pouvaient aller de simples épines génales comme chez *Dalejeproetus owensi* ([Johnson et Fortey, 2012](#)) à de longues épines sur tout le corps comme chez *Kettneraspis prescheri* ([Van Viersen et Heising, 2015](#)). Les épines pouvaient présenter des intérêts variés pour les trilobites que ce soit pour leur défense ou leur mode de vie ([Knell et Fortey, 2005](#)). L'enroulement des trilobites constitue également une phase importante chez les trilobites puisqu'il leur permet notamment de se protéger contre des prédateurs ([Clarkson et Henry, 1973](#)). Il existe différents modes d'enroulement qui jouent sur leur morphologie ([Oudot et al., 2019](#) ; [Suárez et Esteve, 2021](#)).

3.2. Les trilobites : groupe clé en macroévolution

Depuis que [Walch \(1771\)](#) a érigé l'ordre Trilobita au XVIIIème, les trilobites ont été à la base de nombreuses recherches scientifiques. Les trilobites présentent en effet plusieurs avantages pour les paléontologues. Ils sont plus fréquemment préservés dans les dépôts sédimentaires au cours des temps géologiques que la plupart des organismes grâce à leur exosquelette ([Pérez-Huerta et al., 2018](#)). Leur état de conservation est d'ailleurs souvent bon, avec des caractères morphologiques bien visibles. Un autre avantage est que les fossiles de trilobites sont retrouvés en grand nombre, notamment grâce au fait que de nombreuses mues

sont aussi conservées dans le registre fossile. De plus, les traits morphologiques de l'exosquelette des trilobites peuvent être quantifiés à partir de la morphométrie géométrique. Cela permet la quantification possible des caractères morphologiques et la création d'un espace morphologique. Puisque les trilobites présentent un grand nombre de caractéristiques, de formes et de milieux de vie, ils présentent un fort potentiel pour toutes études en macroévolution. Pour ces raisons pratiques, les trilobites ont été très utilisés en paléontologie et ils ont été à la base de grandes avancées sur les modalités macroévolutives, notamment dans l'interprétation des changements de forme en termes évolutif et adaptatif. [Eldredge et Gould \(1972\)](#) s'en sont notamment servis dans le développement du modèle des équilibres ponctués. [Foote \(1989, 1990, 1991, 1993\)](#) a utilisé les trilobites pour améliorer les études sur la disparité morphologique. Foote a ainsi développé des indices de disparité morphologique basés sur l'analyse des espaces morphologiques à partir de l'étude des trilobites ([Foote, 1989, 1990](#)). Leur analyse morphologique a aussi permis de connaître plus en détails les dynamiques de diversification des clades ([Foote, 1991, 1993](#)). L'étude du taux d'évolution des trilobites a apporté des informations sur le timing de l'Explosion cambrienne, qui a probablement débuté vers la transition Ediacarien–Cambrien, avant la multiplication des fossiles ([Paterson et al., 2019](#)). De nombreuses études détaillées sur les stades ontogéniques des trilobites ont également été réalisés, les stades juvéniles étant relativement bien conservés dans le registre fossile et les séries ontogéniques bien identifiées ([Crônier et Feist, 1997](#) ; [Crônier et al., 1999](#) ; [Kim et al., 2002](#) ; [Crônier et al. 2005](#) ; [Lerosey-Aubril et Feist, 2005](#) ; [Webster, 2007](#) ; [Cederström et al., 2009](#) ; [Crônier, 2010](#) ; [Hopkins, 2020](#) parmi d'autres). Par conséquent, des études récentes sur l'ontogénèse ([Hughes et al., 2017](#) ; [Lerosey-Aubril et Laibl, 2021](#)) et la modularité/intégration ([Webster et Zelditch, 2011](#) ; [Gerber et Hopkins, 2011](#) ; [Oudot et al., 2019](#)) ont pris comme support les trilobites. Ils permettent ainsi de mieux comprendre le rôle du développement dans l'évolution. Fort de leur grande abondance dans les sédiments paléozoïques, les trilobites ont également servi de support pour identifier l'influence des différents biais d'échantillonnage en macroévolution ([Tarver et al., 2007](#)).

4. L'Afrique du Nord, région hospitalière du Paléozoïque

Afin d'analyser quantitativement la biodiversité passée et ses réponses face aux changements environnementaux, il est nécessaire également de travailler sur une échelle contrainte spatialement. L'Afrique du Nord étant une région connue pour ses riches contenus fossilifères, elle constitue une région idéale pour examiner la paléobiodiversité. Cela est particulièrement le

cas pour les fossiles paléozoïques qui sont retrouvés en grande quantité dans diverses régions du Maroc et de l'Algérie. Si les dépôts ordoviciens des Fezouata sont les plus réputés pour la qualité exceptionnelle de leurs fossiles (Van Roy et al., 2015), les gisements du Silurien et du Dévonien sont aussi nombreux et pertinents pour leur richesse. En plus des trilobites, les sédiments de cette période abondent d'ammonoïdes (Klug, 2002 ; Allaire, 2017 ; Becker et al., 2019), de poissons (Derycke, 2015), de crustacés (Maillet et al., 2013 ; Jobbins et al., 2020) et bien d'autres organismes (Klug et al., 2008, 2018 ; Frey et al., 2014). Ces fossiles sont en partie exploités à des fins commerciales par les locaux afin d'être vendus à des collectionneurs, mais ils sont également utilisés et analysés par les scientifiques depuis plus d'un siècle. Les premiers travaux sur les trilobites ont été réalisés par des pionniers scientifiques français et allemand (Lecointre, 1926 ; Richter et Richter, 1943 ; Termier et Termier, 1950 ; Le Maître, 1952). De nombreuses études vont suivre dans les années 60 et 70 avant une perte d'intérêt à partir du milieu des années 80. Cependant, durant ces 20 dernières années, les paléontologues se sont de nouveau intéressés aux trilobites d'Afrique du Nord avec les travaux récents de Crônier et al. (2018a, 2018b), Chatterton et al. (2019), Feist (2019) et Van Viersen et Lerouge (2019, 2021) notamment. La plupart des travaux publiés concernent la taxonomie et la systématique avec la description de nouvelles espèces et genres. Ces études sont d'ailleurs réalisées à l'échelle locale, seuls les travaux taxonomiques de Alberti (1969, 1970) ont porté sur une échelle régionale.

La richesse en fossiles en Afrique du Nord du Silurien au Dévonien s'explique par la présence de nombreux dépôts sédimentaires où les conditions d'affleurements sont excellentes (Fig. 7). Il y a 400 millions d'années, cette région était particulièrement hospitalière pour les faunes marines. Le Maroc et l'Algérie étaient situés sur la plate-forme du craton saharien dans la partie nord-ouest du Gondwana (Wendt et al., 1984 ; Wendt, 2021). Cette région était située à des latitudes subtropicales (Scotese et al., 2021). Au Dévonien moyen le Maroc était même situé aux latitudes subtropicales chaudes (Scotese et al. 2021). Aujourd'hui, ces terrains dévoniens affleurent largement en Algérie et au Maroc, on peut les regrouper en huit bassins distincts : la Meseta centrale, le massif du Rehamna, le Tafilalt, le Maïder, le bassin du Tindouf, la vallée du Draa, la Kabylie, le bassin de Béchar et l'Ougarta (Fig. 7). Au Dévonien inférieur, l'Anti-Atlas était une plateforme avec un environnement relativement homogène (Kaufmann, 1998 ; Lubeseder et al., 2010). La phase extensive de l'orogénèse Hercynienne (ou varisque) conduisa à des phases de subsidence dans l'Anti-Atlas menant à une accumulation conséquente de sédiments (Ouanaimi et Lazreq, 2008). Sous l'action de l'orogénèse Varisque l'Anti-Atlas et la zone adjacente de l'Ougarta se sont transformés en une succession de plateformes et

bassins au Dévonien moyen (Wendt et al., 1984 ; Kaufmann, 1998 ; Wendt, 2021). Cette différenciation s'est poursuivie au Dévonien supérieur.

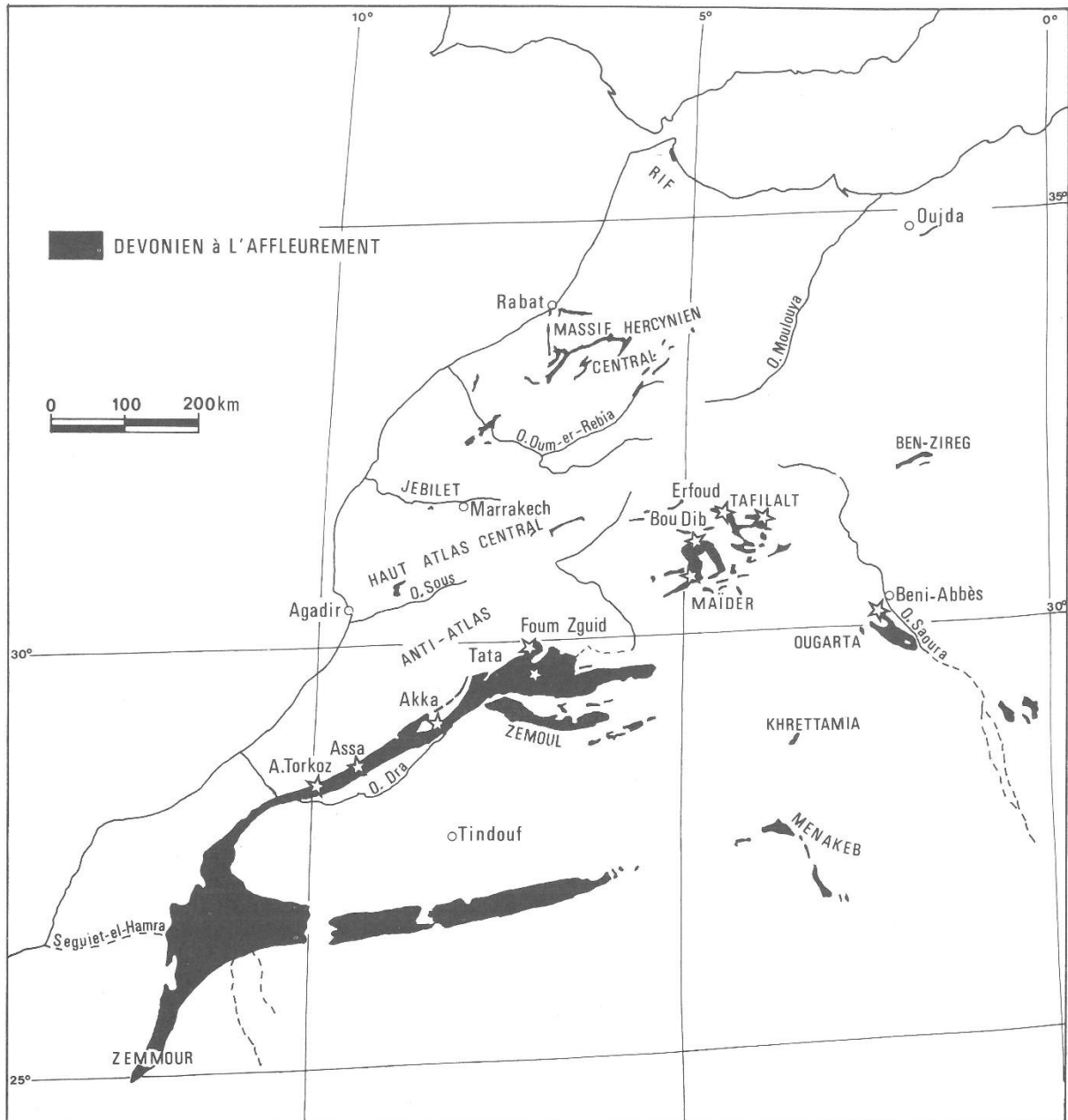


Figure 7 : Principaux affleurements dévoniens du Nord-ouest d'Afrique du Nord (Hollard, 1968).

5. Objectifs de la thèse

Afin de se focaliser sur la paléobiodiversité en temps profond et ses variations spatio-temporelles, trois axes majeurs ont été développés au cours de cette thèse, à savoir un axe concernant la diversité taxonomique, un axe concernant la disparité morphologique, et un axe concernant les dynamiques spatiales. Ces axes ont été considérés à l'échelle globale (chapitre 1) et à l'échelle régionale (chapitre 2).

Chapitre 1. Dynamique des trilobites du Silurien au Permien à l'échelle mondiale

Il s'agit ici d'étudier les tendances globales concernant la distribution et les changements de faunes depuis le Silurien jusqu'au Permien afin de mieux comprendre le contexte dans lequel se placent les trilobites du Dévonien d'Afrique du Nord. L'article 1 « Post-Ordovician trilobite diversity and macroevolutionary history » discute des évolutions fauniques à l'échelle globale qui ont suivi la première extinction de masse qui a lourdement affecté les trilobites. Le but est de quantifier la diversité mondiale mais également de voir comment se sont effectués les renouvellements de faunes au cours de la seconde partie du Paléozoïque. L'influence des nombreux changements environnementaux et écologiques globaux pourrait ainsi être identifiée. Afin de mieux caractériser les faunes de trilobites, il est également nécessaire de caractériser les tendances morphologiques et leurs variations au cours du temps. Pour cela, avant de pouvoir concrétiser une étude à l'ensemble des taxons du Dévonien à l'échelle globale, une première étude (article 2 « Morphological disparity of phacopids ») s'est focalisée sur une famille emblématique du Dévonien : les phacopidés. Cette famille probablement apparue à la fin de l'Ordovicien s'est développée jusqu'au milieu du Dévonien avant de décliner et de disparaître à la toute fin du Dévonien. Cette dynamique de diversité est typique de nombreuses familles post-ordoviciennes et est intéressante à étudier au niveau de la morphologie pour identifier des innovations et la sélectivité ou non des extinctions.

Chapitre 2. Biodiversité et Disparité des trilobites du Dévonien d'Afrique du Nord

Il s'agit ici d'étudier la biodiversité des trilobites présents au Maroc et en Algérie. Ce chapitre est constitué de trois articles : un sur la diversité taxonomique (article 3 « Trilobite biodiversity trends in the Devonian of North Africa »), un sur la disparité morphologique (article 4 « Morphological disparity trends of Devonian trilobites from North Africa ») et le troisième comparant les deux dynamiques diversité vs. disparité (article 5 « No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa? »). L'article 3 (Bault et al., 2021) discute des tendances de diversité au niveau de l'Afrique du Nord. Il repose sur une base de données recensant la centaine de publications portant sur les trilobites d'Afrique du Nord, et permettant ainsi de faire un état des lieux de tout ce qui est connu sur les trilobites nord-africains. La diversité peut être mesurée à différents niveaux taxonomiques aussi bien au niveau des ordres qu'au niveau des espèces. Des tendances différentes peuvent caractériser ces différents niveaux taxonomiques. Ce « zoom » réalisé à l'échelle régionale offre l'opportunité de mieux comprendre les interactions environnement-diversité. La région d'étude est également connue pour ses affleurements riches en ammonioïdes

coexistant sur la même période avec les trilobites. Cet article offre ainsi l'opportunité de comparer une faune nectonique et une faune benthique d'une même région. L'intérêt est d'autant plus grand que les ammonoïdes sont susceptibles d'avoir été des prédateurs de trilobites. La plupart des articles publiés et utilisés pour la construction de la base de données sont des travaux de systématique, offrant ainsi de très nombreuses illustrations des spécimens figurés. Cela permet de rajouter une composante à la richesse taxonomique : la disparité morphologique. C'est l'objet de l'article 4 (Bault et al., accepté avec modifications) basé sur le même jeu de données. Les études morphologiques sont complémentaires de celles de la diversité. L'utilisation de photos implique des études en 2D uniquement, mais cela n'est pas problématique chez les trilobites, leur morphologie ne nécessitant pas forcément la 3D. Ce travail a permis de faire l'état des lieux des formes des trilobites du Dévonien et d'identifier leurs principales variations. Les innovations et les pertes de morphologies des trilobites d'Afrique du Nord ont ainsi pu être identifiées et rattachées aux événements écologiques. L'article 5, quant à lui, se focalise sur la comparaison entre la richesse taxonomique et la disparité morphologiques, ces deux métriques pouvant être couplées ou non. Evaluer leurs dynamiques apporterait des indications précieuses sur les modalités évolutives des trilobites du Dévonien.

La biodiversité ne change pas qu'au cours du temps mais aussi dans l'espace. L'article 6 (« The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria », Bault et al., accepté avec modifications) discute de la diversité paléogéographique qui peut être source de diversité taxonomique et morphologique. Le Maroc et l'Algérie concentrent un grand nombre de bassins caractérisés par des environnements différents qui ont été bien décrits. Cette paléogéomorphologie en bassins et plate-formes résulte d'une tectonique régionale, la région ayant été le siège de l'orogénèse varisque. Cette connaissance du secteur étudié a ainsi offert l'opportunité d'appréhender l'impact de la paléogéographie régionale sur la biodiversité et la distribution des trilobites. En identifiant des associations de trilobites, on peut mettre en évidence leurs affinités du point de vue environnemental et temporel. Des voies de migrations et des barrières géographiques peuvent également être identifiées.

Chapitre 1. Dynamique des trilobites du Silurien au Permien à l'échelle mondiale

Les dynamiques biologiques et environnementales globales ont un effet majeur sur les écosystèmes régionaux. Comprendre les tendances globales permet de connaître le cadre dans lequel les trilobites du Dévonien d'Afrique du Nord se situent et les enjeux. L'objectif est d'identifier l'effet de l'environnement et les changements de population d'abord au niveau taxonomique (article 1) puis au niveau morphologique (article 2).

1.1. Diversité et histoire macroévolutive des trilobites Post-Ordoviens

Article 1: Post-Ordovician trilobite diversity and macroevolutionary history

Pour être soumis à Earth-Science Reviews.

Post-Ordovician trilobite diversity and macroevolutionary history

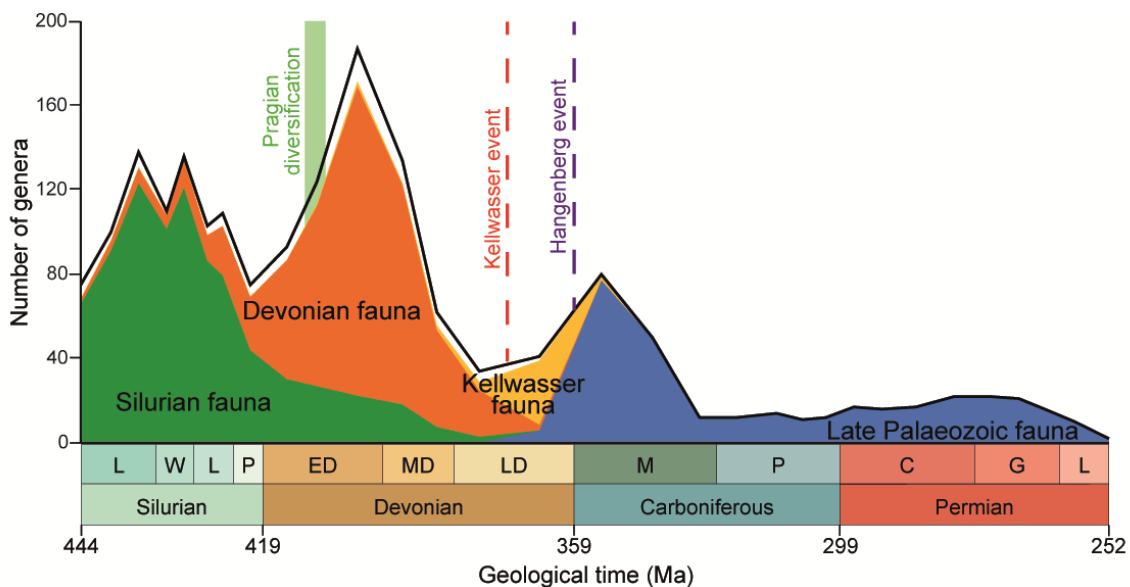
Valentin Bault^{a*}, Diego Balseiro^b, Claude Monnet^a and Catherine Crônier^a

^a*Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France*

^b*Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional de Córdoba, Córdoba (X5016GCA), Argentina*

* Corresponding author at: Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France.

Email address: valentin.bault@univ-lille.fr (V. Bault), dbalseiro@unc.edu.ar (D. Balseiro), claudemonnet@univ-lille.fr (C. Monnet), catherine.cronier@univ-lille.fr (C. Crônier).



Abstract

Trilobites were the successful clade of marine invertebrates during the Palaeozoic as highlighted by Sepkoski's evolutionary faunas. Since the Cambrian they were very abundant, widespread and highly diversified, but they were severely affected by the Late Ordovician extinction event. Our study investigates the evolutionary trends of trilobites after this crisis, especially by evaluating how their diversity recovered and structured itself in evolutionary faunas, as well as the how environments influenced these trilobite faunas. Using occurrences from the Paleobiology Database, we estimated the post-Ordovician paleobiodiversity of trilobites by coverage rarefaction (SQS) and identified the trilobite evolutionary faunas by means of a factor analysis. During the Silurian, the trilobite taxonomic richness was relatively

high and did not undergo important changes; this Silurian Fauna was dominated by the families that appeared in the Ordovician and survived the end-Ordovician extinction. Next, a Devonian Fauna established, progressively since the end of the Silurian, by the diversification of other families and subfamilies, especially in the early Devonian, which records the highest post-Ordovician peak of diversity, probably favoured by the spreading of epicontinental shallow seas. Abrupt sea-level changes and anoxic events during the Middle Devonian strongly reduced the trilobite diversity and brought both Silurian and Devonian faunas close to their disappearance. Then, during the Late Devonian, trilobite diversity was low and dominated by phacopids and proetids. Finally, the Hangenberg event (end-Devonian) affected all existing trilobite clades and the following Tournaisian diversification was the onset of the Late Palaeozoic Fauna, constituted by phillipsiids and brachymetopids. Despite an important diversity decrease in the Viséan–Serpukhovian (early Carboniferous), this fauna was the only one to persist until the doom of trilobites at the end of the Permian.

Keywords:

Trilobites, Palaeozoic, factor analysis, evolutionary fauna, extinction, environmental events, diversity

1. Introduction

Trilobites appeared at the beginning of the Cambrian at the same time as several other metazoan clades (Fortey et al., 1996, 1997; Paterson et al., 2019). They became quickly abundant in the Early Palaeozoic with a maximum diversity between the Late Cambrian and the Late Ordovician (Foote, 1993; Westrop and Aldrain, 1998). In addition to this diversification, the first trilobites showed an increase of morphological disparity until a maximum disparity during the Ordovician (Foote, 1991, 1993; Webster, 2007). These arthropods also developed a wide range of feeding habits (Fortey and Owens, 1999) and various palaeoecological adaptations (Fortey, 2004, 2014, Hopkins, 2014), highlighting their capacity for adaptation and their presence in all fully marine habitats, and even brackish habitats by the Early Ordovician (Mángano et al., 2021; Serra et al., 2021). These ecological adaptations contributed to a resilience against the Palaeozoic extreme environmental changes and thus, the trilobites survived two of the five biggest mass extinction events, i.e., the Late Ordovician and the Late Devonian mass extinctions (Raup and Sepkoski, 1982; Raup, 1986; Bambach et al.,

2004). However, about 250 million years ago, the trilobites became extinct at the end of the Permian (Owens, 2003; Lerosey-Aubril and Feist, 2012).

The Early Palaeozoic faunas and their evolutionary trends have been well studied in the literature. Originally, Adrain et al. (2004) identified three evolutionary faunas from the Ordovician to the Early Silurian, which are characterized by different families showing a similar pattern of diversity. These faunas were identified according to geographical/environmental features such as the latitude or the marine habitats (Adrain et al., 2000, 2004). However, trilobite evolutionary faunas from the Silurian to the Permian remained undefined, although important compositional changes occurred. In the Silurian, although considered relatively stable from an environmental point of view (Calner, 2008; Melchin et al., 2021), environmental changes did take place with temperature variations and transgressive events associated with anoxia. These environmental conditions were favourable for trilobites, which recover from the Late Ordovician mass extinction and become diverse (Adrain et al., 2000). The Early Devonian led to a diversity peak (Chlupáč, 1994; Adrain, 2008; Alroy, 2010b) followed by a sharp decrease in the Middle and Late Devonian, to the extent that only one order survived in the Carboniferous (Feist, 1991; Lerosey-Aubril and Feist, 2012). The Early Devonian represents the only important period of diversification after the Late Ordovician. This period was characterized by several environmental changes, including the displacement of Gondwana towards lower latitudes leading to the increase of carbonate deposits (Scotese and McKerrow, 1990; Scotese, 2021) and important temperature variations (Scotese et al., 2021). Repeated and rapid sea-level changes and anoxic/hypoxic events also affected the planet at this time (House, 1985, 2002; Johnson et al., 1985), leading to the Kellwasser events (Buggisch, 1991; Bond and Wignall, 2008; Carmichael et al., 2019). The Late Palaeozoic was also a period of important ecological changes with the proliferation of nektonic organisms during the Devonian Nekton Revolution (Klug et al., 2010), the colonisation of land by vascular plants (Gerrienne et al., 2016; Capel et al., 2021) and the invasion of the continents by animals (Selden, 2016; Van Straalen, 2021). Because trilobites within changing ecosystems have not responded in the same way to environmental changes over this period, it is important to identify which taxa had similar behaviour in order to identify the causes influencing trilobite richness, their diversifications and their declines.

2. Material and methods

2.1. Dataset

Trilobite occurrences were downloaded from the Paleobiology Database (PBDB, www.paleobiodb.org) on May 21st 2021. Data on diversity data were collected as follows: (1) selection of all the trilobite genera (column “accepted_name” from the “taxa” record) present in each stage from the Silurian to the Permian; (2) subgenera not treated as genera and not taken into account; (3) number of occurrences per stage for each genus counted. In total, 570 genera in 23 families and six orders from the Silurian to the Permian were used. This dataset comprising 13802 occurrences extracted from the “Occurrences” was used for rarefaction methods. In order to better understand the relationship between the environment and the location with the taxonomy, we collected data on habitat affinities and palaeolocation from PBDB. For each occurrence for which some additional data were available, we collected lithological data from the “lithology1” and “lithology2” fields, the environmental data from the “environment” field and latitudinal data from the “paleolat” field. In total 9045 occurrences (66%) record lithological data, 5064 occurrences (66%) environmental data, and 9356 occurrences (68%) latitudinal data. Lithological data were simplified in three categories (Fig. SUPPL. A): siliciclastic (i.e., lithology1 = any clastic lithology AND lithology2 = any clastic lithology or NA), carbonate (i.e., lithology1 = any carbonate lithology AND lithology2 = any carbonate lithology or NA) and mixed (i.e., lithology1 = any carbonate lithology AND lithology2 = any clastic lithology (or *vice versa*). Bathymetrical data were spread in four categories, i.e., shallow, inner platform, outer platform and slope/basin, and latitudinal data in three categories, i.e., low, middle and high latitudes (Fig. SUPPL. A). We followed the International Chronostratigraphic Chart ([Cohen et al., 2013](#)) as the geochronological framework.

2.2. Dataset

Trilobite systematics and phylogenetic relationships remain unclear, especially between major post-Cambrian trilobite clades and their Cambrian ancestors ([Paterson, 2020](#)). The latest studies carried out at the class level were those of [Fortey \(1997\)](#) and [Adrain \(2011\)](#). For more robust analyses, some studies have focused on smaller subsets such as the recent analyses on Asteropygines ([Bignon and Crônier, 2014](#)), Calmoniids ([Abe and Lieberman, 2009](#)), Phacopids ([McKellar and Chatterton, 2009](#)), or the recent redefinition of the order Trinucleida ([Bignon et al., 2020](#)). We have chosen to carry out our analyses based on the taxonomic framework described by [Adrain \(2011\)](#) with some updates. First, we follow [Bignon et al \(2020\)](#) in the

newly erected order Trinucleida separately from Asaphida. Second, although [Adrain \(2011\)](#) created the order Aulacopleurida distinctly from Proetida, the monophyly of the order Proetida, including the superfamily Aulacopleuroidea as one of the three super-families with Proetoidea and Bathyuroidea, has been regularly questioned ([Lamsdell and Selden, 2015](#)). Consequently, we considered Aulacopleuroidea as a super-family of Proetida, not as an order. We followed [Adrain \(2013\)](#) in considering, within the order Proetida, the family Phillipsiidae as a subfamily of Proetidae.

Eleven orders are recognized within trilobites across their evolutionary history (Fig. 1). All of them appeared in the Cambrian-Ordovician. Eodiscida, Ptychopariida, Asaphida, Olenida and Redlichiida disappeared before the Silurian; Trinucleida in the Silurian; and Harpetida, Odontopleurida, Lichida and Corynexochida in the Middle Devonian. If only Phacopida and Proetida survived to the Kellwasser events, Phacopida disappeared with the Hangenberg event at the Devonian-Carboniferous boundary ([Feist, 1991](#); [Chlupáč, 1994](#); [Lerosey-Aubril and Feist, 2012](#)).

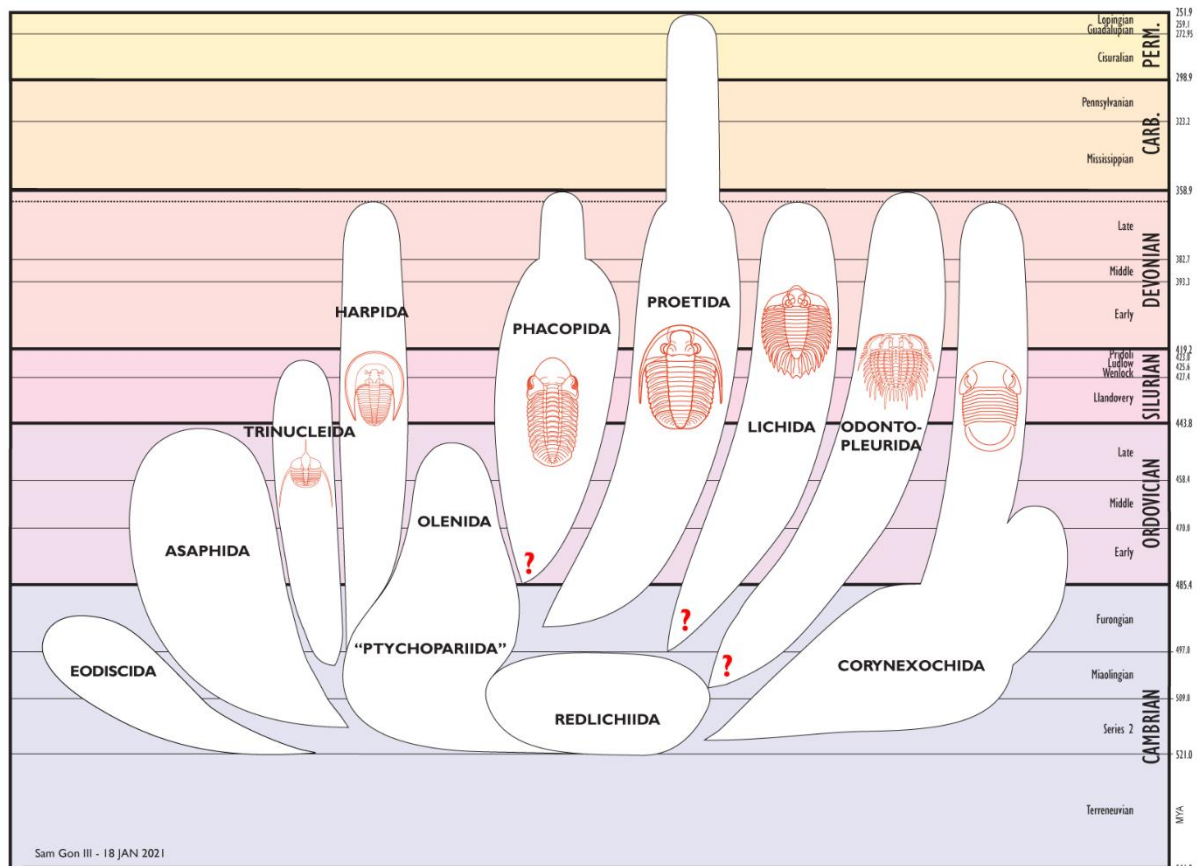


Figure 1. Schematic representation of the evolutionary history of the trilobite orders through time.

The y-axis approximates a log to permit the more detailed illustration of the Cambrian and Ordovician diversifications. Horizontal distance between orders should not be interpreted as phenetic difference no more than the diagram implies maximal phenetic variance in the early part of the Cambrian. Modified from Gon, S.M. (<https://www.trilobites.info>).

Within the orders that crossed the Ordovician-Silurian boundary, some families disappeared (Adrain, 2013). Consequently, post-Ordovician trilobites were spread into the 22 families used for this work. Within the family Proetidae, as there are many subfamilies with different diversity dynamics and temporal distribution, we used them as clades for our analyses, represented by Cornuproetinae, Crassiproetinae, Cyrtosymbolinae, Dechenellinae, Drevermanniinae, Eodrevermanniinae, Mirabolinae, Proetinae and Warburgellinae.

As the taxonomic assignments in the PBDB are not systematically updated, a revision of the taxonomy has been carried out. Some subfamilies have been reassigned to families. Trepidocoryphidae has been considered as a distinct family comprising Eremiproetinae, as in recent studies (Helling and Schöllmann, 2018; Feist and Belka, 2018), although this subfamily has sometimes been assigned to Proetidae. We considered that the Scutelluidae are different from the exclusively Ordovician Styginidae (Holloway, 2007). Therefore, the trilobites assigned to the Styginidae in the database were transferred to the Scutelluidae.

In the same way, some genera have been reassigned to families and subfamilies. Some issues of junior synonyms were also solved. Reassignments were made using the statements of Jell and Adrain (2002) and subsequent updating. The following proetid genera *Constantina* Cisne, 1970, *Ormistonina* Maksimova, 1978, *Pseudoproetus* Poulsen, 1934 and *Schaderthalaspis* Alberti, 1983 not assigned to a subfamily were not used in the Factor Analysis. A database with updated taxonomy is given in Appendix A.

2.3. Diversity

Attempts to reconstruct taxonomic richness face several biases (Smith, 2001; Alroy, 2010b) but the development of modern methods have helped palaeontologists to estimate diversity in the fossil record using resampling methods (Alroy, 2010a, Close et al., 2018). Here, trilobite diversity is estimated at genus level from the Silurian to the Permian using two different methods. First, we calculated the Range-Through diversity including single-interval taxa (RT), which is the raw count of actually documented taxa per stage plus interpolated discontinuous taxon ranges (Foote, 2000). Indeed, some genera had an irregular presence through time with virtual absence between two stages of occurrences due to the incompleteness of PBDB. As we are working at the global , we corrected this issue by assuming presence in all stages between the first and last appearance. For this estimation, and given that many trilobite genera have short longevities, we chose to include singletons. Second, we performed a Shareholder Quorum

Subsampling (SQS) diversity (Alroy, 2009). This is a subsampling method that aims to overcome uneven sampling between intervals. We further estimated net change rates corresponding to the difference in logged diversity between successive intervals. Net changes highlight periods of gain and loss of genera.

Diversity indices are computed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.) using R statistical environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>).

2.4. Factor Analysis

Factor Analysis (FA), a multivariate statistical method, was used to describe Phanerozoic evolutionary faunas (Sepkoski, 1981) and was further been applied for more specific analyses of faunas or floras (Figueirido et al., 2012; Cleal and Cas-Miñana, 2014; Morales et al., 2015; Capel et al., 2021). To assess the inter-sample relationships in trilobites, we performed a Q-mode factor analysis (Mulaik 1972). This method allows decreasing space dimensionality in the original database to a smaller number of variables known as factors. We implemented Sepkoski’s (1981) approach to the raw-normalized diversity of Silurian-Permian trilobites, consisting of the number of genera in each family or subfamily per stage. We obtained factors (orthogonal vectors) with their associated eigenvalues (factor loadings) and the percentage of explained total variance. The importance of each family or subfamily to each factor is indicated by its score. The composition of each fauna is therefore defined as the group of families or subfamilies that record the highest scores in each factor. A varimax rotation (Kaiser, 1958) was used to clarify the relationship among factors and to maximize the sum of the variances of the squared correlations between variables, i.e., families and subfamilies, and factors to avoid nonsense associations determined by raw eigenvectors. Hence, this rotation clearly segregates the variables onto different factors. The selection of the number of factors used can be done in different ways. Sepkoski (1981) chose to select the factors located before the slope break of the successive factor eigenvalues plotted logarithmically. As our data do not show a break, we chose the number of factors explaining 95% of the variance, i.e., four factors.

Because a family or subfamily could record high scores in more than one single factor, we also performed a Hierarchical Cluster Analysis (HCA). We used the UPGMA linkage method (Sokal and Michener, 1958) and the Morisita’s similarity index (Morisita, 1959), which is insensitive to the sample size. This clustering method linked families and subfamilies according to their temporal distribution.

Alroy (2010c) suggested to study the different faunas on the basis of changes in diversity and not just on taxonomic richness. For this analysis we used the logarithmic transformation of taxonomic richness [$\text{Log}(N+1)$], because differences in counts of the logged data are equivalent to net turnover rates (Foote, 2000; Alroy, 2000). Since FA could not be used with this type of data due to the presence of zeros, we used a PCoA of an Euclidean distance matrix of log ratios without undefined values in order to highlight the correlation between the faunas (Alroy, 2010c). FA, HCA and PCoA were carried out using the software PAST version 3.14 (Hammer et al., 2001).

2.5. Environmental impact

The latitudinal distribution of trilobites played a major role in their survival in the first half of the Palaeozoic (Westrop and Ludvigsen, 1987). A preferential extinction among families living in high latitudes affected Late Ordovician communities, while families living in lower latitudes survived and radiated into the Silurian (Adrain et al., 2004). We estimated the latitudinal distribution of families and subfamilies through time as well as the distribution of each fauna. We divided each hemisphere in three latitudinal bins: 0-30°, 30-60° and 60-90°.

Several sea-level changes occurred between the Silurian and Permian (Walliser, 1996; House, 2002; Calner, 2008; Haq and Schutter, 2008) and affected the benthic fauna, including trilobites. Moreover, it has been shown that bathymetry played a major role in replacement patterns (Jablonski and Bottjer, 1991; Adrain et al., 2004). In order to understand the impact of such events, we analysed the evolution of trilobite diversity at different bathymetry: shallow, inner shelf, outer shelf and slope/basin. The latter two are relatively deep environments, while shallow and inner shelf are rather shallow. Bathymetrical distributions for each factor were also estimated.

Type of sedimentation had an impact on the Palaeozoic benthic fauna (Balseiro and Powell, 2020). Substrate type has also shown to be important for macroevolutionary dynamics of origination and extinction (Foote, 2006; Kiessling et al., 2010), and faunal replacements (Tomašových, 2006; Miller and Connolly, 2001). Climate change and environmental events such as sea-level changes or perturbations of the carbon cycle also affected the biodiversity through time (Walliser, 1996; House, 2002). Thus, we compared the temporal trends in diversity for trilobite families and for described faunas (=factors) between siliciclastic and carbonate environments.

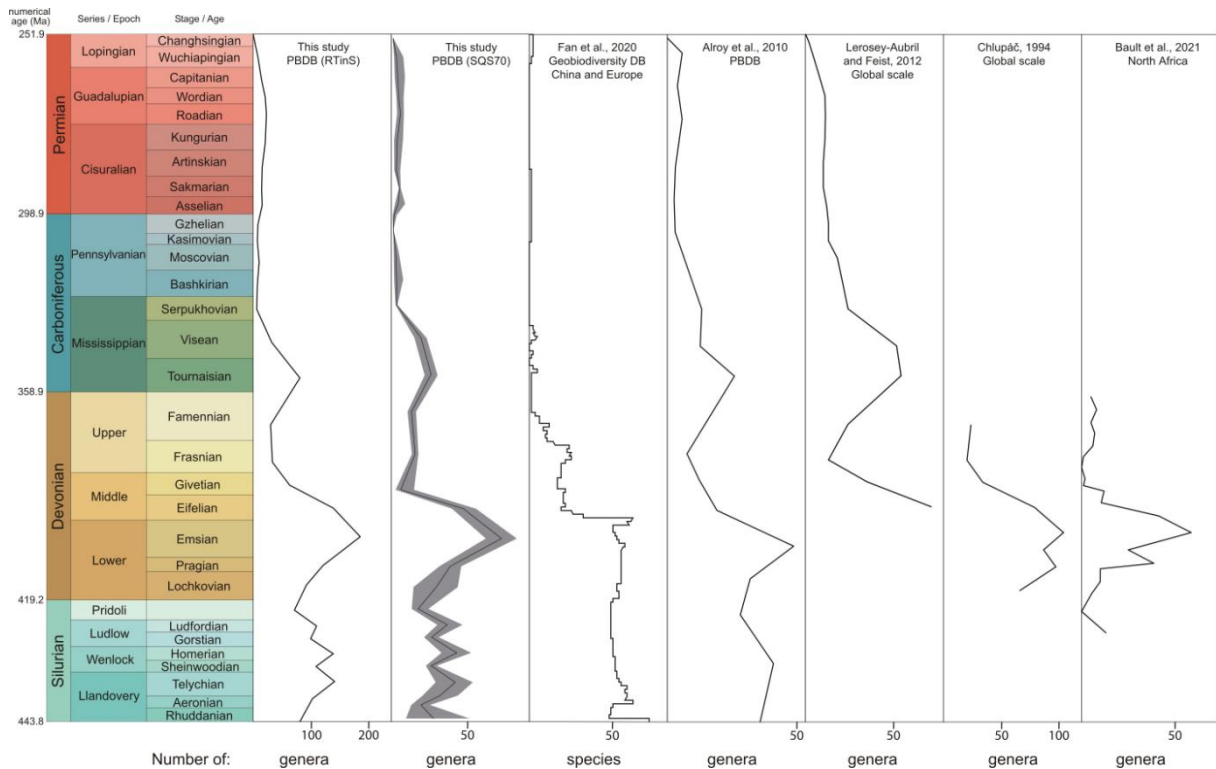
We also studied the relationship between trilobite total diversity with different environmental proxies estimated for the Palaeozoic from the literature. Because most trilobites lived along continental margins, changes in coastal length related to the collision of continents and the opening of new oceans (Scotese and McKerrow, 1990; Scotese, 2021) may have influenced their diversity. A fragmentation index estimated by Zaffos et al. (2017) was used as proxy for the amount of continental coastal environments available. Different isotope ratios were used as environmental proxies (Veizer et al., 1999). We used $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (McArthur et al., 2012) as a proxy for seafloor spreading and/or continental weathering (Jones et al., 1994; Capo et al., 1998); $\delta^{18}\text{O}_{\text{apatite}}$ (Veizer and Prokoph, 2015) as a proxy for temperature change and $\delta^{13}\text{C}$ (Saltzman and Thomas, 2012) as a proxy for the global carbon cycle variation linked to changes in primary production and climate variations. We also compared total diversity and diversity of each fauna to pCO_2 (Foster et al., 2017) and the mean tropical sea-surface temperatures (Song et al., 2019; mean values from Scotese et al., 2021). We further used the Palaeozoic sea-level estimated by Haq and Schutter (2008) to identify faunal changes linked to the extent of continental flooding. The volume of sediments on the continental margins and ocean basins (Hay et al., 2006) was also analysed. Finally, we performed pairwise correlation tests of detrended values of these environmental proxies with detrended raw diversity values (McKinney, 1990; Alroy, 2000) in order to identify if some proxies could explain some trends in diversity. For detrending of time series we used the generalized differencing approach using the `gen.diff()` function for R (Lloyd, 2008). Correlations were done for the whole dataset together and for each fauna individually. Pairwise correlation tests were performed using Spearman's r as correlation index. As multiple comparisons were done between each diversity series and the eight environmental series, we used the False Discovery Rate approach (Benjamini and Hochberg, 1995) to reduce the risk of detecting false correlations. Analyses were carried out in the R statistical environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>).

3. Results

3.1. Diversity

Both Range-through (RT) and Shareholder Quorum Subsampling (SQS) diversities (Fig. 2) show similar trends except for the Mississippian, where the diversity peak lasted until the Viséan according to SQS, in agreement with Lerosey-Aubril and Feist (2012). Trilobite

diversity increased in the Llandovery and remained high in the Wenlock despite slight variation in richness. A decrease in diversity occurred in the Ludlow-Pridoli before a sharp diversification in the Early Devonian to reach a maximum richness for the studied period with more than 180 genera referenced in the Emsian (Fig. 2). The Middle Devonian events appear to have the strongest impact, with SQS subsampling suggesting a very low Givetian diversity (Fig. 2). A sharp decline affected Middle Devonian trilobites with the loss of 80% of the number of genera before a period of low diversity in the Late Devonian. A final peak in diversity was documented



in the Tournaisian but after another important decline, the trilobite diversity remained low until the end of the Permian despite a slight increase of diversity in the Middle Permian (Fig. 2).

Figure 2. Diversity dynamics of trilobites from the Silurian to the Permian. Taxonomic richness from the PBDB estimated as Range-through diversity including single-interval taxa (RT) and the Shareholder Quorum Subsampling (SQS) diversity, estimation for a quorum of 70. Other curves correspond to the diversity estimated by Fan et al. (2020), Alroy et al. (2010c), Lerosey-Aubril and Feist (2012), Chlupáč (1994) and Bault et al. (2021) at regional or global. Diversity is estimated for each stage at the generic level except for Fan et al. (2020) who used the species level. Age from Cohen et al. (2013, updated).

Positive net diversity changes were registered four times between the Silurian and Permian, namely the Early Silurian, the Early Devonian, the Mississippian and the Cisuralian. Four

periods of negative turnover occurred: in the Late Silurian, the Middle Devonian, the Viséan and at the end of the Permian (Fig. 3). Peaks of both maximum positive and negative net changes occurred both in the Devonian with a gain of 28 genera in the Pragian and a loss of 44 genera in the Eifelian respectively.

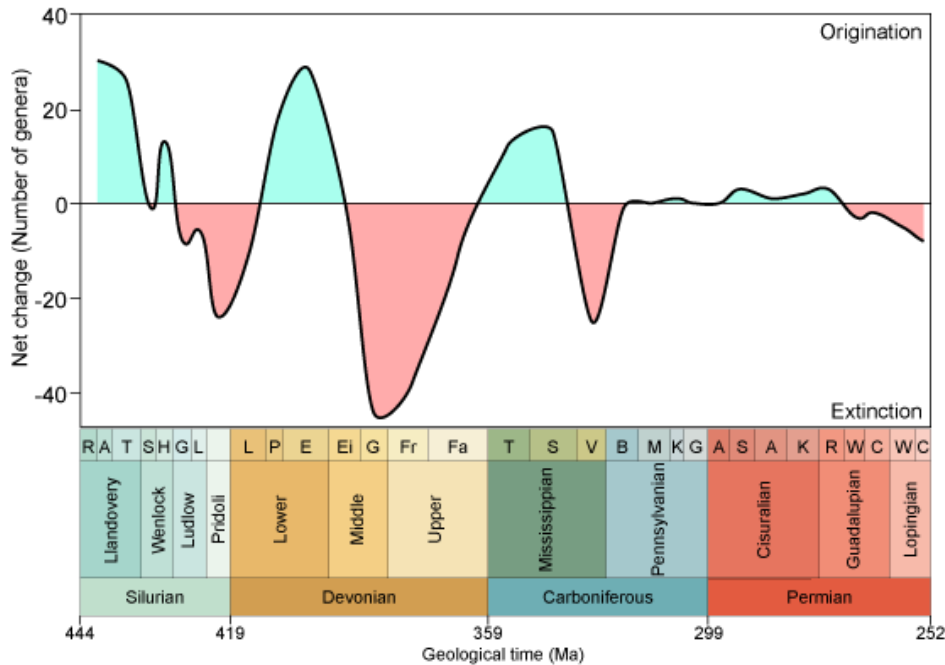


Figure 3. Net change of trilobites between the Silurian and the Permian. Net change per stage correspond to the number of origination of genera minus the number of extinction of genera. Positive net change indicates a period of origination and negative values indicate period of extinction. Age from Cohen et al. (2013, updated).

3.2. Trilobite faunas

We defined trilobite faunas following a factor analysis, where each selected factor represents a single fauna (Sepkoski, 1981; Figueirido et al., 2012). Four factors accounting for the 97% of the variance of the trilobite diversity were selected (Fig. SUPPL. B). The first factor explains 52% of the total variance, the second 35% while factors 3 and 4 are less important with respectively 7% and 3% of the explained variance. These four trilobite faunas developed from the Silurian to Permian (Fig. 4). Each fauna dominated a period before giving another fauna diversified. The Silurian Fauna lasted from the Rhuddanian to Famennian, but was dominant only until the Pridoli (Factor 2 of FA, Fig. SUPPL. C; Fig. 4). The Devonian Fauna was present during the same period but became important only from the Lochkovian to the Givetian (Factor 3 of FA, Fig. SUPPL. C; Fig. 4). The Kellwasser Fauna was present only for short period, from the Eifelian to the Tournaisian, and became important only in the Late Devonian particularly in the Famennian (Factor 4 of FA, Fig. SUPPL. C; Fig. 4). Finally, a Late Palaeozoic Fauna

emerged in the Famennian, became dominant in the Tournaisian and lasted until the end of the Permian (Factor 1 of FA, Fig. SUPPL. C; Fig. 4).

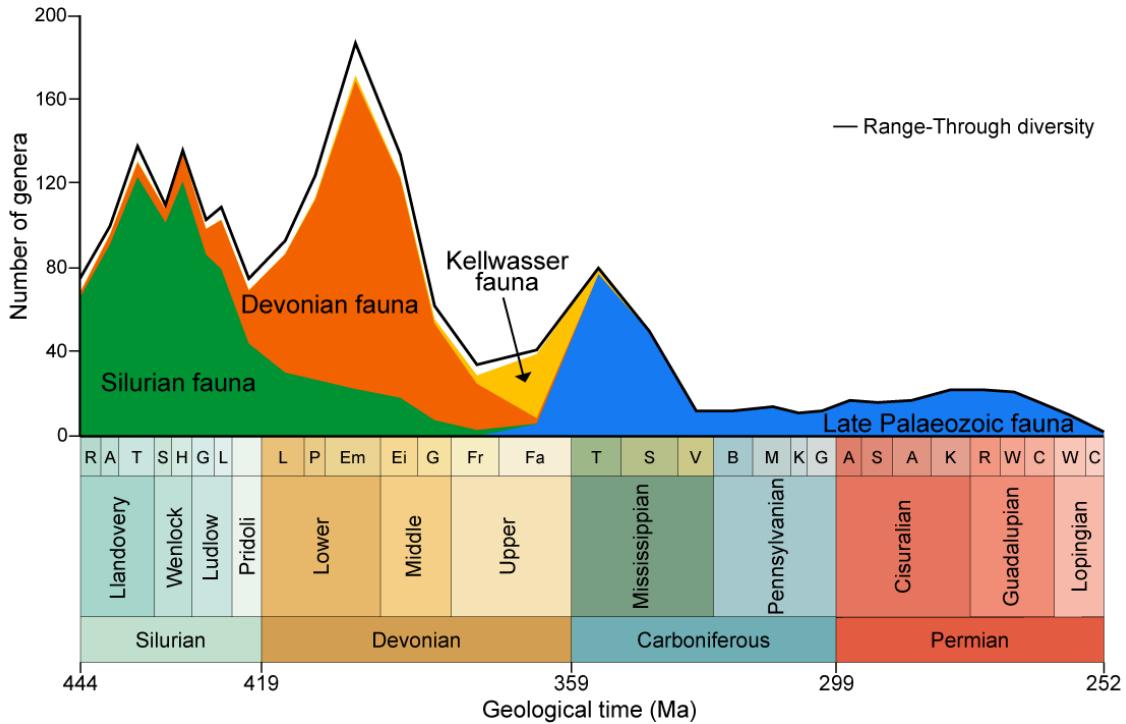


Figure 4. Diversity of each of the four trilobite evolutionary faunas from the Silurian to the Permian. Evolutionary faunas estimated with *Sepkoski (1981)*'s method. Black line represents the Range through diversity and the white part corresponds to the part of the diversity not explained by the model. Age from *Cohen et al. (2013, updated)*.

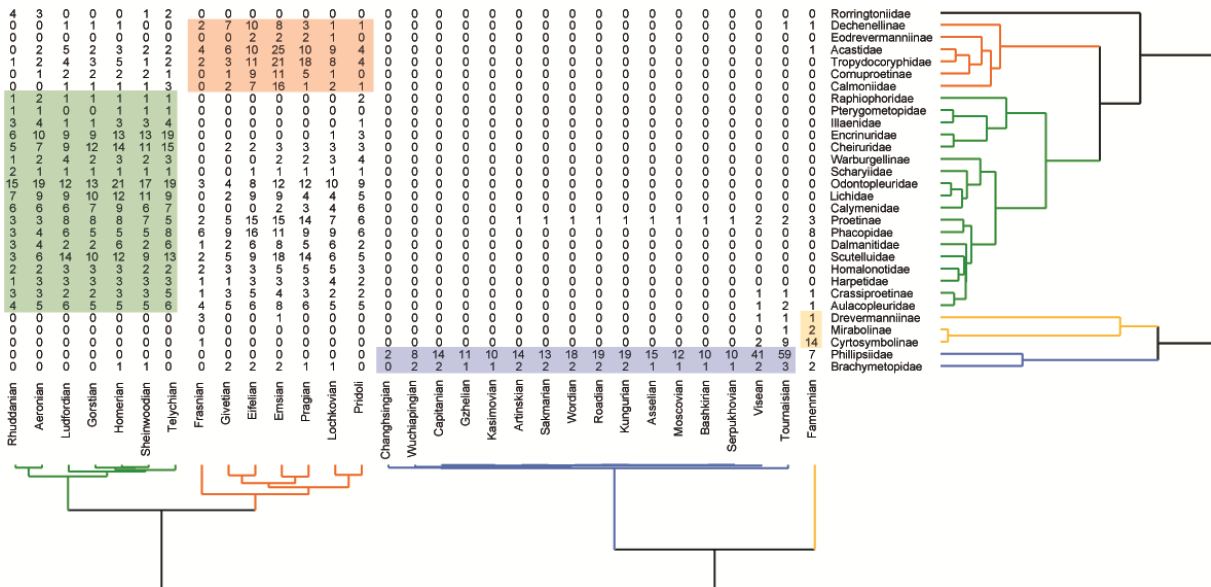


Figure 5. Hierarchical Cluster Analysis of the Post Ordovician trilobite families and subfamilies according their temporal distribution. Method used is UPGMA (*Sokal and Michener, 1958*) and the similarity index is Morisita's (*Morisita, 1959*).

Scores	Factor 1	Factor 2	Factor 3	Factor 4
>2	Phillipsiidae (5.5) 81%	Odontopleuridae (3.2) Encrinuridae (2.4) Cheiruridae (2.1) 40%	Acastidae (2.5) Tropydocoryphidae (2.3) Phacopidae (2.2) 33%	Cyrtosymbolinae (4.4) Phacopidae (2.6) 46%
>1		Lichidae (1.8) Calymenidae (1.5) Scutelluidae (1.3) 64%	Proetinae (1.9) Dechenellinae (1.4) Scutelluidae (1.4) Encrinuridae (1.1) Aulacopleuridae (1.1) 65%	Tropydocoryphidae (1.2) 49%
>0,5	Brachymetopidae (0.6) 89%	Aulacopleuridae (0.7) Illaenidae (0.6) Proetinae (0.6) Warburgellinae (0.5) 77%	Calmoniidae (0.9) Cornuproetinae (0.8) Homalonotidae (0.8) Dalmanitidae (0.7) 81%	Scutelluidae (0.8) Drevermanniinae (0.7) Mirabolinae (0.6) Cornuproetinae (0.6) Calmoniidae (0.6) Aulacopleuridae (0.5) 79%

Table 1. Factor scores of the four evolutionary faunas. Family and subfamilies with a score higher than 0.5 are noted and distributed in to classes (>0.5, >1 and >2).

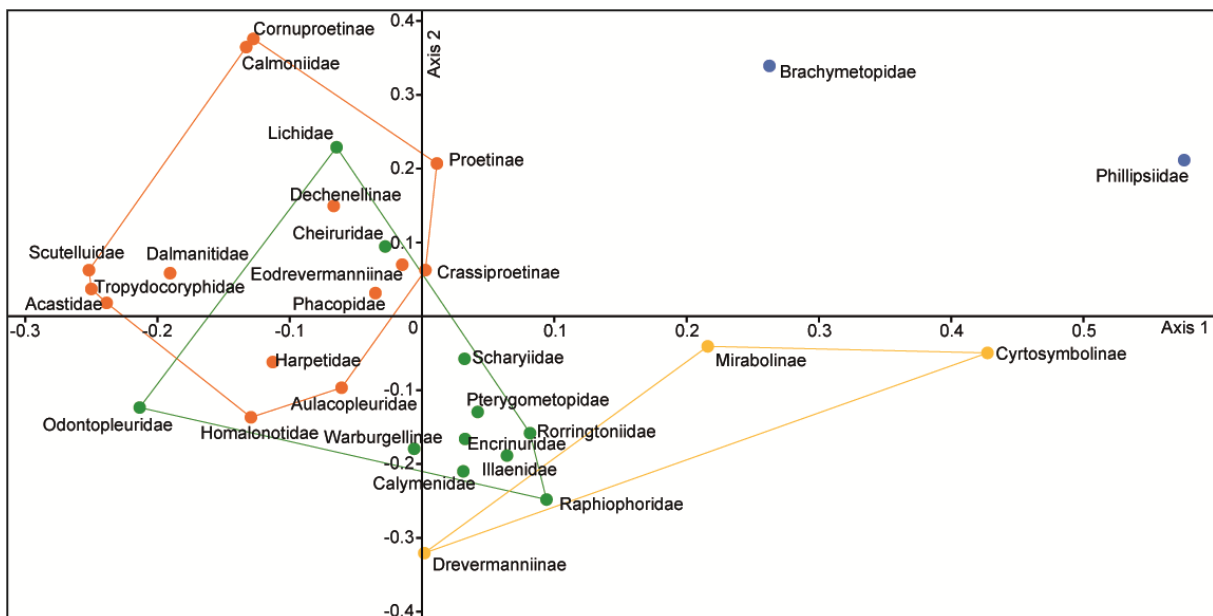


Figure 6. PCoA of a Euclidean distance between trilobite families and subfamilies according to their net change through time. Faunas defined by the factor analysis. Method from [Alroy \(2010c\)](#).

All families and subfamilies were distributed into different faunas according to their scores in each of the four factors (Table 1). The Silurian Fauna was dominated by cheirurids, Encrinurids and Odontopleurids, while the main components of the Devonian Fauna were tropydocoriphids, acastids and phacopids. Phacopids and cyrtosymbolines were the main members of the Kellwasser Fauna and finally the Late Palaeozoic Fauna was dominated by phillipsiids. A few families, however, had equivalent scores in more than one factor. Scutelluids, pterygometopids, harpetids and crassiproetines were components of the Silurian

and Devonian faunas. Similarly, phacopids were distributed between the Kellwasser and the Devonian faunas but represented a higher proportion of the Kellwasser Fauna (Fig. SUPPL. D). HCA helped to classify them into the fauna with which they were most related (Fig. 5).

PCoA shows that families and subfamilies were relatively equally distributed either based on their total diversity or change in diversity (Fig. 6). Cyrtosymbolinae, Mirabolinae, Brachymetopidae and Phillipsiidae show the highest PCoA1 values while the last two stand out with higher PCoA2 values (Fig. 6). PCoA groups families and subfamilies belonging to the Silurian and Devonian Faunas defined by the factor analysis. However, there is a relatively good separation between most families in the ordination belonging to the Silurian fauna which scattered along positive PCoA1 and negative PCoA2 values and most families from the Devonian Fauna which have negative PCoA1 and positive PCoA2 scores (Fig. 6). The only differences were that Drevermanniinae were closer to the Silurian Fauna and Phacopidae, Lichidae, Odontopleuridae and Cheiruridae closer to the Devonian Fauna.

Based on the abundance and turnover analyses, we could associate each family or subfamily with the fauna with which it had more affinity. The Silurian Fauna was composed of 11 families and subfamilies, i.e., Calymenidae, Cheiruridae, Encrinuridae, Illaenidae, Lichidae, Odontopleuridae, Pterygometopidae, Raphiophoridae, Rorringtoniidae, Scharyiidae, and Warburgellinae (Fig. 7). This fauna reached its maximum of diversity in the Silurian before a long decline until the end Devonian. The Devonian Fauna was composed of eight families and five subfamilies, i.e., Acastidae, Aulacopleuridae, Calmoniidae, Cornuproetinae, Crassiproetinae, Dalmanitidae, Dechenellinae, Eodrevermanniinae, Harpetidae, Homalonotidae, Proetinae, Scutelluidae and Tropydocoryphidae (Fig. 7). Most of these clades already existed in the Silurian but the diversity peak of this fauna was in the Early Devonian. The Kellwasser Fauna was composed of Cyrtosymbolinae, Drevermanniinae, Mirabolinae and Phacopidae, with a combined diversity increasing from the Silurian to the Late Devonian before a steep decline. The components of the Late Palaeozoic Fauna were Phillipsiidae and Brachymetopidae, which diversified mainly in the Early Carboniferous and survived until the end of the Permian (Fig. 7).

Different faunas coexisted at the same time, but one of them was generally dominant, except in the Pridoli-Lochkovian. The three main peaks in diversity from the Silurian to Permian can be explained by the emergence of one new fauna each time (Fig. 4). The Kellwasser Fauna, on the other hand, dominated during a period of reduced diversity is not related to a diversification event. Once a fauna lost its dominance it never regained it again. The decline of faunas was not similar for different faunas. While the Silurian Fauna progressively declined through more than

60 million years, the Devonian and Kellwasser faunas disappeared abruptly in less than 20 million years. After a rapid and significant loss of diversity in the Mississippian, the Late Palaeozoic Fauna survived for nearly 150 million years before becoming extinct.

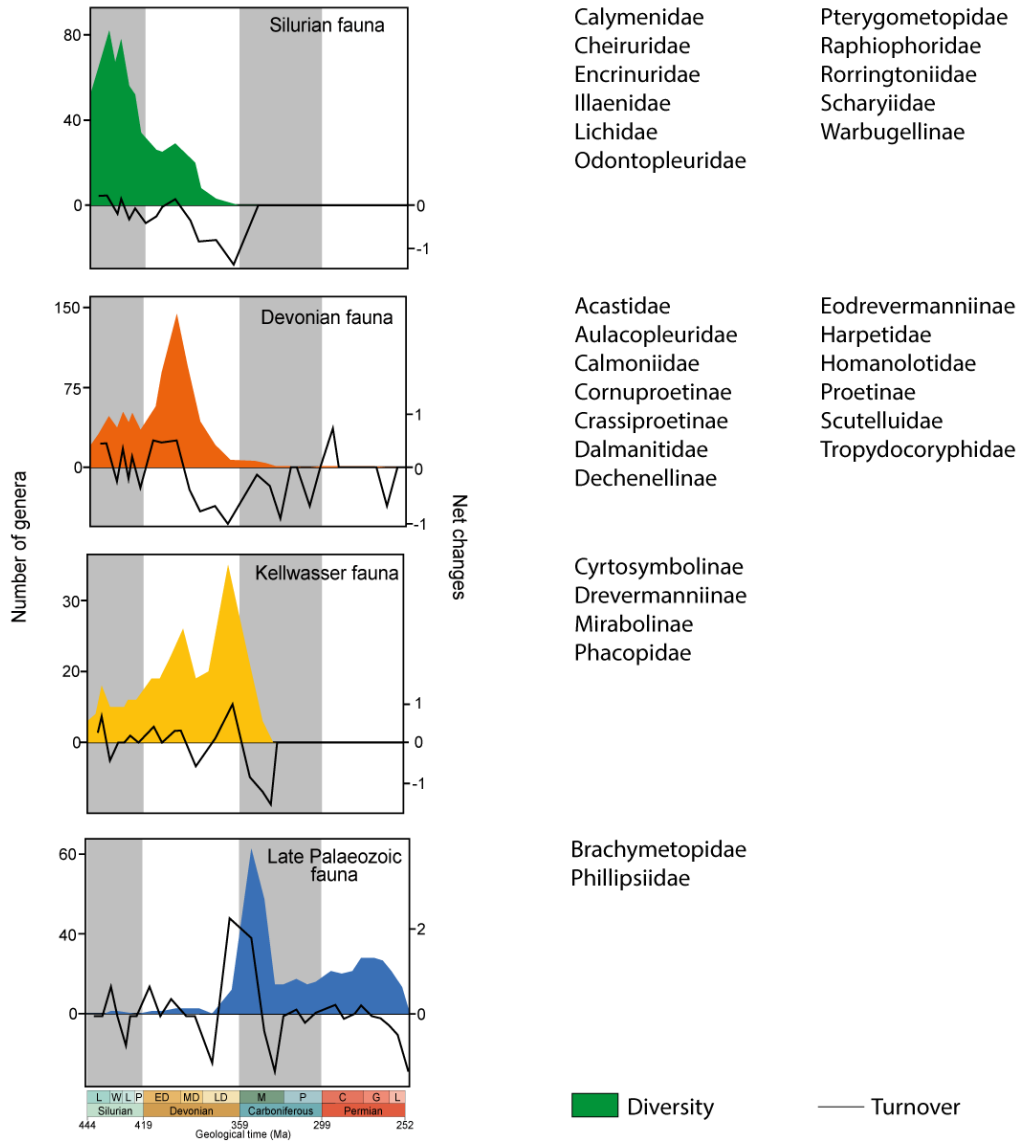


Figure 7. Detail of the composition of each trilobite evolutionary fauna. Diversity of faunas corresponds to the sum of the Range-through diversity of all the family and subfamily components. Black lines correspond to the net change (logged) for each fauna. Age from *Cohen et al. (2013, updated)*.

3.3. Latitude

Most trilobite genera lived at low latitudes from the Rhuddanian to the Givetian (Fig. 8A). For the same period, the proportion of trilobites living/dwelling beyond 60° latitude increased until the end of the Silurian, although it remained largely minor. High latitude habitats were

progressively depopulated by trilobites before being abandoned in the Frasnian. High latitude data from the Givetian to the Cisuralian should be taken with caution because there are no collections at all from these areas at this time; it could be a sampling bias. Frasnian corresponds to the only period when diversity became more important in the middle latitudes (Fig. 8A). The trend has been reversed since the Famennian with increasing numbers of trilobites dwelling at low latitudes (Fig. 8A). It is difficult to analyse post Mississippian data because they are based on the presence of only a few genera, leading to considerable uncertainty, but most trilobites appeared to live at low latitudes. However, some trilobites seemed to invade the high latitudes again in the Permian.

The latitudinal distribution of each fauna somewhat mirrors latitudinal trends for all trilobites (Fig. 8B). Small differences are found Kellwasser Fauna, which records a large proportion of genera at high latitudes during the Silurian (Fig. 8B). The Devonian Devonian Fauna shows a greater proportion of diversity at high latitudes (above 60° latitude), probably related to the

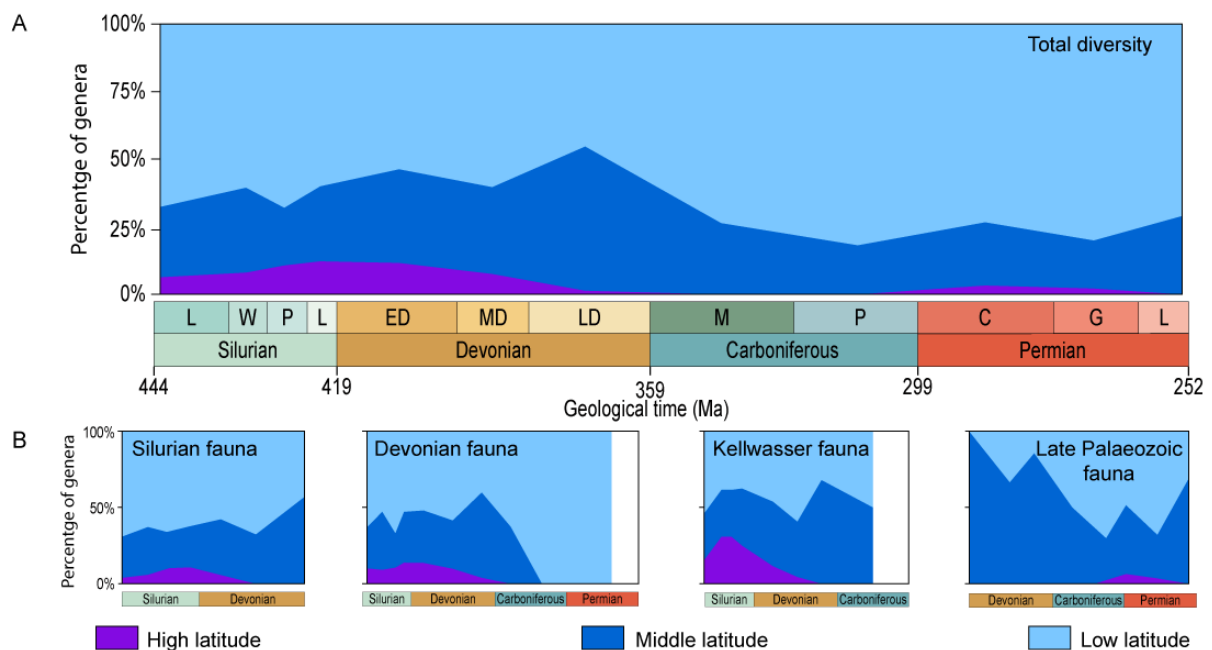


Figure 8. Latitudinal repartition through time of trilobites for the total diversity and for the four evolutionary faunas. Repartition is expressed in the percentage of genera. Age from *Cohen et al. (2013, updated)*.

diversification of Calmoniids (*Abe and Lieberman, 2009*). Interestingly, genera belonging to the Devonian Fauna that survived after the Late Devonian crisis, were constrained to low latitude habitats. The Late Palaeozoic Fauna developed initially at mid latitudes, and only later diversified in high and low latitude environments. Unfortunately, the low abundance of this fauna prevents any definitive interpretation. In the Carboniferous and Permian only the Late Palaeozoic Fauna was present beyond 30° latitude (Fig. 8B).

3.4. Bathymetry

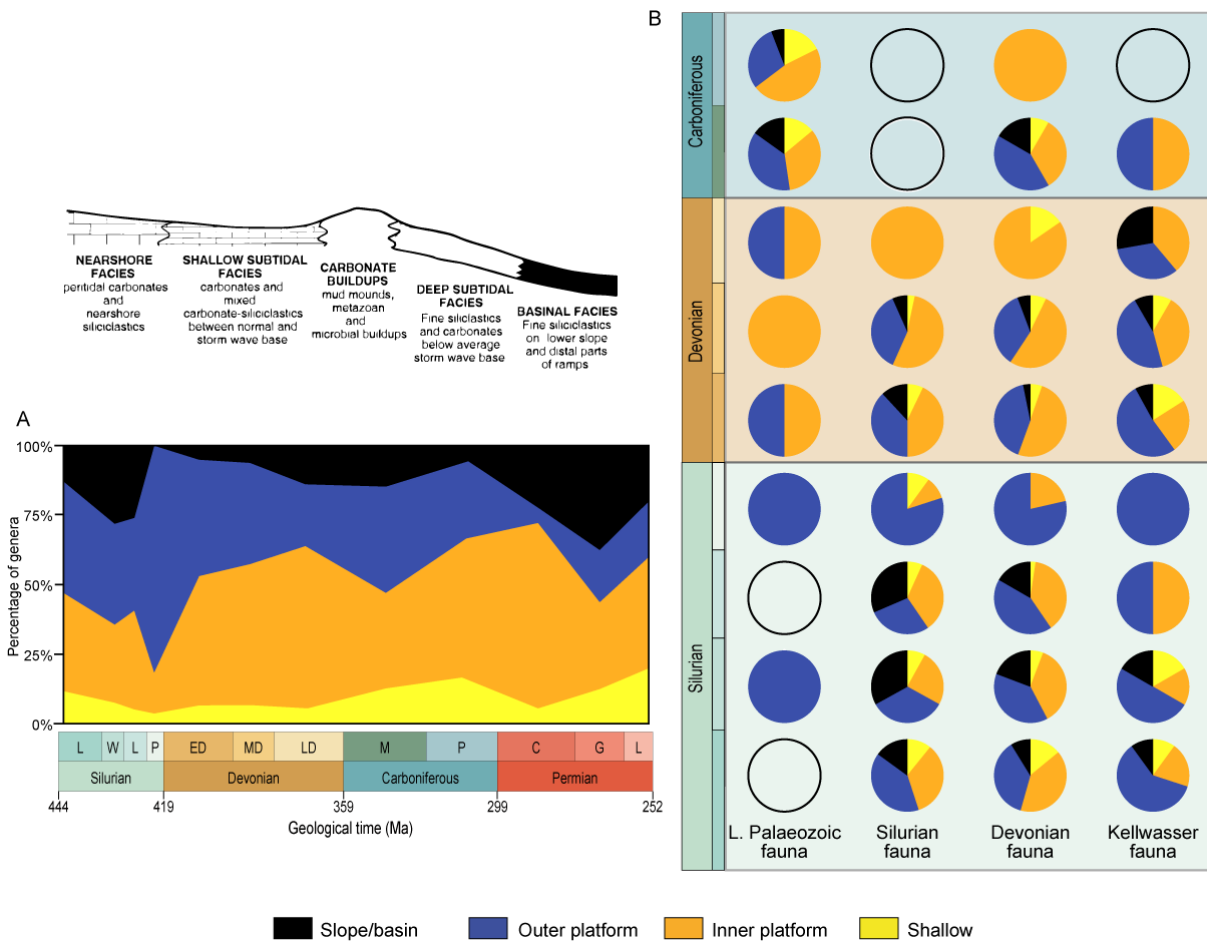


Figure 9. Lithological repartition through time of trilobites (A) for the total diversity and (B) for the four evolutionary faunas. Diversity corresponds to the number of genera. Age from [Cohen et al. \(2013, updated\)](#).

The bathymetrical distribution of trilobites changed over time (Fig. 9B). Trilobites living in deep water (i.e., Outer Platform and Slope/Basin facies) were an important part of the Silurian period before losing their importance in the Devonian. During this Period, trilobites developed preferentially in shallower environments (i.e., Shallow and Inner platform) but the Late Devonian corresponded to an increase in trilobites living in basinal environments (Fig. 9B). The importance of deep-water trilobites continued to increase in the Mississippian, but later they became rarer, excepted in the Guadalupian (Fig. 9B).

Most faunas showed similar bathymetric trends from the Silurian to the Middle Devonian. The Late Paleozoic Fauna, however, seems to have diversified in outer platform environments during this interval (Fig. 9C). Interestingly, during the Late Devonian only the Kellwasser

Fauna was present in the deep-water facies (Fig. 9C). It was not until the Carboniferous that the Late Paleozoic fauna accessed to shallow and deep-water environments, therefore dominating the whole bathymetric gradient.

3.5. Depositional environment

In the analysed dataset, most trilobites inhabited carbonate environments in all studied intervals (Fig. 10A). Diversity was almost equivalent between uniquely carbonate and siliciclastic or mixed environments during the Silurian. Nevertheless, trilobites with a carbonate affinity became particularly important from the Middle Devonian (Fig. 10A, Fig. SUPPL. E). Beyond this trend, the number of trilobites shows that diversification and extinction events occurred in any type of environments (Fig. 10A). After the Serpukhkovian crises few trilobites lived in siliciclastic environments (Fig. 10A).

The Silurian Fauna did not show a preference for either lithology throughout its history. Both the Devonian and Kellwasser faunas, however, showed no evident preference during the Silurian but occurred primarily in carbonates in the Devonian. With the exception of the Pennsylvanian, the Late Palaeozoic Fauna was preferentially recorded in carbonate environments (Fig. 10A).

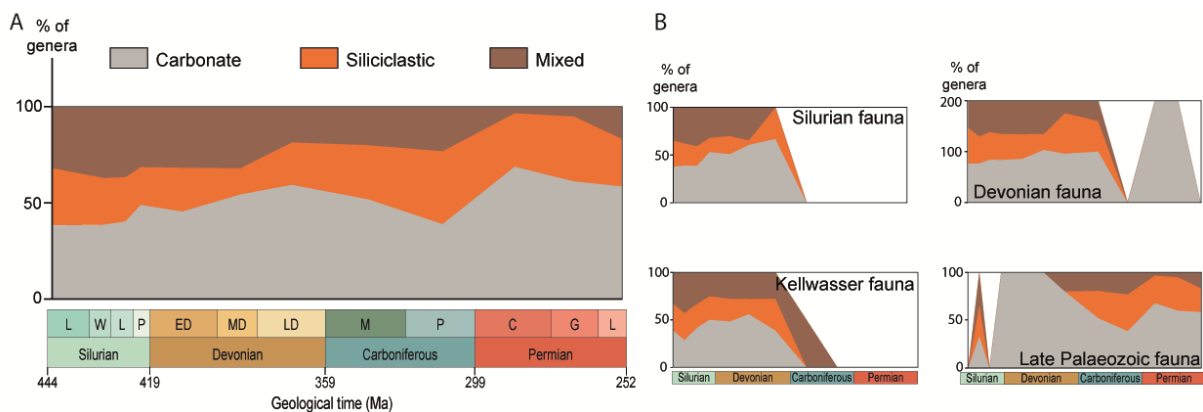


Figure 10. Environmental repartition through time of trilobites (A) for the total diversity and (B) for the four evolutionary faunas. Repartition is expressed in the percentage of genera. Age from [Cohen et al. \(2013, updated\)](#).

3.6. Correlation with environmental proxies

Total trilobite diversity and evolutionary faunas were not correlated to any proxy (Table 2). Changes of a single proxy could not explain diversity dynamics.

	Total		Silurian		Devonian		Kellwasser		Carboniferous	
	p	rho	p	rho	p	rho	p	rho	p	rho
dSr	0.95	-0.04	0.95	-0.08	0.60	-0.29	0.57	0.70	0.84	0.11
Sea-level	0.83	0.12	0.54	0.38	0.72	0.21	1	0	0.43	0.33
d13C	0.95	0.02	0.95	-0.06	0.54	-0.33	0.43	0.80	0.43	0.33
Sedimentation	0.43	0.31	0.43	0.48	0.43	0.42	0.83	-0.40	0.69	-0.20
Fragmentation	0.95	0.05	0.86	-0.13	0.95	0.03	0.43	0.90	0.43	0.44
Temperature	0.83	0.11	0.64	-0.30	0.83	-0.15	0.43	0.80	0.66	0.21

Table 2. Results of the pairwise correlation tests of detrended (first differences) values of these environmental proxies with detrended raw diversity. Diversity at the global and by evolutionary faunas were compared to environmental proxies. Pairwise correlation tests were performed using Spearman's r as correlation index and p values were corrected because of multi correlation tests.

4. Evolutionary faunas

4.1. Late Ordovician mass extinction and the early Silurian recovery

The Late Ordovician extinction event resulted in the disappearance of about 60% of genera and 25% of families (Sepkoski, 1996). It was probably a consequence of an important glaciation and a subsequent sea-level fall (Sheehan, 2001; Harper et al., 2014). Although trilobites were highly diverse in the Early Palaeozoic, this extinction strongly affected them, particularly the Cambrian faunas (Owen et al., 1991; Sheehan, 2001). All the families that successfully crossed the Ordovician-Silurian boundary without significant losses originated in the Ordovician (Owen et al., 1991; Adrain et al., 1998; Sheehan, 2001). Calymenids, cheirurids, encrinurids, illaenids, lichids, odontopleurids, pterygometopids, raphiophorids, rorringtoniids, scharyiids and warburgellines survived Late Ordovician events (Sepkoski, 1996; Sheehan, 2001; Harper et al., 2014) and have proliferated in many places since the Llandovery (Figs. 4, 7). These families and subfamilies were components of the Silurian Fauna, which is a subset of the Whiterock Fauna, as Adrain et al. (1998) already underscored (Adrain et al., 2000, 2004). The families and subfamilies of the Silurian Fauna were not the only ones to live in Silurian waters and some families and subfamilies of the Devonian Fauna were already present, such as acastids, scutellids, aulacopleurids and proetines (Fig. 7). The recovery was quick, the diversity of the Early Silurian trilobites was similar to that of the Cambrian and Ordovician at local (i.e., alpha diversity), despite a decrease in provincialism and β diversity (Adrain et al., 2000; Chatterton and Ludvigsen, 2004).

Polar areas were devoid of trilobites in the Rhuddanian (Fig. 4) because the Late Ordovician extinction strongly affected high latitude trilobites (Adrain et al., 2004). Consequently, the Early Silurian radiation occurred preferentially at low latitudes (Adrain et al., 1998). Similarly,

many Silurian trilobites lived in shallow environments (Thomas and Narbonne, 1979; Siveter, 1995; Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Stocker et al., 2019; Wendruff et al., 2020; Yuan et al., 2020) because the Hirnantian extinction had a lesser impact on shallow water communities than on deep-water ones (Adrain et al., 2000).

4.2. Silurian

No important trilobite diversity changes occurred in the Silurian due to the relative climate stability in terms of environmental changes (Tinn et al., 2020). Nonetheless, Silurian trilobites were subject to minor taxonomic changes at low taxonomic ranks linked to environmental variations. The earliest events happened locally in the early Llandovery of the Northwestern Canada (Chatterton et al., 1990). This minor extinction affected the global diversity anyhow (Fig. 2). The first important event occurred at the Llandovery-Wenlock boundary and is known as the Ireviken event (Jeppsson, 1987; Munnecke et al., 2003). During this event, there was a sea-level fall associated with a positive excursion of $\delta^{13}\text{C}$ linked to anoxia and dysoxia. These environmental changes affected different biota as conodonts, corals, ostracods for example (Aldridge et al., 1993). 50 % of the trilobites of Gotland disappeared (Ramsköld, 1985). Although the Ireviken event was mainly spotted in Scandinavia, it occurred elsewhere in the world (Calner, 2008; Molloy and Simpson, 2012; Noble et al., 2012). It corresponded to the most important period of extinctions and migrations for Silurian trilobites of Northwestern Canada (Chatterton et al., 1990) and central USA (Mikulic and Kluessendorf, 1999). The global diversity was affected by this event (Fig. 2). In the early Ludlow, another important facies shift associated with positive excursion of $\delta^{13}\text{C}$ and sea-level drop occurred. It was the Mulde event, which led to diversity decrease. However, this event had a stronger impact on pelagic fauna as graptolites than on the benthic biota, which were mainly characterized by faunal changes (Calner, 2008). Therefore, trilobites were not strongly affected by this event and were found in the sediments deposited during this event (Jarochowska et al., 2014; Spiridonov et al., 2017). In addition, trilobites took advantage of the new conditions as odontopleurids arrived in Poland and in Scandinavia just after this event (Porębska et al., 2004; Calner et al., 2006).

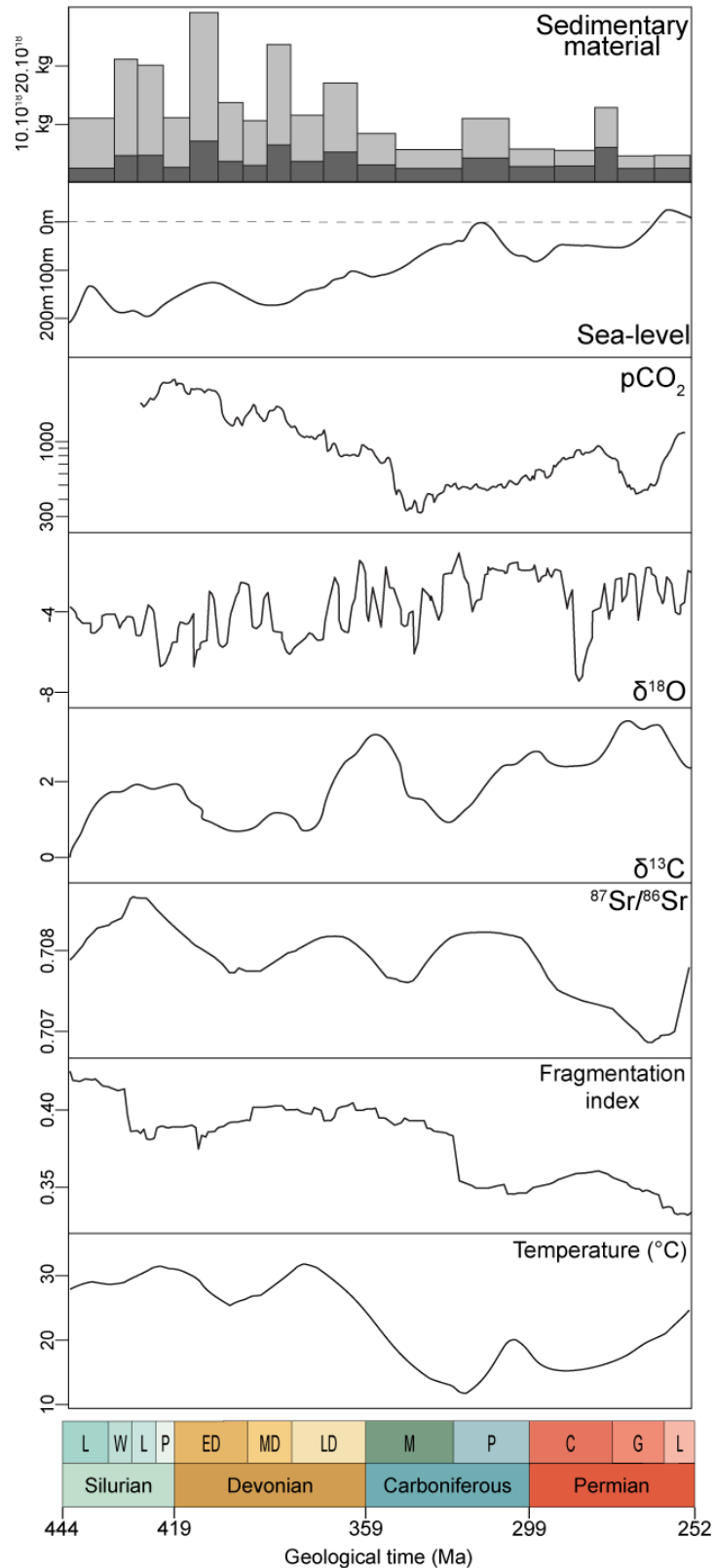


Figure 11. Trends of multiple environmental proxies. Existing (dark grey) and reconstructed (light grey) mass of continental and oceanic sediments from [Hay et al. \(2006\)](#). Sea-level from [Haq and Schutter \(2008\)](#); pCO₂ from [Foster et al. \(2017\)](#); δ¹⁸Oapatite from [Veizer and Prokoph \(2015\)](#); δ¹³C from [Saltzman and Thomas \(2012\)](#); ⁸⁷Sr/⁸⁶Sr ratio from [McArthur et al. \(2012\)](#); Fragmentation index from [Zaffos et al. \(2017\)](#) and mean tropical sea-surface temperatures ([Song et al., 2019](#), mean values from [Scotese et al., 2021](#)). Age from [Cohen et al. \(2013, updated\)](#).

No important environmental affinity occurred during this relatively stable period. Since the Aeronian, trilobites started to develop beyond 60° latitude in Gondwana and Baltica, with several families restricted to high latitudes (Adrain et al., 1998). During the whole Silurian, high latitudinal trilobites were thus well-represented (Fig. 9). Latitudinal distribution partly explains the important proportion of Silurian trilobites in both mixed and siliclastic environments. Indeed, polar trilobites proliferated preferentially in siliciclastic environment whereas fauna living in carbonate deposits proliferated at low latitudes (Cocks and Fortey, 1990). Moreover, the Silurian was a period of large deposits of sedimentary material with a high $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (Fig. 11), indicating a period of important erosion and weathering (Capo et al., 1998). Colder and humid episodes occurring in the Silurian (e.g., P-episodes postulated by Jeppsson, 1990) increased weathering and erosion; the products of these weathering and erosion flowed into the oceans and led to more clastic deposits. The Silurian was also the last period of important erosion and sedimentation due to limited land plant cover (Hay et al., 2006), before the development of vascular plants in the Devonian (Pawlik et al., 2020). Consequently, there were large terrigenous inputs to the continental margins, which explains why many trilobites diversified in siliciclastic environments. Nevertheless, carbonate environments were also appreciated by Silurian trilobites (Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Hughes and Thomas, 2011; Wendruff et al., 2020; Fig. 10). Silurian trilobites were all benthic contrary to the Ordovician ones (Thomas and Lane, 1984), the substrate type had a strong effect on benthic communities (Henderson and Dann, 2010; Hopkins, 2014). Silurian trilobites also developed in relatively deep environments until the Ludlow (Fig. 9). Aulacopleurids were the first groups to diversify in high depth (Fortey and Owens, 1975). They were followed by many families until deep environments concentrate a relevant proportion of the total diversity (Storey et al., 2016). Trilobite proliferation in deep environment coincided with the Silurian long-term transgression until the Wenlock (Haq and Schutter, 2008). Differentiated trilobites biofacies could be recognized along the whole bathymetric profile, proliferating in various facies (Thomas, 1979; Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004) both carbonate and clastic (Fig. 10).

A third relatively important event struck the Silurian: the Lau event in the Ludfordian. This event had the most important impact on Silurian trilobites (Fig. 2) and corresponded to the beginning of the decline of the Silurian Fauna (Fig. 4). The Lau event was mostly spotted in central and Northern Europe (Lehnert et al., 2003; Antoshkina, 2018) and was characterized by a sea-level fall before a transgression and a perturbation in the carbon cycle as in the Ireviken and Mulde events (Calner, 2008; Munnecke et al., 2010; Bowman et al., 2019). Trilobites were

affected by this event as were many other groups like acritarchs, chitinozoans, polychaetes, tentaculids and ostracods in Scandinavia but also in Canada, in Poland and in Britain (Jeppsson and Aldridge, 2000 and references therein; Eriksson et al., 2009). At the same time, a decrease of trilobite diversity occurred in North Africa even if the Lau event has not yet been recorded in this region (Bault et al., 2021). Decrease of diversity also concerned trilobites of Uzbekistan and Tajikistan between Ludlow and Pridoli (Ivanova et al., 2009) and in the Prague basin, there were trilobite extinctions in the Kozlowskii zone, just after the Lau event (Manda and Kříž, 2006). However, the impact of this event on trilobites concerned mainly taxonomic changes and trilobites were among the fauna participating to the recovery in the Prague basin (Lehnert et al., 2003; Manda and Frýda, 2014). Long-term sea-level drop began also in the Ludlow (Haq and Schutter, 2008). The effects associated with environmental changes (i.e., sea-level fall and carbon isotope disruption) particularly affected shallow environments and fauna at low latitudes (Calner, 2008). Thereby, Pridoli trilobites were mainly found in deep environments at higher latitudes. In addition, Calner (2008) highlighted important changes in carbonate platforms after the Lau event, explaining why trilobites living in carbonate environment were affected. Within the Silurian Fauna, Raphiophoridae and Encrinuridae disappeared shortly after the Pridoli (Chlupáč, 1994). The decline of the Silurian Fauna also corresponded to a reduction of continental margins, as suggested by a decrease of the fragmentation index (Fig. 11), partly due to the closure of the Iapetus Ocean and the collision of Baltica and Laurentia (Roberts, 2003; Scotese, 2021). As many Silurian trilobites lived along the coasts of these two continents (Cocks and Fortey, 1990; Adrain et al., 1998, 2000), these two palaeogeographical changes may have played a role in the weakening of the Silurian Fauna. Moreover, although the Silurian began with an icehouse climate with glaciations events (Calner, 2008; Munnecke et al., 2010; Trotter et al., 2016; Cuervo et al., 2018), a progressive warming of the oscillating climate occurred (Azmy et al., 1999; Gambacorta et al., 2019) to reach high temperatures in the Late Silurian and Lochkovian (Joachimski et al., 2009). Thus, the drop of the Silurian Fauna occurred when the climate no longer resembled to the one during its peak.

In parallel with the gradual decline of the Silurian Fauna, a gradual increase in the Devonian Fauna occurred since the Ludfordian (Fig. 4). The passage from one fauna to the other constituted a temporally diffuse turnover, the Devonian Fauna having a strong positive diversification from the Ludlow while the Silurian Fauna did not rebound after the Pridoli decline (Fig. 4). As for trilobites, a progressive faunal turnover occurred for decapods, another marine arthropod clade, in response to sea-level fluctuations and explosive radiations (Schweitzer and Feldmann, 2015). Schweitzer and Feldmann (2015) suggested a potential

competition between decapods to explain such faunal turnover. This hypothesis could explain the Silurian-Devonian faunal transition among trilobites.

4.3. Early Devonian

The Devonian Period was characterized by vast continental seas with many carbonate environments (Tinn et al., 2020) and a climate that continued to warm (Torsvik and Cocks, 2013). The transition between the Silurian and the Devonian did not show important taxonomical changes and only low extinction rates (Chlupáč, 1994). Many families diversified in the Lochkovian such as acastids, which lived in shallow siliciclastic environment (Morzadec, 1992; Chlupáč, 1994). Proetids, scutelluids and dalmanitids also diversified in this stage (Chlupáč, 1994), although they already existed in the Silurian. These families belonged to the Devonian Fauna, which became the dominant fauna. Diversity increased in the Pragian (Fig. 2). The global regressive event at the Lochkovian-Pragian boundary possibly led to this diversification (Chlupáč and Kukal, 1986; Chlupáč, 1994) with the increase in speciation rates by vicariance (Abe and Liebermann, 2009). This diversification was registered worldwide with the increase of diversity in the Pragian of North Africa (Bault et al., 2021), Czech Republic (Chlupáč et al., 1985) and Falklands Islands (Carvalho, 2006) for instance. Subsequently, trilobites diversified more in shallower environments (Fig. 9) in this period of global sea-level lowstand (Haq and Schutter, 2008), while the Silurian Fauna showed little preference for these shallow environments. Therefore, such changes accelerating the decline of the Silurian Fauna to the benefit of the Devonian Fauna. At the Pragian-Emsian transition, a transgression known as the Basal Zlichov Event occurred (Johnson et al., 1985; House, 2002), leading to a decrease of provincialism (Chlupáč, 1994). After this event, the early Emsian coincided with a slightly less diverse period. The following Daleje event corresponded to a worldwide sea-level rise and sedimentological changes (House, 1985, 2002; Chlupáč and Kukal, 1986) influencing trilobites (Chlupáč, 1994). After the transgression, blind and reduced-eyes trilobites developed as well as offshore trilobites, but shallower fauna remained highly diverse (Fig. 8). This led to a peak of low taxonomic rank richness in the late Emsian (Fig. 2, Chlupáč, 1994; Bault et al., 2021). It was particularly the time of the adaptive radiation of calmoniids (Eldredge and Branisa, 1980; Eldredge and Cracraft, 1980) and Chlupáč (1994) also noticed the increasing diversity during the Early Devonian of proetids, homanototids, aulacopleurids, dalmanitids, scutelluids, acastids (asteropygines) and harpetids. Taxa of the Devonian Fauna were thus the main taxa responsible for the Early Devonian diversification. Phacopids, which are major taxa

of the Kellwasser Fauna, also participated in the diversification of the Devonian (Fig. 6) with a maximum diversity in the Middle Devonian (Chlupáč, 1975; Crônier et al., 2011). The Emsian also showed higher diversity in different places like Ardennes (Crônier and Van Viersen, 2007), Colombia (Morzadec et al., 2015) or Morocco (Crônier et al., 2018), although it was not the case everywhere (Khaldi et al., 2016; Van Viersen and Taghon, 2020). The high diversity reached in the Early Devonian was the maximum post-Ordovician diversity (Adrain, 2008).

Carbonate and reef environments were widespread throughout the Devonian, favoured by the greenhouse climate and the presence of large epicontinental seas (Copper and Scotese, 2003; Joachimski et al., 2009; Copper, 2011; Tinn et al., 2020). Consequently, since the Early Devonian trilobites proliferated more in these carbonate environments (Chlupáč, 1994) relative to siliciclastic environments (Fig. 10). This interval also records the highest diversity in high latitude regions, with the flattest latitudinal diversity gradient. This pattern is probably related to the greenhouse climate (Cocks, 2007; Joachimski et al., 2009), as it is known that greenhouse intervals record rather flat latitudinal biodiversity gradients (Mannion et al., 2014). The Devonian Fauna diversification also occurred at high latitudes, notably with the development of calmoniids in the cold waters of the Malvinokaffric Realm (Carvalho and Ponciano, 2015). A diversification occurring at different latitudes characterized the trilobites because the Whiterock fauna originated at different place during its Ordovician radiation (Adrain et al., 2004). Such a biogeographic macroevolutionary pattern, however, is not the most frequent one, as highest origination rates occur frequently in the tropics (Jablonski, 1993; Brown, 2013).

Simultaneously to the Early Devonian diversification of the Devonian Fauna, a slowdown in the decline of the Silurian Fauna is observed between the Lochkovian and Eifelian (Fig. 4), during a period of diversification (Chlupáč, 1994), but without an increase in diversity. Between the Lochkovian and Eifelian, cheirurids, lichids and odontopleurids proliferated (Chlupáč, 1994).

4.4. Middle Devonian

No important changes in trilobite fauna characterized the transition to the Middle Devonian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) but the Middle Devonian events affected trilobite diversity negatively (Fig. 2). It was the onset of the decline of the Devonian Fauna while the Silurian Fauna fall accelerated (Fig. 7). A first event (i.e., the basal Choteč event), corresponding to a deepening associated to anoxia and dysoxia (House, 2002), occurred in the early Eifelian. These environmental changes affected the trilobites at the global with migrations

and extinctions despite a stable rate of diversification (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Trilobite families did not react in the same way because at the opposite of the decline of many families, Lichidae, Acastidae and Proetidae showed important innovations (Lerosey-Aubril and Feist, 2012). Transgression and anoxia could be more important at the regional as in North Africa (Klug et al., 2000; Ouali Mehadji et al., 2004), leading to a sharper decline of trilobites (Bault et al., 2021). At the opposite, the sea-level rise offered new shallow carbonate areas where trilobites proliferated (Fig. 10) and diversity increased (Crônier and Van Viersen, 2007; Bignon et al., 2008). The following Kačak event and its oxygen-depleted conditions also influenced Devonian Fauna (House, 1985, 2002; Walliser, 1996) including trilobites with extinctions and migrations (Feist, 1991; Morzadec, 1992; Chlupáč, 1994). However, Eifelian events were not the most devastating Middle Devonian events. The middle Givetian Taghanic event is associated with an important sea-level rise that killed many taxa, particularly ammonoids (House, 1985, 2002; Walliser, 1996). Trilobites were severely affected by this event, particularly those living in shallow environments. Lichids, cheirurids and calmoniids as well as some proetid and aulacopleurids subfamilies went extinct (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), whereas deep-water clades survived (Feist, 1991).

The decrease in the diversity in deep-water environments (Fig. 9) and high latitude (Fig. 8) was gradual. It was a consequence of a long-term effect (Haq and Schutter et al., 2008) and the succession of rapid sea-level transgressions. The decline in high latitudes was possibly linked to the progressive climate cooling in the Early and Middle Devonian (Joachimski et al., 2009; Scotese et al., 2021) affecting cold-water taxa. A cooler climate is associated with a steeper latitudinal gradient, possibly related to a decrease in high latitude diversity (Mannion et al., 2014). Furthermore, northward migration of Gondwana (Scotese and McKerrow, 1990; Scotese, 2021) must also have resulted in a decrease in high latitude coastlines. No lithological selectivity happened with the Middle Devonian events because both carbonate and clastic environments were involved in the decline (Fig. 6). Therefore, the disappearance of the Devonian Fauna corresponded to the decline of the trilobites rather than a faunal replacement, as it was the case for the Silurian Fauna.

4.5. Late Devonian

After the Taghanic event, no important changes affected trilobites which reached the late Frasnian without drastic changes (Fig. 2). The generic diversity remained low with few originations (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Absent in the

Givetian, the Kellwasser Fauna replaced the Devonian Fauna in the Late Devonian (Fig. 4). The Kellwasser Fauna, primarily phacopids and cyrtosymbolines, began to become highly diverse in the Frasnian (Fig. 4) with the adaptive radiation of phacopids present in shallow neritic to outer shelf habitats (Feist, 1991). The only event occurring in this period was the Frasnian event which affected both pelagic and benthic organisms (Walliser, 1996). This event only had a low impact on trilobites (Lerosey-Aubril and Feist, 2012). On the other hand, the Upper Kellwasser event occurring at the end of the Frasnian was one of the five mass extinctions (Raup and Sepkoski 1982; McGhee et al., 2013). This event was characterised by sea-level changes with a transgression followed by a regression and an important episode of anoxia (House, 2002; Bond and Wignall, 2008; Carmichael et al., 2019; Lu et al., 2021). The impact on the biota was important and many clades were severely affected (Buggish, 1991). This event had a strong effect on both low and high taxonomic levels of trilobites. Indeed, three of the five orders still living in the Frasnian disappeared: Corynexochida, Harpetida and Odontopleurida (Lerosey-Aubril and Feist, 2012). These orders were already impoverished in genera after being severely affected by the Taghanic event and the disappearance of their last genera at the end of the Frasnian led them to their extinction (McNamara and Feist, 2006; Feist and McNamara, 2007; McNamara et al., 2009). Subsequently, the Silurian Fauna disappeared with the Frasnian-Famennian crisis and the extinction of Odontopleuridae (Feist, 1991; Feist and McNamara, 2007).

Only two orders survived to the Kellwasser events, i.e., Phacopida and Proetida, but many of their families and subfamilies vanished: Asteropyginae, Cornuproetinae and Tropicocoryphinae (Chlupáč, 1994). After the Kellwasser biocrisis, the first trilobite to recover worldwide was the phacopid *Pulvinocephalus* in the early *triangularis* zone (Feist, 2019). Then, drevermanniines and cyrtosymbolines appeared in the *crepida* zone of the early Famennian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). However, trilobite diversity remained low until the late-early Famennian when the recovery really happened, giving a Famennian taxonomic richness similar to the Frasnian one (Fig. 2).

These trilobites took advantage of the Late Devonian environmental changes and invaded shallow and deep environments globally (Brauckmann et al., 1992; Lerosey-Aubril and Feist, 2005; Feist et al., 2003, 2009; Crônier et al., 2013). The Kellwasser Fauna became the dominant fauna in the Famennian. It was the only fauna that diversified in a context of a global decrease in diversity and with a short existence. This evolutionary fauna could be characterized as an opportunistic (Levinton, 1970) or crisis fauna.

Although the Kellwasser event severely affected offshore communities, recovery largely occurred in deep environments (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Temperature and bathymetry seemed to be two key parameters in the evolutionary fauna change although none of the fauna were strongly correlated with these parameters (Table 1). Indeed, the Silurian and the Kellwasser faunas that succeeded each other are faunas with different bathymetry affinities. In addition, they evolved in a different global temperature context. Temperature started to increase in the Frasnian (Fig. 11), to reach Lochkovian values, i.e., before the diversification of the Devonian Fauna. The affinity of the Kellwasser Fauna for warm waters seems to explain why the recovery occurred in a carbonate environment first and not in high latitudes (Figs. 8, 10). The higher faunal diversity at middle latitudes was related to a lower latitudinal gradient during greenhouse periods (Mannion et al., 2014). During its origins in the Silurian, the Kellwasser Fauna was mainly composed of high latitude genera in contrast to its Late Devonian distribution. A greater intensity of Middle and Late Devonian events in the tropics could lead to the migration of extratropical genera toward low latitudes. Indeed, reef communities representing complex ecosystems were strongly affected by the Frasnian-Famennian extinction event, resulting in greater consequences at low and middle latitudes (Buggish, 1991; McGhee, 1996; Walliser, 1996; Gong, 2002; Bond et al., 2013; Barash, 2017, Huang et al., 2018). Another explanation for the displacement of the Kellwasser Fauna towards lower latitudes could be related to the ecology of extratropical Silurian phacopids. Some of them were adapted to relatively deep environments near the storm wave base (Holloway, 1980; Sánchez et al., 1991; Rustán et al., 2011b; Fig. 9). Thus, after the deepening linked to the Devonian events, they could invade other places deserted by previous evolutionary faunas.

In addition to the taxonomic changes, important morphological changes affected trilobites around the Frasnian-Famennian boundary. Eyes reduction and blindness occurred in different taxa and in different parts of the globe (Feist, 1991, 2019; Crônier et al., 2004; McNamara and Feist, 2008, 2016; Lerosey-Aubril and Feist, 2012; Schoenemann, 2018) and were related to deepening and turbidity causing decrease of light (Feist et al., 2009). This common explanation is not enough in few cases and a propensity to an endobenthic behaviour were suggested for reduced-eyes and blind trilobites (Feist and Clarkson, 1989; McNamara and Feist, 2016). A size reduction could also affect trilobites (Feist and McNamara, 2016). The first Famennian trilobites were the phacopids *Pulvinocephalus* (*Cryphopsides*) and *Nephranops* appeared in the early Famennian in the *triangularis* zone in deep offshore environment (Feist, 2019). This reflected the post-Kellwasser trend of trilobites to move toward deeper habitats (Chlupáč, 1994; Feist et al., 2009; Lerosey-Aubril and Feist, 2012; Bault et al., 2021) as slope or basins (Fig. 8).

Nonetheless, many trilobites still occurred in shallow environment (Fig. 8; Crônier et al., 2020). Subsequently, other anoxic/hypoxic events and sea-level changes happened, i.e., Condroz and Annulata events (Walliser, 1996; House, 2002), with a low impact on trilobites. A second diversification occurred in the late Famennian during the Dasberg event among both Proetida and Phacopida (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), following a transgressive event implying diversification in nektic fauna such as Gonioclymeniina (House, 2002). Near the Devonian/Carboniferous boundary, another important biotic turnover linked to anoxia/dysoxia and sea-level fall occurred (Walliser, 1996; House, 2002; Kaiser et al., 2016; Zhang et al., 2020). Trilobites were strongly affected by this event (Fig. 2), with the disappearance of the order Phacopida as well as blind and reduced-eyes Proetida trilobites (Lerosey-Aubril and Feist, 2012). The Hangenberg event was lethal for both shallow and deep water trilobites (Chlupáč, 1994), but it had a stronger impact on deeper trilobites and consequently, survivors mostly lived in shallower areas (Feist and Petersen, 1995). Important faunal changes coincided with this event (Brauckmann et al., 1992). The Kellwasser Fauna almost disappeared with the Hangenberg event at the end of the Devonian, resulting in the extinction of phacopids (Lerosey-Aubril and Feist, 2012) and the decline of cyrtosymbolines, so that this subfamily was considered extinct for a long time (Feist, 1991). Climate cooling and glaciation at the Devonian-Carboniferous boundary (Isaacson et al., 2008; Kaizer et al., 2016) affected more severely a fauna accustomed to warmer temperatures.

4.6. Carboniferous and Permian

The early Carboniferous recovery was achieved with the survival of two families, namely Brachymetopidae and Phillipsiidae, which characterized the Late Palaeozoic Fauna (Figs. 4, 7). While the brachymetopids already existed in the Devonian, the phillipsiids emerged and diversified in the Tournaisian (Owens, 1990; Lerosey-Aubril and Feist, 2012; Vanderlaan and Ebach, 2015), and were largely responsible for the peak in diversity of the latest trilobite evolutionary fauna. The diversification of this fauna was very rapid after the Late Devonian extinction events and could be considered as a recovery fauna. Tournaisian diversity recovered to the higher taxonomic richness values since the Eifelian (Fig. 2). This rise of diversity was not homogeneous at the global and trilobite diversity remained low in China (Fan et al., 2020). This diversity peak was mainly due to the great radiation of phillipsiids whereas the other families remained low diversified (Owens, 1990). With this diversification, trilobite and especially phillipsiids occupied various environment from reef to outer platform (Fig. 8; Owens,

1990). There were no differential trends in bathymetric repartition because no long-term sea-level changes affected the Famennian-Tournaisian transition (Haq and Schutter, 2008). Tournaisian diversification coincided with a higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (Fig. 11), indicating a possible increase in continental supply due to erosion. As a result, trilobites invaded the siliciclastic environments whereas they previously preferred shelf carbonate environments (Owens, 1990; Lerosey-Aubril and Feist, 2012; Fig. 10). While the Late Palaeozoic Fauna was restricted to the mid-latitudes in the Devonian, it invaded the low latitudes deserted by other trilobite evolutionary faunas in the Carboniferous. The high latitudes remained deserted in a context of low temperatures (Scotese et al., 2021).

Contrary to pelagic clades, Trilobites survived anoxia and sea-level changes of the Mid-Tournaisian event (Walliser, 1996). Subsequently, the decline of phillipsiids corresponded to the decline of the Late Palaeozoic Fauna in the Viséan and Serpukhovian (Fig. 2) in all depositional environments and at all depths. Then, trilobite diversity stagnated while other benthic faunas could strongly diversify in the second part of the Carboniferous (Shi et al., 2021). As this fauna never reached a similar taxonomic richness again and remained essentially undiversified for the next tens of millions of years, it could be considered as a ‘dead clade walking’ (Jablonski, 2002; Barnes et al., 2021). From the Serpukhovian, the fauna developed preferentially in low latitudes due to the establishment of a progressive icehouse climate (Cocks, 2007; Shi et al., 2010; Fig. 8). Since the Mississippian, only a small proportion of trilobites were found in deep-water facies due to the decline of phillipsiids in basinal environments (Fig. 8; Owens, 1990). The Mid-Carboniferous events (Saunders and Ramsbottom, 1986; Walliser, 1996) led to the extinction of many benthic and pelagic taxa. However, the trilobite diversity was already low at this time and no significant changes happened (Lerosey-Aubril and Feist, 2012). Then, the beginning of the Pennsylvanian was characterised by another period of origination and a rise of diversity, but not in the same magnitude as the Tournaisian (Fig. 2). Trilobites followed a global trend resulting in the diversification of numerous clades at this period, boosted by the closure of the Rheic ocean and advantageous environmental changes (Shi et al., 2021). A higher proportion of trilobites lived in siliciclastic environments than in carbonate environments. This was a consequence of the cooling of the Late Palaeozoic Ice Age, which had an impact on the carbonate factory (Balseiro and Powell, 2020). With this cooling, tropical faunas slightly decline (Fig. 9). Powell (2005) noticed that brachiopods from low latitudes were the most affected too, suggesting that tropical taxa disappeared because they had a narrower latitudinal distribution. At the end of the Pennsylvanian another diversity decrease occurred (Lerosey-Aubril and Feist, 2012). Trilobites

did not show important diversity changes in the end of the Carboniferous and the beginning of the Permian (Lerosey-Aubril and Feist, 2012) during a period characterized by important glaciation and low marine invertebrate diversity (Alroy et al., 2008). Since the Asselian, the Late Palaeozoic Fauna developed again preferentially in carbonate environments (Fig. 10). With the climate warming, trilobite diversity slightly rose in the Sakmarian-Artinskian (Lerosey-Aubril and Feist, 2012). The reappearance of the high latitude fauna in this warmer phase during a period of glaciation is notable (Cocks, 2007; Haig et al., 2014, 2017). Then, another decrease linked to very low origination rates because of unfavourable environment (Lerosey-Aubril and Feist, 2012). The Late Palaeozoic Fauna disappeared at the Permian-Triassic boundary sealing the fate of the trilobites (Lerosey-Aubril and Feist, 2012; Song et al., 2013).

5. Ecological changes

The Devonian was a key period in the Palaeozoic history with important changes in both marine and terrestrial ecosystems. On the continents, land plants diversified and invaded continental environments (Cleal and Cas-Miñana, 2014; Pawlik et al., 2020; Dahl and Arens, 2020). Land plants are suspected to be a major driver of environmental changes occurring from the Devonian to the Permian. In the Late Devonian, vascular plants developed on lands with the consequence of increased burial of organic carbon in marine sediments and the enhancement of the silicate weathering (Algeo and Scheckler, 1998, 2010; Pawlik et al., 2020; Dahl and Arens, 2020). These upheavals dropped the atmospheric CO₂ levels and positive $\delta^{13}\text{C}$ shift in marine carbonates (Fig. 11) leading to climate cooling (Algeo and Scheckler, 1998; Algeo et al., 2001), although effect of land plants was not the only mechanism evoked for weathering (Goddéris et al., 2017; Racki et al., 2018; McDonald et al., 2019). However, recent studies argued that land plants hampered weathering (D'Antonio et al., 2020) leaving the land plant effect an ongoing debate. Diversification of vascular plants affected marine environments with the supply of nutrient fluxes and plant litter in epicontinental seas leading to increase of primary productivity and thus, eutrophication and anoxia (Algeo and Scheckler, 1998; Zhang et al., 2020; Lu et al., 2021). Trilobites and particularly those of the Devonian Fauna were affected by anoxic events. In addition to these changes, diversification of vascular land plants could lead to a late Famennian glaciation and especially the Carboniferous-Permian glaciation (Algeo and Scheckler, 1998). Environmental changes induced by continental plants affected trilobites in the same way as changes in marine ecosystems did, particularly the Kellwasser Fauna, which

appreciated warm climate. Therefore, changes in ecosystems in the second part of the Palaeozoic challenged trilobites, which never regain their former diversity despite the Tournaisian diversification.

In parallel to the plant terrestrialization, the Devonian Nekton Revolution (Klug et al., 2010) occurred in the oceans with the diversification of many nektonic animals, although the nekton was diversified prior to the Devonian (Whalen and Briggs, 2018). Development of such fauna could influence trilobite diversity in two different ways. Nektonic organisms could be new predators for trilobites or new concurrent for food resource. Concerning predation, Palaeozoic trophic links remains largely unknown (Brett and Walker, 2002) but some assumptions are made on the possible predators. Besides, the number of durophagous predators sharply increased in the Devonian (Signor and Brett, 1984; Brett, 2003). In parallel, trilobite ecdysis was different from other arthropods and implied longer intermoult periods, enhancing their vulnerability to predators (Brandt, 2002). Babcock (2003) envisaged different trilobite predators appearing progressively in the Palaeozoic seas: phyllocarids, eurypterids, malacostracans, jawless and jawed fishes, cephalopods, some echinoderms, and even other trilobites. There was a rise of predator diversity from the Middle Devonian with the diversification of nautiloids, placoderms, elasmobranchs and Sarcoptrigii/Actinopterygii (Klug et al., 2010) contemporary to the decrease of the Devonian Fauna. Ammonoids appeared in the Emsian while nautiloids developed (Klug et al., 2010). Nautiloids were suspected to hunt trilobites since the Early Palaeozoic (Brett and Walker, 2002; Brett, 2003; Bicknell et al., 2019), their increasing diversity could mean increasing predation on trilobites. Concerning ammonoids, their potential predation on trilobites remained uncertain, particularly because there is no evidence that ammonoids had jaws and radula in the Palaeozoic (Nixon, 1996; Tanabe et al., 2015). Despite the lack of strong evidence, jawed fishes were able to eat chitinous arthropods and shelly benthic organisms (Mark-Kurik, 1995; Brett and Walker, 2002). Consequently, frequency of healed bite marks and peeling on trilobite exoskeletons increased since the Devonian (Brett, 2003). Crustaceans, asteroids and gastropods could also have predator/scavenging behaviour (Gale, 1987; Brett and Walker, 2002). Marine predators could also play a major role in the Mississippian trilobite dynamic, particularly regarding the Viséan-Serpukhovian extinction in the absence of important environmental events. Camerate crinoids showed the same diversity trends as trilobites with a Tournaisian diversification followed by a strong decline in the Viséan (Sallan et al., 2011). After the Late Devonian extinctions, the predators were scarce and benthic prey including trilobites and crinoids could diversify. Subsequently, predators and especially durophagous fishes proliferated, strongly affecting their prey diversity. Consequently, camerate

crinoids dropped (Sallan et al., 2011) and a similar pattern could occur with trilobites, explaining the short Tournaisian recovery.

In response to increasing predation, trilobites adopted different strategies. In the Devonian, many trilobites tended to develop spines, which were supposed to be helpful against predators. Spines functioned as defensive structures to protect trilobites or to camouflage oneself (Kloc, 1992, 1993, 1997; Pates and Bicknell, 2019). However, spines were inefficient against predators with large jaws, which developed from the Late Devonian and in the Mississippian (Brett, 2003; Sallan et al., 2011). Another way to escape from predation could be size changes. A size reduction of prey could occur, as it was the case for crinoids (Waters and Maples, 1991; Brett, 2003). Indeed, it seems that the larger trilobites were more attacked than the others (Bicknell et al., 2019). Conversely, predation is avoided by achieving larger body too. An enlargement could be done with the development of spines (Johnsen et al., 2013) without a strong increase in biomass. Cryptic behaviour as infaunal moulting could also be considered as defensive behaviour (Rustán et al., 2011a; Rustán and Balseiro, 2016). Moreover, many Kellwasser Fauna genera were characterized by eyes reduction, which could be interpreted as endobenthic behaviour (Feist and Clarkson, 1989; McNamara and Feist, 2016). Consequently, changes in predation affected trilobite faunas, taxa with infaunal moulting and small size abilities were thus better equipped to cope with increasing predation.

From the Silurian to the Permian, the nekton fauna and benthic trilobites were decoupled, as the nekton diversity was low in the Early Devonian, the Devonian Nekton Revolution persisted throughout the Devonian environmental events and the Mississippian showed opposite trends between nekton and benthos (Klug et al., 2010; Sallan et al., 2011; Whalen and Briggs, 2018). This decoupling was not only due to predation but also to different reaction facing Devonian environmental events as it was suggested for North Africa (Ebbighausen et al., 2011; Bault et al., 2021). Indeed, similar benthic fauna showed the same variation as trilobites, like brachiopods (Carlson, 2016).

An increase in resource competition with the appearance of new clades could affect trilobites, similarly as in other communities, by impeding diversification (Bailey et al., 2013) leading to extinctions (Smith and DeSantis, 2020), or the opposite, inducing adaptive radiation (Meyer and Kassen, 2007; Bailey et al., 2013). In trilobites, resource competition could partly explain the Early Devonian diversification. Indeed, a strong resource competition in a dense population or with new ecological opportunities could favoured inter and intraspecific diversification (Rainey and Travisano, 1998; Bailey et al., 2013; Aristide and Morlon, 2019). Conversely, the arrival of new competitors with the same food niche could

lead to the decline or demise of a taxon (Smith and DeSantis, 2020). With the diversification of predators (Klug et al., 2010), the predator/scavenger trilobites saw the arrival of new competitors in the Devonian. The predator/scavenger behaviour concerned trilobites from the four evolutionary faunas and especially Corynexochida, Lichida, Odontopleuridae, Calymenoidea, Phacopina and secondarily conterminant Proetida, Fortey and Owens, 1999). However, the trilobite clades that persisted in the Late Palaeozoic were probably all predators or scavengers (Fortey and Owens, 1999), so the competition was potentially enhanced for the particle feeding (e.g., aulacopleurids) and the filter (e.g., harpetids, raphiophorids) trilobites. Thus, resource competition could explain the low diversity of trilobites from the Middle Devonian and the inability of radiating afterwards, except for the moderate Tournaisian peak. Phases of low resources accentuated the competition effects on the demise of taxa (Vakulenko et al., 2018). Consequently, the extinction of potential prey because of the Devonian events, which affected several taxa (Buggish, 1991; Walliser, 1996; House, 2002), and the decrease of nutrient supply in the Middle and Late Devonian (Large et al., 2015) could participate in the decline of trilobites in the late Palaeozoic.

It is complicated to know whether predation, resource competition or asymmetrical effect of Devonian events, but faunal changes occurring in the Devonian-Permian clearly affected trilobites.

6. Conclusion

On the basis of abundance and faunal turnover over time, we identified four evolutionary faunas characterizing trilobites from the Silurian to the Permian:

1. The Silurian Fauna was inherited from the Ordovician fauna that survived the Hirnantian extinction events and was dominant until the Pridoli. This evolutionary fauna was dominated by Cheiruridae, Encrinuridae and Odontopleuridae but several other families and subfamilies developed in this diverse fauna. The Silurian trilobites developed more at high latitudes and in a siliciclastic environment than later faunas. This evolutionary fauna progressively lost its dominance with the Devonian environmental changes, although it may have survived until the Frasnian-Famennian boundary.
2. Another evolutionary fauna has progressively dominated the trilobite community since the Pridoli, represented mainly by Acastidae and Tropydocoryphidae. This is the Devonian Fauna, whose members already existed at the beginning of the Silurian. This evolutionary fauna developed mainly in the Devonian with the environmental changes, i.e., a greenhouse

environment, an increasing carbonate environment and drowned epicontinental seas. The development of this fauna led to an important diversification of trilobites to the highest post-Ordovician taxonomic richness. However, the Devonian Fauna was challenged by environmental and ecological changes. Several Middle Devonian events affected the trilobites, leading to a sharp decline in diversity and the disappearance of the Devonian Fauna at the end of the Frasnian.

3. The Kellwasser Fauna had the shortest life span, only in the Late Devonian and Tournaisian. This is the only evolutionary fauna that is characterized by low diversity, as the Middle Devonian environmental changes decimated the ancient evolutionary faunas. Dominated by Phacopidae and Cyrtosymbolinae, this evolutionary fauna invaded both shallow and deep environments. The taxa of this fauna are characterized by important morphological changes such as the eye-reduction. At that time, trilobites appreciated warm and carbonate environments. The gradual cooling that began in the Famennian and the Hangenberg event at the Devonian-Carboniferous boundary led to the disappearance of this evolutionary fauna.

4. Only the order Proetida developed in the Late Palaeozoic Fauna, dominated by Phillipsiidae. Although trilobites were able to recover in the Tournaisian, a further decline in the late Mississippian left them poorly diversified despite their survival until the Permian-Triassic crisis.

Acknowledgements

This work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic time’, to the project ECOS Sud-MINCYT A17A01 (Argentina), and to the French CNRS UMR 8198 Evo-Eco-Paleo. The authors want to thank the Région Hauts-de-France and the Ministère de l’Enseignement Supérieur et de la Recherche (CPER Climibio) for their financial support.

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Supplementary figures

Latitude	PBDB
Low	0-30°N and S
Middle	30-60°N and S
High	60-90°N and S

Environment	PBDB
Carbonate	Floatstone, dolomite, framestone, wackestone, packstone, rudstone, mudstone, marl, lime-mudstone, grainstone, bindstone, « carbonate », « limestone », « reef rock »
Clastic	« shale », « siliciclastic », chert, siltstone, sandstone, schiste, quartzite, conglomerate, claystone

Bathymetry	PBDB
Shallow	Coastal indet., delta front, delta plain, deltaic indet., foreshore, lagoonal, lagoonal/restricted shallow subtidal, paralic indet., prodelta, sand shoal
Inner platform	Marginal marine indet., open shallow subtidal, perireef or subreef, peritidal, reef, builder or bioherm, shallow subtidal indet., shoreface, transition zone/lower shoreface
Outer platform	Deep subtidal indet., deep subtidal ramp, deep subtidal shelf, offshore ramp, offshore shelf, platform/shelf-margin reef, offshore, offshore indet.
Slope/basin	Basinal (carbonate), basinal (siliceous), basinal (siliciclastic), deep-water indet., slope, slope/ramp reef
Not known and not used	Submarine fan, terrestrial indet., marine indet.
Reefal	perireef or subreef, reef, builder or bioherm, slope, slope/ramp reef, platform/shelf-margin reef

Figure SUPPL. A. Table of the attribution of each PBDB category to latitudinal, environmental and bathymetrical categories used in this article.

PC	Eigenvalue	% Variance
1	16.109	51.97
2	10.92	35.23
3	2.105	6.79
4	0.790	2.55
5	0.320	1.03
6	0.228	0.74
7	0.156	0.5
8	0.107	0.35
9	0.068	0.22
10	0.058	0.19

Figure SUPPL. B. Eigenvalues for the first ten eigenvectors given by the CABFAC factor analysis of trilobite family and subfamily diversity from the Silurian to the Permian.

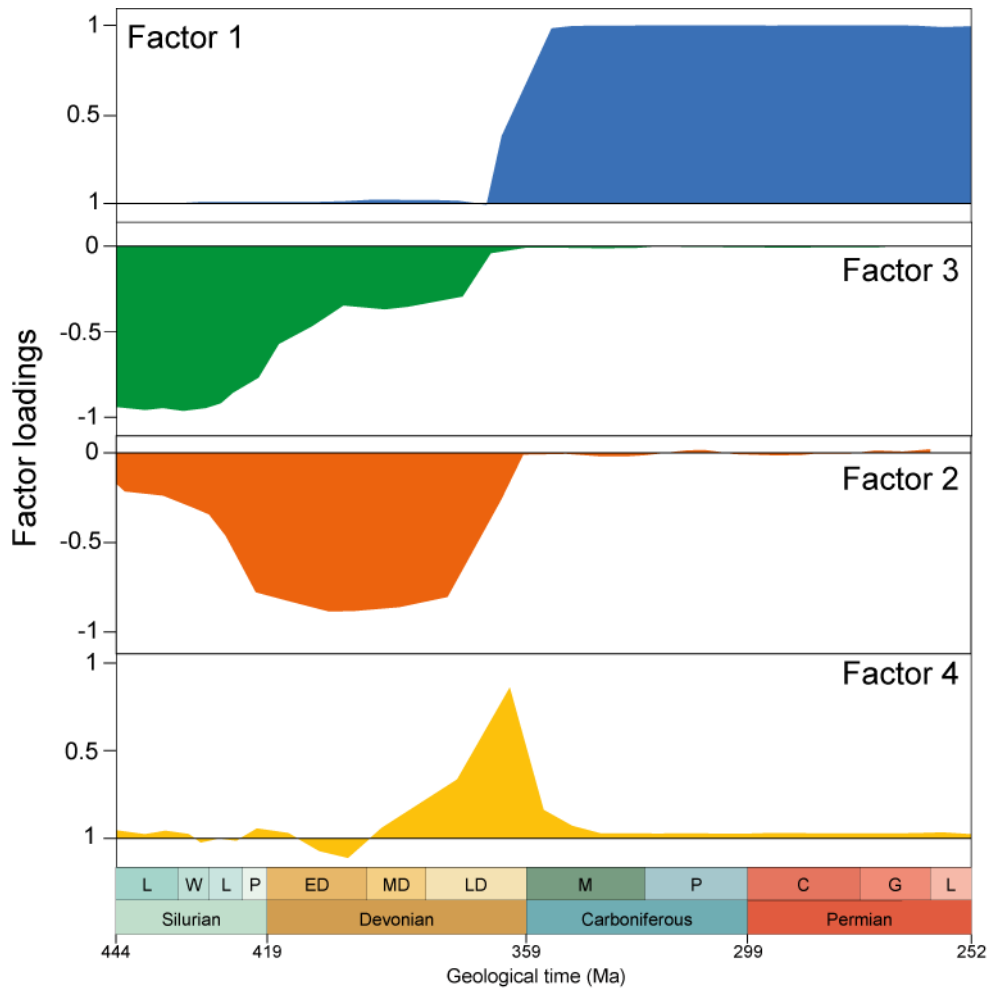


Figure SUPPL. C. Factor loadings of the first four factors generated by the CABFAC factor analysis. Age from *Cohen et al. (2013, updated)*.

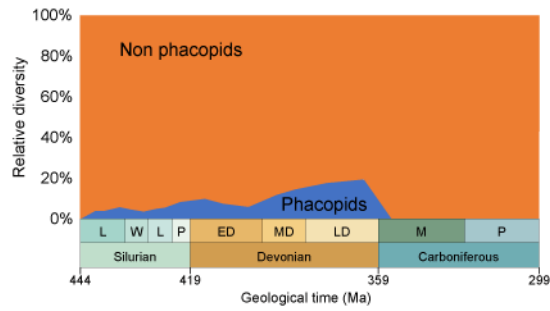


Figure SUPPL. D. Percentage of phacopids from the Silurian to the Carboniferous. Age from *Cohen et al. (2013, updated)*.

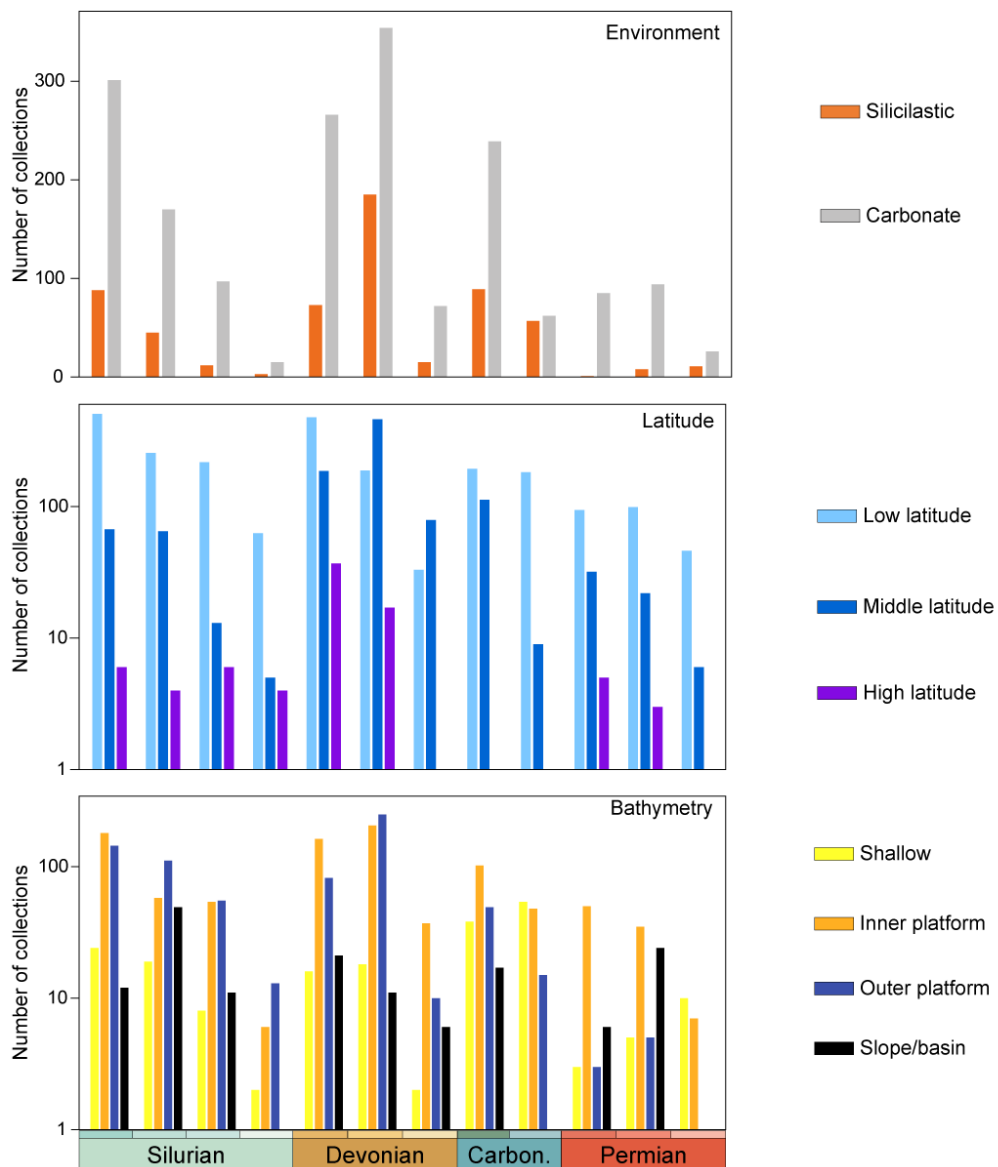


Figure SUPPL. E. Number of collection recorded in the PBDB for each environmental category.

1.2. Disparité morphologique des phacopidés

Article 2 : Morphological disparity of phacopids

Pour être soumis à Lethaia

MORPHOLOGICAL DISPARITY OF PHACOPIDS

Valentin Bault^{1*}, Catherine Crônier¹, Claude Monnet¹, Beatriz Waisfeld², Diego Balseiro², Fernanda Serra², Juan José Rustán² and Arnaud Bignon².

¹ *Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France*

² *Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional de Córdoba, Córdoba (X5016GCA), Argentina*

valentin.bault@univ-lille.fr, catherine.cronier@univ-lille.fr, claudemonnet@univ-lille.fr,
bwaisfeld@efn.uncor.edu, dbalseiro@unc.edu.ar, fserra@unc.edu.ar,
juanjorustan@gmail.com, arnaudbignon@yahoo.fr

* Corresponding author

ORCID:

Valentin Bault <https://orcid.org/0000-0002-9225-5195>

Catherine Crônier <http://orcid.org/0000-0002-7606-0822>

Claude Monnet <http://orcid.org/0000-0002-0899-8392>

Abstract:

Phacopidae was a successful family of the Silurian-Devonian period. Their morphologies were analysed by using Procrustes analyses and morphometric disparity indices. Results showed some morphological variations between the genera and through time. Phacopids differ from each other by the position of the facial suture linked to the visual complex size, the shape of the genal angle and the elongation of both cephalon and pygidium. The morphological disparity of the cephalon was high since the Silurian contrary to that of the pygidium. Subsequently, the morphological disparity increased in the Early Devonian with the development of narrow cephalons and triangular pygidia. The peak of morphological disparity was reached in the Emsian for both cephalons and pygidia, more than 50 Myr after the phacopid origination. This late diversification was favoured by the appearance of new environmental opportunities. Strong decrease of morphological disparity occurred in the Middle Devonian, caused by sea-level changes and anoxic events. Although the diversity increased until the Eifelian, taxonomic richness declined strongly in the Givetian. These extinction phases were non-random affecting particularly blind morphologies. Despite morphological changes in the Frasnian with a progressive eye reduction, the morphological disparity remained low. An important recovery occurred in the Famennian with the important increase of both diversity and morphological disparity. A Famennian trend toward reduced-eyes and blindness was confirmed and the pygidia became more elongated. Once again, environmental changes led to the morphological dynamics. However, the last Devonian event caused the final extinction of phacopids.

Keywords:

Trilobites, Palaeozoic, phacopids, morphological disparity, diversity, diversification, extinction

1. Introduction:

Phacopidae is a typical family of the Siluro-Devonian epicontinental platforms, and an important component of the marine benthos, represented worldwide, especially in Europe and North Africa. This family originates at the end of the Ordovician (Campbell 1967, Adrain 2013), probably derived from the Pterygometopidae family (Ludvigsen & Chatterton 1982). The first phacopid was *Sambreusaspis* Lespérance in Lespérance and Sheehan 1988, the most primitive member of the whole family (Ramsköld and Werdelin 1991). After this genus all phacopid genera developed, firstly a few in the Silurian, then several in the Devonian, to

reach its highest diversity in the Middle Devonian (Crônier et al. 2011). While the Phacopidae was one of the rare trilobite families to survive the Frasnian-Famennian extinction, they vanished at the end of the Devonian with the Hangenberg event (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Throughout their long evolutionary history, phacopids underwent several environmental changes (Walliser 1996; House 2002; Calner 2008; Qie et al. 2019) including the second of five mass extinctions described by Raup & Sepkoski (1982), i.e., the Kellwasser events (Buggisch 1991; Carmichael et al. 2019). These events positively influenced their diversity as for example the Pragian regression which led to the Pragian diversification of phacopids as well as many other trilobite clades (Chlupáč 1994), or negatively such as for example the Late Devonian events which led to the extinction of many genera (Feist 1991).

In this Epoch, this family, by its great diversity in genera and species (McKellar and Chatterton 2009; Crônier and François 2014), occupied numerous habitats of the epicontinental platforms from the shallow depths to beyond the photic zone, and they showed strong bathymetrical and palaeogeographical affinities (Crônier & François 2014). Their morphology but also their behaviour were affected by environmental changes and particularly at the Frasnian-Famennian boundary with the development of blind forms living in deeper-water environment and/or endobenthic (Feist et al. 2009).

Phacopidae firstly described by Hawle & Corda (1847) are characterised by a glabella broadening markedly forward with lateral glabellar furrows S2 and S3 obsolescent, and S1 often transglabellar leading to an ‘intercalating ring’, genal angles rounded without genal spines, and a visual complex often well-developed. The phacopid pygidium is well rounded, semicircular or shorter, without lateral or marginal spines (Harrington et al. 1959). The morphological diversity among Phacopidae is expressed especially in the shape of both the vincular furrow and visual complex and in the course of the facial suture (Fig. 1). Systematic clusters are based primarily on these characters (Crônier et al. 2011). Chlupáč (1977) identifies two sub-families, i.e., Phacopidellinae Delo, 1935 characterised by a cephalic doublure without a vincular furrow and Phacopinae Reed, 1905 characterised by a cephalic doublure with a deep and continuous vincular furrow. McKellar & Chatterton (2009) proposed a distribution of genera and sub-genera in tribes based on the work of Flick & Struve (1984), Haas (1998) and Struve (1970, 1972, 1976, 1982, 1989, 1990, 1992, 1995). This distribution is in disagreement with the previous work of Chlupáč (1977): numerous members belonging to Phacopidellinae or Phacopinae are in the same tribe. Moreover, all taxa belonging to this family, listed in the exhaustive list of Jell & Adrain (2003), have not been taken into consideration.

Environmental changes are reflected in the variations of the exoskeleton of trilobites and

their evolutionary history, which is essentially adaptive. Trilobites seem to represent a potential to analyze trends and evolutionary processes (Foote 1989, 1990, 1991a, 1993, Gerber & Hopkins 2011, Webster & Zelditch 2011). Some analyses focused at the family or the subfamily level, such as the analysis of Pterocephaliidae (Hopkins 2013) but not in Phacopidae.

Therefore, the present study aims to investigate the morphological evolution of all phacopids from their origination in the Silurian to the end of Devonian, by analysing their cephalic and pygidial shapes at the genus level. Here, the morphological disparity is investigated for the first time at the global and using the stage as temporal .

2. Material and methods:

2.1. Datasets

To explore the morphology of the Phacopidae family, we have compiled two datasets respectively to investigate the two main structures in the trilobites, i.e., the cephalon and the pygidium (Whittington et al. 1997), and, we have selected most of genera confirmed by Jell & Adrain (2002). Updates since this publication were taken into account such as the replacement for *Cultrops* Struve, 1995 to *Struvephacops* (Ghobadi Pour 2015) as well as the description of new genera: *Morocops* (Basse, 2006), *Enigmapyge* (Feist et al. 2016), *Magreanops* (VanViersen & Vanherle 2018) and *Feistops* (Crônier et al. 2020). The Late Devonian *Phacops* Emmrich, 1839 being significantly different from previous ones (Crônier et al., 2011), we separated them into a distinct genus named: *Phacops sensu lato*. Moreover, the Pterygometopidae *Calyptaulax* Cooper, 1930 was also included. The Pterygometopidae family is considered as the sister group of the Phacopidae family (Ludvigsen & Chatterton 1982) and one of its genera, i.e., *Calyptaulax* was used as outgroup in cladistics to study the relationships within phacopids (McKellar & Chatterton 2009; Oudot et al. 2019). Nevertheless, some poorly known and badly illustrated genera were excluded (*Somatrikelon* McMurtrie, 1819 without illustration in both datasets; *Enygmopyge* Feist et al., 2016 without cephalon in ‘cephalon’ dataset; *Adastocephalum* Mitchell, 1919, *Afrops* Alberti, 1983, *Burtonops* Struve, 1990, *Cryphops* Richter & Richter, 1926, *Portlockia* McCoy, 1846, *Spinicryphops* Crônier and Feist, 2000, *Struvephacops* Ghobadi Pour, 2015, *Tangbailaspis* Xiang & Zhang, 1983 in Zhang 1983, and *Zaplaops* Baldis & Blasco, 1976 in Baldis et al. 1976 without pygidium in ‘pygidium’ dataset). For each genus, a representative specimen was selected, most often the holotype of the type species, unless the illustrations were insufficient. Because of the lack of illustration, the

species of six genera were not the same between cephalon and pygidium: *Nephranomma* Erben, 1952, *Pedinopariops* Struve, 1970, *Prokops* Chlupáč, 1971, *Struveaspis* Alberti, 1966, *Teichertops* Struve, 1992 and *Weyerites* Crônier & Feist, 2000. 72 cephalata and 63 pygidia representing different genera were analyzed, all at a holaspid stage (Appendix A). For each genus, the stage of the first appearance and the last appearance are noted.

For the assessment, two components that can influence the shape distribution have been tested: the specimen selected and the measurement error. In order to evaluate the impact of the selected species representing the genus, we analysed 10 specimens representing 10 different species for the genus *Morocops*. Furthermore, one randomly selected cephalon was also digitized 10 times to identify the part of variation attributed to measurements (Bartlett & Frost 2008). To compare the variation between the different subgroups (i.e. measurement error, inter-specific variability and inter-generic variability), we measured the variance of the distance to the centroid size of each subgroups.

2.2. Landmarks and geometric morphometrics

To describe the 2D morphology of cephalata and pygidia, we used a morphometric approach based on homologous points, i.e., landmarks (Bookstein 1991; Rohlf & Marcus 1993; Adams et al. 2004; Mitteroecker & Gunz 2009; Zelditch et al. 2012). This method is regularly used on trilobites for macroevolutionary topics (Gerber & Hopkins 2011, Webster & Zelditch 2011; Oudot et al. 2019; Bault et al. 2021, submitted). The x - and y - coordinates of 13 landmarks and 4 semi-landmark curves of 30 points on the cephalon and 8 landmarks and one semi-landmark curve of 24 points on the pygidium were digitized (Fig. 1) using the software TPSDig 2.32 (Rohlf 2006, 2015). For the cephalon, the semi-landmark curves represent respectively the glabella shape, the facial suture shape and the cephalic outline (Fig. 1). For the pygidium, the semi-landmark curve represents the pygidial outline (Fig. 1). The landmark 2D coordinates were exported in the standard TPS file format (Rohlf 2012). For all configurations of landmarks, a generalized Procrustes analysis (GPA) was performed to remove effects of size, position and orientation in order to minimize the distances between each landmark of configurations (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O'Higgins 2000; Zelditch et al. 2012). All configurations of landmarks were d to unit centroid size. The centroid size is the square root of the sum of squared distances between the centroid and each landmark of the configuration (Dryden & Mardia 1998). Thereby the d configurations are then superimposed, i.e., translated and rotated. Then, we projected the superimposed configurations to a linear tangent space at the

full Procrustes mean (Rohlf 1999; Kendall 1984). The superimposed configurations constitute a data set corresponding to Procrustes residuals, i.e., x -, and y -coordinates of each landmark of configurations superimposed on a reference configuration, and describing only the shape of each landmark configuration.

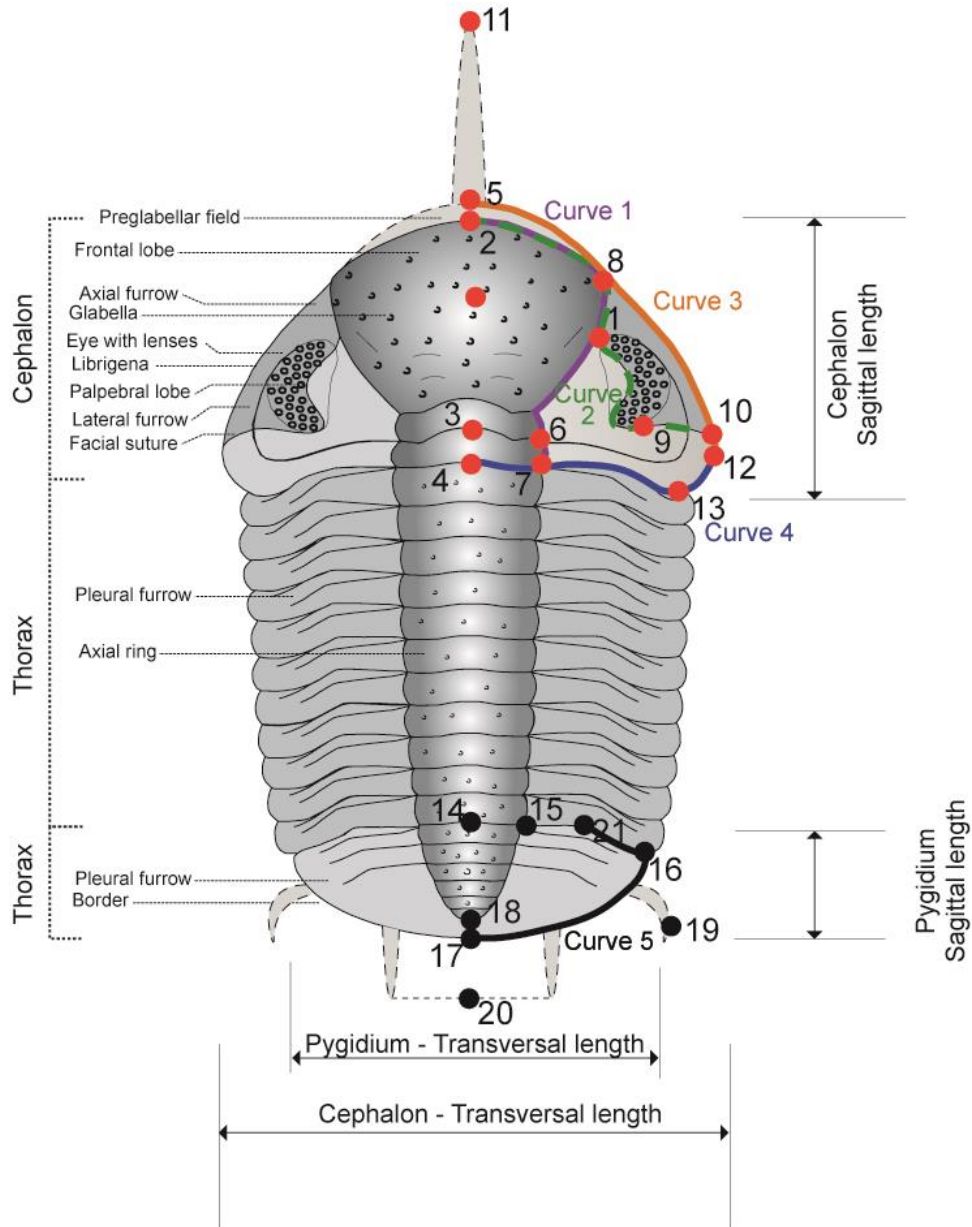


Figure 1. Thirteen landmarks and four semi-landmark curves of 30 points defined on the cephalon and 8 landmarks and one semi-landmark curve of 24 points on the pygidium.

A principal component analysis (PCA; Ringnér 2008; Abdi & Williams 2010) was performed on the variance-covariance matrix of Procrustes residual coordinates to identify the major trend of the morphological variation. Each specimen was represented by eigenvalues in a morphospace, positioned along Principal Components (PCs, eigenvectors) ordered by shape variance explained. Series of virtual shapes were reconstructed to illustrate the largest shape

changes for PC1 and PC2. Empirical morphospace were established for each stage from the Late Ordovician to the end of the Famennian (Adrain 2013; Lerosey-Aubril & Feist 2012). Because of the low number of genera before the Devonian, the Silurian is considered as a unique time bin.

Additionally, in order to identify morphological changes related to eye-reduction or blindness in the cephalon but also in the pygidium, blind and oculated genera were illustrated separately in PCA.

Morphological analyses have been computed with the software R (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>) and the packages ‘geomorph’ (v. 3.2.1; Adams & Otárola-Castillo 2013) and ‘epaleo’ (v. 0.8.41; Monnet, unpub.).

2.3. Morphological disparity indices

To quantify accurately the morphological disparity changes through time based on the obtained morphospaces, disparity indices were used: the sum of range (SoR), the sum of variance (SoV) and Nearest Neighbour Distance (NND) (Foote 1991b; Ciampaglio et al. 2001; Wills 2001; Guillerme et al. 2020); disparity indices already used in trilobites (Foote 1990, 1993; Hopkins 2013). Disparity indices have been estimated for the Silurian as a whole and for each stage of the Devonian. Morphological indices have been performed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.) on the software R (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>).

Two indices were used to estimate the size of the morphospace, i.e., the Sum of Range (SoR), corresponding to the total range of morphologies, and the Sum of Variance (SoV) corresponding to the average dissimilarity between morphologies. The overall first-order Nearest Neighbour Distance (NND) is the shortest Euclidean distance between two points of the morphospace and characterises the density of the morphospace. The mean values per stage for PC1 and PC2 were computed to identify potential morphospace displacement.

Finally, the confidence intervals on the obtained disparity values were obtained with a bootstrap approach, by randomly resampling with individual points in the morphospace and calculating SoR, SoV and NND again (Foote 1993). This was iterated 1000 times, creating a distribution from which 2.5 and 97.5 percentile values were used as lower and upper confidence intervals.

3. Results:

3.1. Global morphospace

The measurement errors and the interspecific variation tests indicated a smaller (one order of magnitude) variation than the inter-generic variation analysed thereafter, although some variations existed.

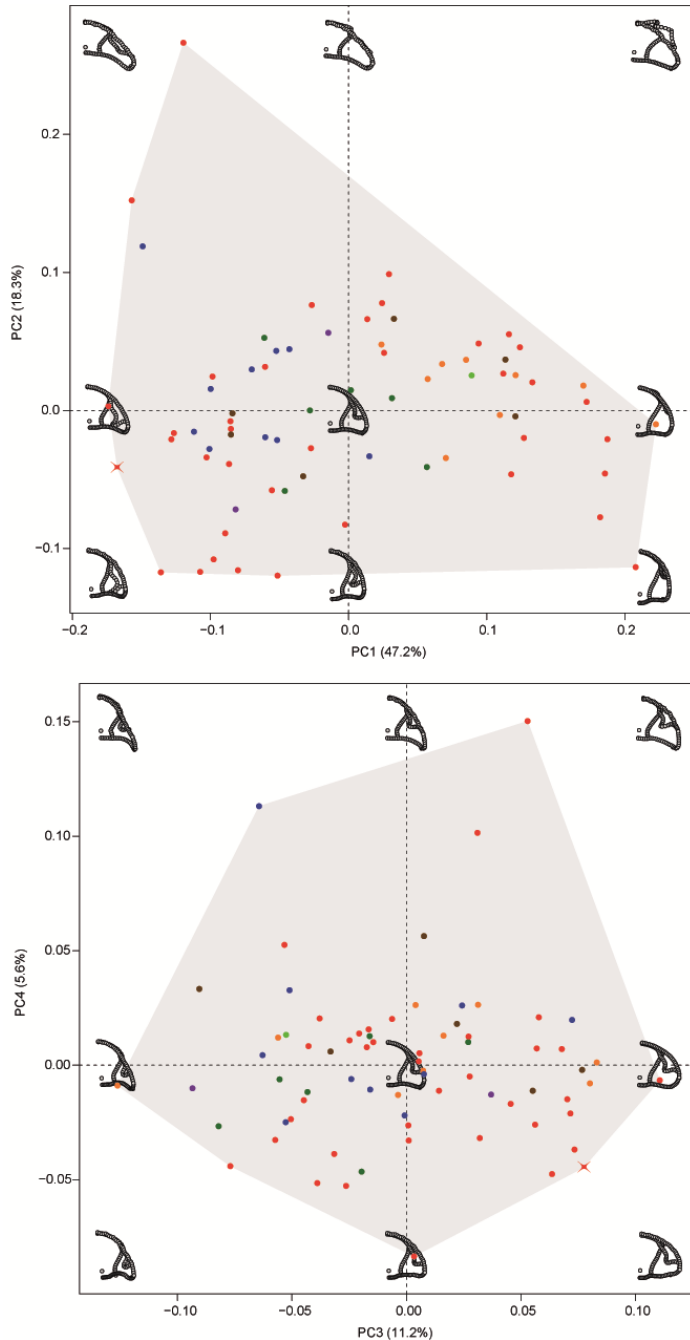


Figure 2. Global morphospace for phacopid cephalon computed by performing a PCA based on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 66% of the variance; (B) the PC3 and PC4 axes explain 17% of the variance. Tribes according to McKellar & Chatterton (2009): Anaspini Haas, 1998 (Brown); Cordapeltini Struve, 1989 (Dark green); Cryphopini Struve, 1989 (Orange); Geesopini Flick & Struve, 1984 (Blue); Phacopini Flick & Struve, 1984 (Light green); Reedopini Struve, 1989 (Purple) and Incertae sedis (Red). The pterygometopid *Calyptaulax* is represented by a red cross. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaped to landmark data.

Cephalon shape. The total variance among occulated cephala was explained by 71 principal components (PC's). The four first axes (Fig. 2) explain 82% of the total shape variance as

following: PC1 (47%), PC2 (18%), PC3 (11%) and PC4 (6%). The first axis PC1 (Fig. 2) depicts changes in the position of the facial suture and the visual complex. The higher PC1, the more the suture is close to the lateral margin and more the visual complex is reduced. The second axis PC2 (Fig. 2) depicts changes associated with the width/length ratio: narrow (transversal) cephalia in negative values to elongated (tr.) cephalia in positive values. The distribution of genera is relatively fairly homogeneous in the morphospace with the exception of three outliers characterised by low PC1 and high PC2 values: *Illaenula* Chlupáč, 1977, *Teichertops* and *Zaplaops*; and no taxa for high PC1 and high PC2 values. The pterygometopid *Calyptaulax* has the lowest PC1 values but is not distinct from phacopids with an average PC2 value. The global morphospace (Fig. 2) forms a triangle reflecting the influence of the three cephalic parameters (width/length ratio, facial suture and visual complex location). The bottom-left part of the morphospace corresponds to narrow cephalia with a more developed visual complex, the bottom-right part to narrow cephalia with a more reduced visual complex, and the top-left part to elongated cephalia. The shape of the genal angle is depicted by PC1 and PC2. The more PC1 is low and PC2 high, the more the genal angle is curved, and conversely, with high PC1 values, the genal angle is rounded.

Along the PC3 axis (Fig. 2), the cephalic variations are associated with the genal angle shape and the cheek proportion: cephalia with an elongated genal angle and larger cheeks relative to the cephalic shield in negative values and cephalia with rounded genal angle and smaller cheeks relative to the cephalic shield in positive values. Along the PC4 axis (Fig. 2), the cephalic variations are associated with genal spines (high PC4 values) or their absence (low PC4 values). The distribution of genera is relatively fairly homogeneous in the morphospace with the exception of three outliers characterised by high PC4 values: *Acernaspis*, *Babinops* Feist & Becker, 1997 and *Drotops* Struve, 1990.

Pygidium shape. The total variance among pygidia was explained by 60 PC. The four first axes (Fig. 3) explain 91% of the total shape variance as following: PC1 (60%) PC2 (18%), PC3 (9%) and PC4 (4%). The first axis PC1 (Fig. 3) depicts changes in the pleural field proportion and the lateral border angle. The lower PC1, the more the pleural field is important and the lateral border angle acute. The second axis PC2 (Fig. 3) depicts changes associated with the position of the greatest width: backward in negative values to forward in positive values. A higher PC2 value indicates a higher width/length ratio. The distribution of genera is relatively fairly homogeneous in the morphospace (Fig. 3). *Calyptaulax* has the highest PC1 values but is not distinct from phacopids with an average PC2 value.

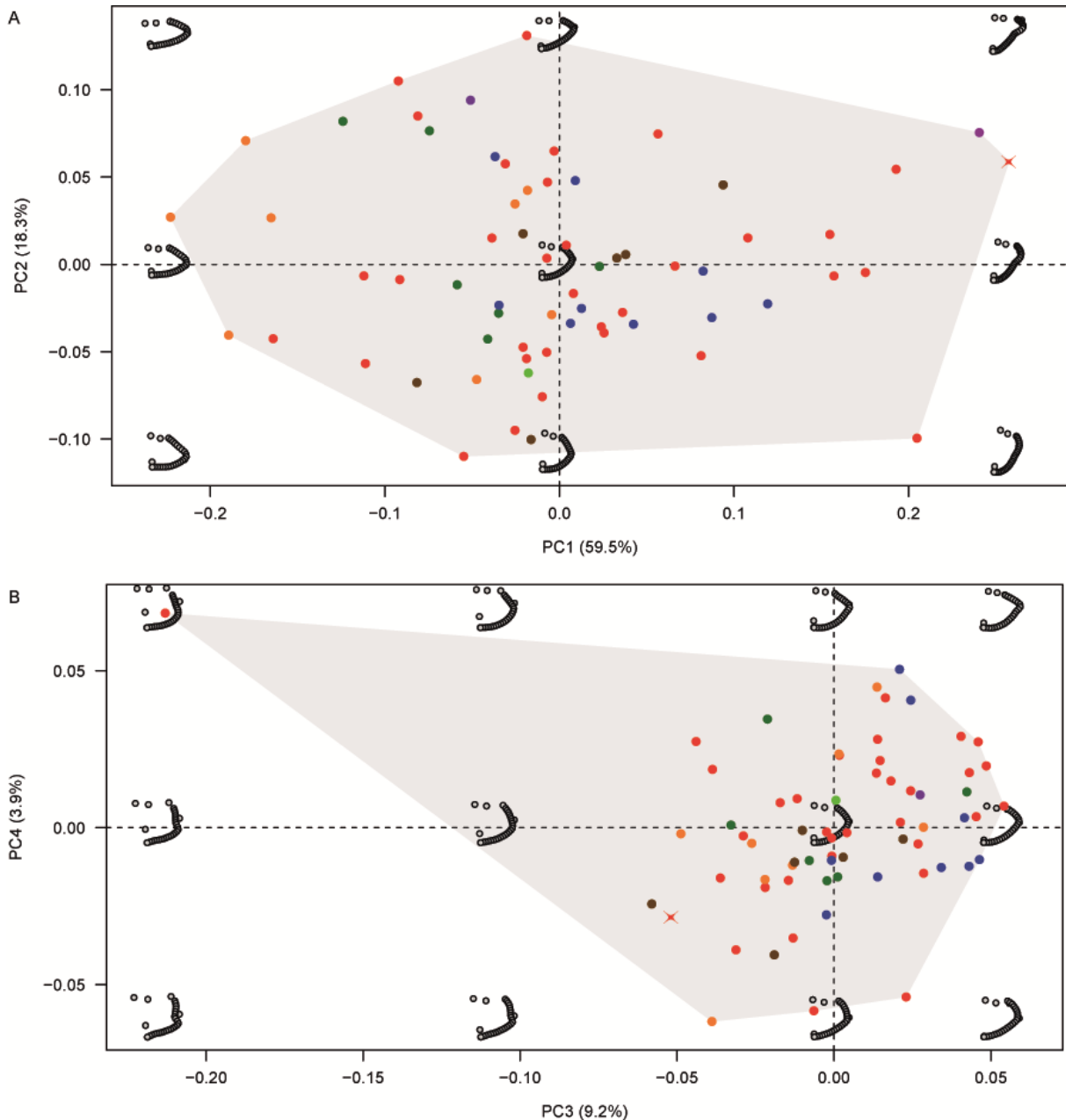


Figure 3. Global morphospace for phacopid pygidium computed by performing a PCA based on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 78% of the variance; B) the PC3 and PC4 axes explain 13% of the variance. Tribes sensu McKellar & Chatterton (2009): Anaspini Haas, 1998 (Brown); Cordapeltini Struve, 1989 (Dark green); Cryphopini Struve, 1989 (Orange); Geesopini Flick & Struve, 1984 (Blue); Phacopini Flick & Struve, 1984 (Light green); Reedopini Struve, 1989 (Purple) and Incertae sedis (Red). The pterygometopid *Calyptaulax* is represented by a red cross. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaped to landmark data.

Along the PC3 axis (Fig. 3), the pygidial variations are associated with the position of the rachis relative to the pygidial posterior border: rachis more (high PC3 values) or less (low PC3 values) close to the posterior border of the pygidium. Along the PC4 axis (Fig. 3), the pygidial variations are associated with the lateral outline. All genera are clustered in the morphospace in

high PC3 values except *Enigmapyge* characterised by high PC4 and low PC3 values: with a short (sag.) rachis and a maximum pygidial width located backward with a linear lateral border (Fig. 3).

Tribes. The Phacopid tribes were widespread in the morphospace and there were mingled each other. Nevertheless, some trends exist, Cryphopini being restricted in the positive PC1 values of the cephalon (Fig. 2) and negative PC1 values of the pygidium (Fig. 3). Conversely, Geesopini occupies negative PC1 values of the cephalon and positive PC1 values of the pygidium.

3.2. Global morphospace with blind taxa

Absence of eyes strongly affected the shape of phacopids cephalon ($p=0.001$, $r^2=0.09$). Most of blind and reduced-eyed trilobites are gathered in the highest PC1 values, while the oculated trilobites are gathered in the lowest PC1 values (Fig. 4). However, some blinds genera are characterised by lower PC1 values comparable to eyed trilobites. Nevertheless, these blind taxa correspond to shape with a facial suture close to the antero-lateral margin. Trilobites with eyes

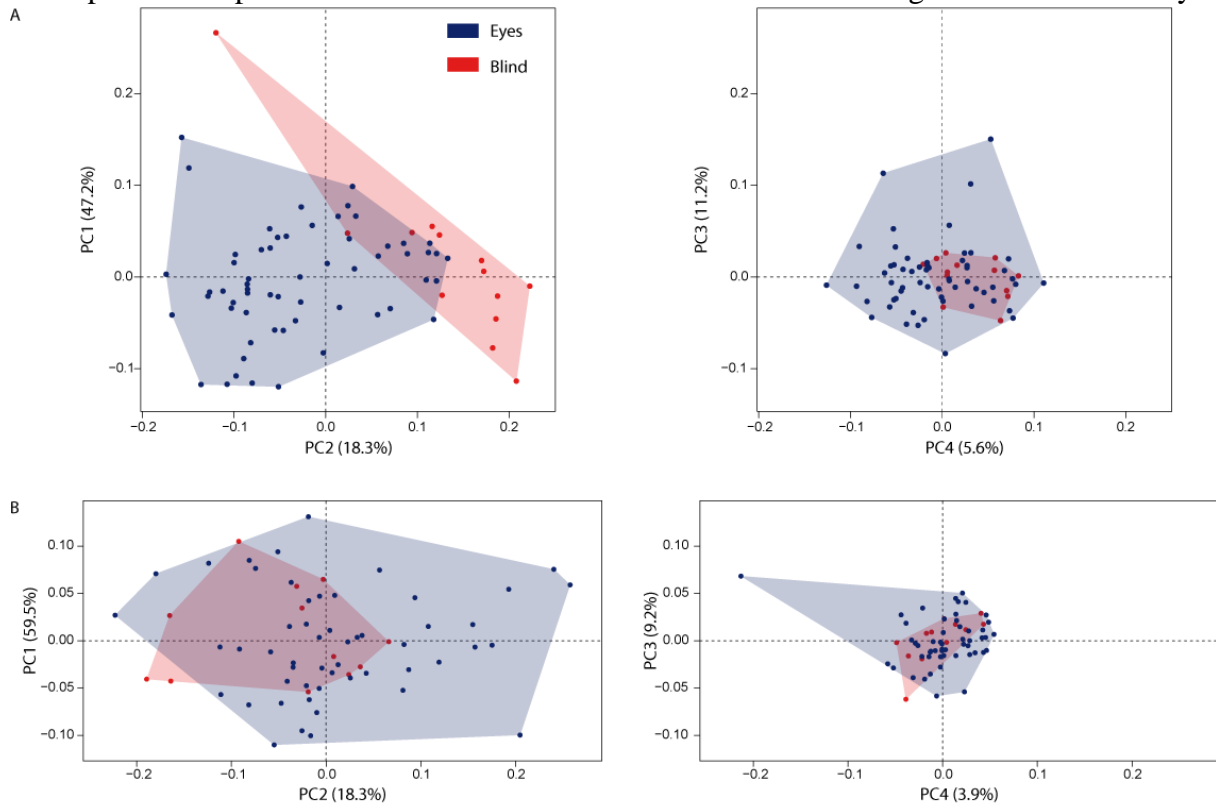


Figure 4. Location of: cephalon (A) and pygidia (B) according visual abilities of phacopids in the global morphospace defined according to the four first principal component axes performed on Procrustes residuals.

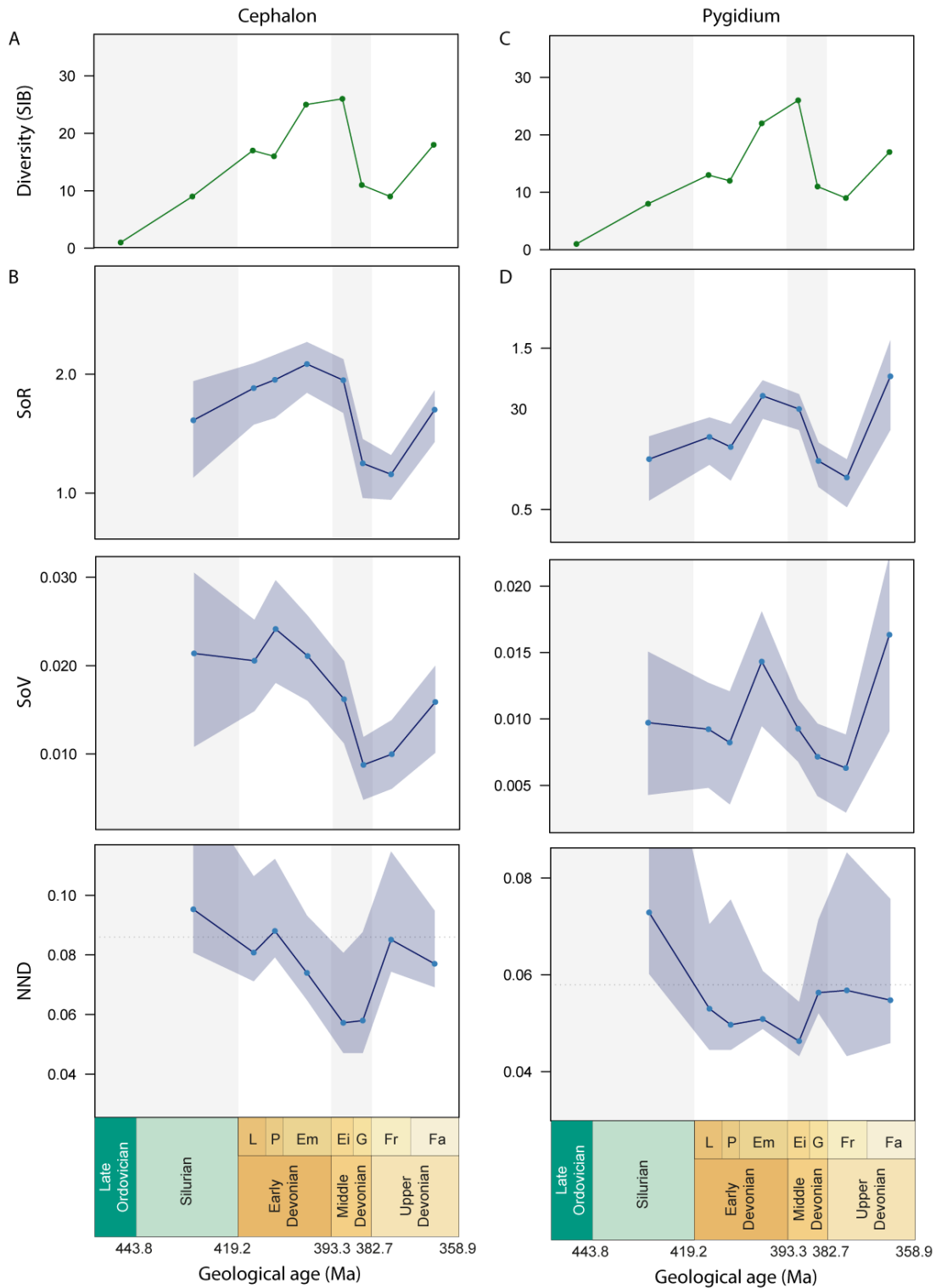


Figure 5. Fluctuations of the morphological disparity and taxonomic diversity of phacopids through time, respectively based on the cephalon and the pygidium. (A) Cephalon: taxonomic richness; (B) Cephalon: morphological disparity. (C) Pygidium: taxonomic richness; (D) Pygidium: morphological disparity. SoV: Sum of Range SoV: Sum of variance, NDD: Nearest-Neighbour Distance Solid lines correspond to mean values from 1000 bootstrap replicates and shaded areas represent 95% confidence intervals. See text for the explanations of the indices. Ages from [Cohen et al. 2013, updated](#).

or not are distributed along PC2 except for *Illaenula*, characterised by the highest PC2 values. Only *Nephranops* Richter & Richter, 1926 and *Pulvinocephalus* Feist, 2019 were included in the area of sighted trilobites. Blind taxa are distributed along PC3 and PC4: blind trilobites being restricted to positive PC3 values and average PC4 values.

The blindness observed in cephalata did not imply a different morphology of pygidia ($p=0.112$, $r^2=0.03$). However, the pygidia associated with blind cephalata are all gathered in the part of PC1 with the lowest values (Fig. 4). This indicates that blind phacopids did not display or a rounded lateral border either a large pleural field. The type of vision had no effect on PC2, PC3 and PC4.

3.3. Diversity, disparity indices and morphospaces through time

Diversity. Phacopids were poorly diversified in the Silurian but their taxonomic richness increased almost continuously until the Eifelian (Fig. 5). Only a slight decrease occurred in the Pragian. In the Givetian, the diversity decreased strongly from 26 to 11 genera. This decline continued in the Frasnian before a substantial increase in the Famennian. No phacopids survived in the Carboniferous.

Disparity. Bootstrapped confidence intervals indicate a relative robustness of the morphological disparity indices through time (Fig. 5). However, evolutionary interpretations of poorly diversified time bins (i.e., Silurian to Emsian) should be made with caution. This is particularly the case with the NND for both cephalata and pygidia, but also with the SoV for pygidia.

Cephalon. From the Late Ordovician to the Pragian, the morphospace occupation moved toward higher PC1 values, while the average PC2 values did not change through the Silurian and the Devonian (Fig. 6). The Late Ordovician pterygometopid *Calyptaulax* is characterised by a glabella with a hypertrophic frontal lobe anteriorly with well-developed S3 and a subtriangular pygidium. In the morphospace, *Calyptaulax* is located on one extremity of the morphospace, with one of the lowest PC1 value (Fig. 7). In the Silurian, the phacopid shapes appeared (Fig. 7) with the appearance of more rounded cephalata and a facial suture closer to the anterolateral border such as in *Denckmannites* Wedekind, 1914 and *Orygmatos* Sandford, 2000. The morphospace enlarged progressively in the Early Devonian with new morphologies in the Pragian: cephalata characterised by a narrow (tr.) cephalic shield associated with antero-lateral facial sutures. The appearance of *Afrops* at the right edge (i.e. high PC1 values) of the morphospace illustrated this trend. In the Emsian, the morphospace is almost entirely occupied

except the top-left part of all phacopid distribution (Fig. 7). Thus, the morphological disparity increased (see SoR, Fig. 5). In the same time, the NND and the SoV tend to decrease (Fig. 5).

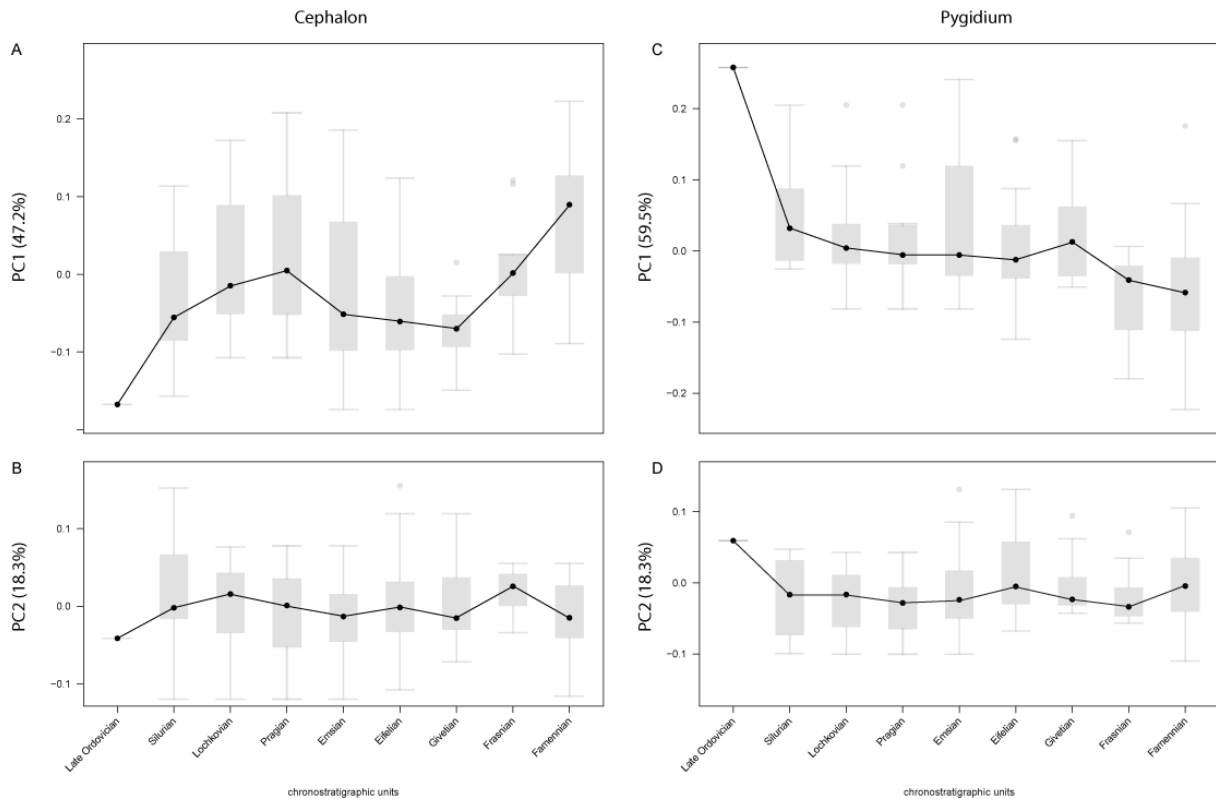


Figure 6. Location of the morphospace occupation on PC1 and PC2 through time. (A and B) Average values of PC1 and PC2 on the cephalon. (C and D) Average values of PC1 and PC2 on the pygidium.

During the Middle Devonian, the morphospace occupation moved to opposite values, i.e., lower PC1 values; no real displacement on PC2 (Fig. 6). The morphological disparity strongly decreased (see SoR and SoV, Fig. 5). This collapse of the occupied part of the morphospace was only reduced in the Eifelian (Fig. 5, 7). Firstly, shapes with a facial suture located close to the lateral border, such as *Altaesajania* Maksimova, 1978a and *Angulophacops* Maksimova, 1978b are no longer present and disappeared at the Emsian-Eifelian boundary. Conversely, no new genera appeared. The Eifelian was also characterised by the lowest NND despite the presence of two outliers *Illaeula* and *Teichertops*. These outliers were located in the top-left part of all phacopid distribution during the Eifelian (Fig. 7). Subsequently, the morphospace collapsed in the Givetian (Fig. 7) because of the extinction of genera, such as *Nandanaspis* Zhang & Yin in Yin & Li, 1978, *Eocryphops* Richter & Richter, 1931, *Plagiolaria* Kegel, 1952 and *Reedops* Richter & Richter, 1925. Their morphology implied a facial suture near the antero-lateral border and a rounded genal angle. Subsequently, *Geesops* Struve, 1982 and *Nyterops* Struve, 1972 disappeared at the end Givetian and they are characterised by a cephalon with

acute genal angles and a posterior section of the facial suture close to the posterior border (Fig. 7). The occupied part of the morphospace is limited to the bottom-left part of all phacopids distribution (Fig. 7).

Finally, during the Upper Devonian, the morphospace occupation shifted again to higher PC1 values to reach the highest values with more elongated pygidial shapes (Fig. 6); once again there is no real displacement on PC2 (Fig. 6). The morphological disparity increased (see SoR and SoV, Fig. 5). Nevertheless, the morphospace occupation remain reduced in the Frasnian but with a displacement of the occupied part of the morphospace. The morphological disparity was minimal (see SoR, Fig. 5), while SoV and NDD remain almost unchanged (Fig. 5). This displacement is due to the successive origination of *Acuticryphops* Crônier & Feist, 2000 and *Trimerocephaloides* Feist et al., 2009 in the Frasnian, which spread in the middle-

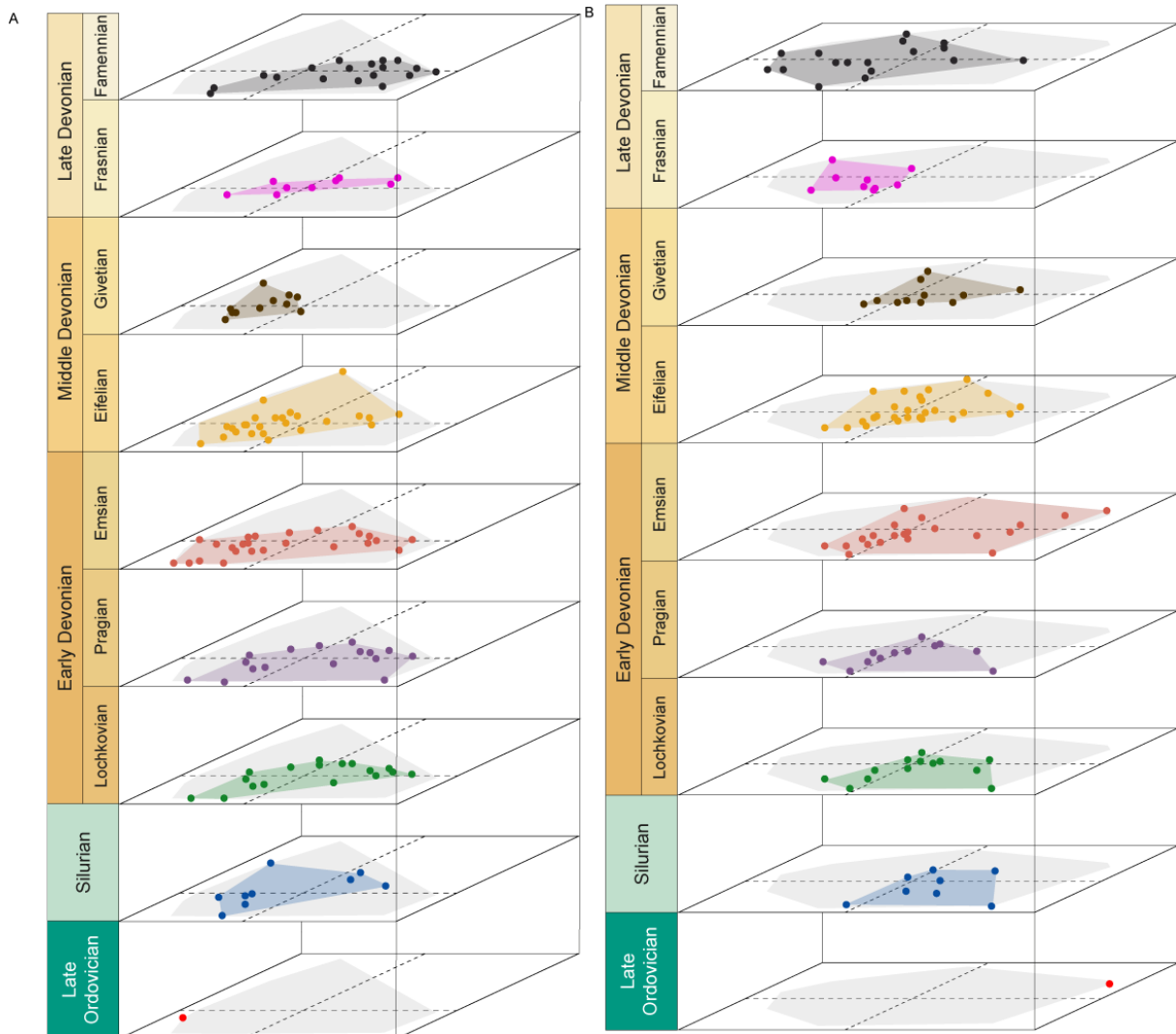


Figure 7. Morphological occupation of the (A) cephalon and (B) the pygidium through time (PCA based on Procrustes residuals). Ages from Cohen et al.2013.

right part of the morphospace with their antero-lateral facial sutures and a narrow cephalon with rounded genal angles (Fig. 7). New genera appeared in the Famennian, such as *Dianops* Richter & Richter, 1923, *Ductina* Richter & Richter, 1931, *Struveops* Crônier & Feist, 2000 and *Trimerocephalus* McCoy, 1849. They contributed to refill partially the morphospace (Fig.7). These taxa exhibit the facial suture closest to the lateral margin border, a small (tr.) cheek and a rounded genal angle. In the Famennian, the morphological disparity strongly increased (see SoR, Fig. 5), SoV still increased, and NND decreased slightly (Fig. 5).

Pygidium. From the Late Ordovician to the Silurian, the morphospace occupation moved toward lower PC1 and PC2 values to stay stable until the Emsian (Fig. 6). *Calyptaulax* by its a subtriangular pygidium is located, on one end of the morphospace, as for the cephalon (Fig. 7). In the Silurian, the phacopid shapes appeared (Fig. 7) with the appearance of more enlarged (tr.) pygidia with a larger pleural field. This morphospace occupation (mainly the bottom-middle right part) persisted until the Pragian. Thus, the morphological disparity remained almost stable, except a decrease of the NND (Fig.5). In the Emsian, the morphological disparity increased (see SoR and SoV), while NDD remained almost stable (Fig. 5). Consequently, some innovations occurred with the origination of *Austerops* McKellar & Chatterton, 2009, *Rhinophacops* Kaneko, 1990 and *Toxophacops* Zhou & Campbell, 1990 for instance. It corresponds to their triangular pygidial shape and weakly curved posterior border. The morphospace became filled and almost occupied except the extreme left part of morphospace (Fig. 7).

During the Middle Devonian, the morphospace occupation shifted slightly to opposite values, i.e., higher PC1 values; no real displacement on PC2 (Fig. 6). The morphological disparity decreased (see both SoR and SoV, Fig. 5); and NND tends to increase (Fig. 5). The occupied part of the morphospace was relatively expanded in the Eifelian, with the disappearance of taxa in the top-right and the bottom-right parts of the morphospace (Fig. 7). *Echinophacops* Zhou, 1983 and *Rhinophacops* were no longer present and disappeared at the Emsian-Eifelian boundary; they are characterised by narrow (tr.) pygidia with small pleural fields (Fig. 7). Subsequently, the morphospace collapsed in the Givetian (Fig. 7) because of the extinction of *Morocops*, *Signatops* Přibyl & Vaněk, 1971 and *Viaphacops* Maksimova, 1972 in the left part of the morphospace. Therefore, the occupied part of the morphospace was limited to the left part of all phacopids distribution (Fig. 7).

Finally, during the Upper Devonian, the morphospace occupation shifted again to reach the lowest PC1 values (Fig. 6) whereas there is no real displacement on PC2 once again (Fig. 6). In the same time, the morphological disparity increased (Fig. 5) although the morphospace

occupation remained reduced in the Frasnian. Only a displacement of the occupied part of the morphospace to the left occurred (Fig. 7). As for the cephalon, the morphological disparity is minimal (see SoR and SoV (Fig. 5), while NDD remained almost unchanged (Fig. 5). This displacement is due to the appearance of genera characterised by an elongated (tr.) pygidium, such as *Acuticryphops*, *Chlupacops* Feist et al., 2016 and *Phacops s.l.*. In the Famennian, new genera appeared such as *Dianops* Richter & Richter, 1923, *Trifoliops* Crônier, 2003, *Trimeroccephalus* McCoy, 1849 and *Weyerites* for instance and contributed to refill partially the morphospace (Fig. 7). All taxa exhibit an elongated (tr.) pygidium. The morphological disparity strongly increased to reach highest values (see both SoR and SoV, Fig. 5), SoV still increased, and NND decreased slightly (Fig. 5).

4. Discussion:

4.1. Morphological disparity – cephalon vs. pygidium shapes

Phacopids did not exhibit a large morphological variation. This absence of strong difference among phacopid genera and tribes explains the difficulties encountered by the scientists to determine their systematic structure (McKellar & Chatterton 2009). Only one genus differs strongly from the others: *Echinophacops* is the only phacopid, which developed prominent spines on the cephalon (Zhou 1983). This genus occurred with ammonoids, conodonts, brachiopods, gastropods and corals (Hua-Zhang & Cook 2003) in the Lower Devonian from calcareous sandstones of the Zhusileng representative of subtidal environments (Zhou & Campbell 1990). In this kind of environment, spinose asteropygines, another Phacopida subfamily, proliferated also at the same time (Morzadec 1992, 2001). Other phacopids co-occurred with *Echinophacops* in the same horizon (i.e. *Rhinophacops* and *Toxophacops*), and *Zhusilengops* Zhou & Campbell, 1990 and *Atopophacops* Zhou & Campbell, 1990 above the Zhusileng (Zhou & Campbell 1990). Contrary to *Echinophacops*, these genera did not have spines. Nevertheless, an intermediate morphology existed between taxa with long spines (i.e., *Echinophacops mirabilis* Zhou, 1983) and taxa without spines: *Rhinophacops schlizoma* Zhou, 1983.

Among phacopids, very few have a very differentiated morphology like *Enigmapyge* from the Famennian of Algeria (Feist et al. 2016). Although incompletely preserved, its cephalon shows all the characteristics of a phacopid. Nonetheless, its pygidium is unusual among this family with a large pygidial margin and a short (sag.) pygidial axis ending at a considerable distance from the posterior edge (Feist et al. 2016). The morphology of the cephalon of

Teichertops and *Zaplaops* was also uncommon. These two genera are represented by very few specimens in the literature and a deformation of the landmarked fossils is possible. The specimen of *Teichertops* was found in black marls (Struve 1970) where distortions are susceptible to happen (Webster & Hughes 1999). The ordinary shape of the pygidium of *Teichertops* tends to confirm this assumption although the cephalon and the pygidium of a same taxon show different distribution in a morphospace (Bault et al. 2021, submitted). For its part, *Zaplaops* could be a junior synonym of *Ananaspis* Campbell, 1967 (Holloway & Rustán 2012), which is not an outlier. This latter genus is characterised by an elongated cephalon as in *Zaplaops* (negative PC1 value) but without a downward genal field (average PC2 value), probably a consequence of a deformation. *Acernaspis*, *Adrisiops*, *Babinops*, *Drotops* and *Viaphacops* are the five genera differentiated by an elongated genal angle. Genal spines could develop from this configuration, as it is the case for *Babinops* (Feist & Becker 1997), *Viaphacops* (Eldredge 1973) and *Drotops armatus* (Struve 1995). Usually, phacopids had a genal spine during the early stages of their development, but these spines then reduced (Crônier & Courville 2003). Contrary to the Early Devonian tendency among Trilobita (Bault et al. 2021, submitted), this development of genal spines among phacopids was not a temporal trend because trilobites with genal spines existed throughout the evolutionary history of phacopids. Only the presence of the strongly spinose *Echinophacops* coincided with the Early and Middle Devonian trends in spiny marine faunas (Brett 2003). The presence of such genal spines could be linked to the ecology of trilobites for stabilization on soft substrates (Brett 2003).

Except the few taxa described above, most phacopid genera showed slight differences between them. The main variation concerns the position of the facial suture. That corresponds to a line of weakness facilitating the moulting process (Daley & Drage 2016; Drage 2019). This allows the separation between the cranidium and the free cheeks during the ecdysis (Drage 2019). Among trilobites, the phacopids have a proparian suture, the posterior section of which intersects the lateral cephalic margins in front of the genal angles (Harrington et al. 1959). The position of this facial suture constituted a trade-off between the ability to moult and a resistance to burrowing loads (Esteve et al. 2021). However, among phacopids, the size of the visual complex influences the location of the facial suture. Blindness or reduced-eyes implicate a facial suture situated close to the lateral margin. Indeed, the reduction and ‘migration’ of the visual complex caused the displacement of the associated dorsal facial sutures (Feist 1995). Consequently, the facial sutures of blind taxa are located on the anterolateral margins related to a macroevolutionary pedomorphic process (Feist 1995;

Crônier & Courville 2003; Crônier 2013). This ‘migration’ occurred although the facial sutures became brittle in such position (Esteve et al. 2021). In addition to the facial suture displacement with the visual complex reduction, blind trilobites have a less curved genal angle, except *Illaenula*. A marginal facial suture and weakly arched genal angles characterised blind trilobites but also some sighted genera. There were reduced-eye trilobites such as *Eocryphops* (Holloway 2005), that showed the suture displacement described by Feist (1995). Concerning the pygidium, blind trilobites did not imply a new morphology as it was the case for the head. Nevertheless, the morphology of blind phacopids was limited to a particular shape of pygidium: those with high width/length ratios.

The second most important morphological variation in phacopids concerned the curvature of the genal angle and the cheek width. A vaulted cephalon also found in other clades was supposed to prevent the trilobite from sinking into mud (Richter 1920; Feist & Clarkson 1989). The phacopids with the most vaulted cephalon lived in a muddy environment like *Echidnops taphomimus* (Rustán & Balseiro 2016), *Illaenula struvei* (Basse & Müller 2000), *Nephronomma sweeti* (Sandford 2003), *Orygmatus yanyeani* (Sandford 2000), *Teichertops soetenicus* (Struve 1970) and *Zaplaops zaplensis* (Baldis et al. 1976). However, some trilobites with a vaulted cephalon occurred in limestone deposits, such as *Lochkovella misera* (Chlupáč 1977). Consequently, the type of substrate is not the only factor influencing the shape of the cephalon. The shape of the glabella also changed with the shape change of the cephalon. If the phacopids are characterized by a similar shape of glabella, narrower (tr.) at the base and wider (tr.) at the front, the glabella is even wider at its front with a less curved genal angle for vaulted cephalon, The base/frontal part width ratios are partly due to the predatory/scavenger habit of phacopids, a forwardly expanding glabella allowing ingestion of higher volumes (Fortey & Owens 1999). This pattern contrasts with the morphological changes observed during the ontogeny for which the maximal width of the glabella/minimal width of the glabella ratio increases while the genal spines reduce (Crônier & Fortey 2006; Crônier 2007).

The elongation of the pygidium was also a major variation in phacopids. Some genera had an elongated pygidium with a width/length ratio greater than 2 (e.g., *Trifoliops*) while others had a ratio less than 1 such as *Enygmapyge* (Feist et al. 2016). It is noticeable that the genera with the most elongated pygidium are not the same as those with the largest cephalon. There is a decoupling at the level of innovations between cephalon and pygidia. The pygidium shape was probably less suitable for stabilizing the organism on the seafloor. The morphology of organisms being the result of trade-offs between different tasks (Shoval et al. 2012; Ou et al.

2020), the pygidial organization was dedicated to other functions. For example, the enrolment influenced both cephalon and pygidium morphology, but it had probably a stronger effect on the pygidium, which was dedicated to fewer tasks (Oudot et al. 2019; Suárez & Esteve 2021). The length of the pygidial axis also changes between different phacopids. However, except *Enigmapyge* discussed above, only a short (sag.) postaxial area characterised the phacopid family.

4.2. Evolutionary history

The shape of *Calyptaulax* is positioned at the edge of phacopid morphologies but is not completely different, being close to the shape of the first phacopid *Acernaspis* (Chlupáč 1975). The assumption that Pterygometopidae is a sister taxa of phacopids seems relevant (Ludvigsen & Chatterton 1982). Similarities between ontogenetic trajectories of this genus and some phacopids (Jacobs & Carlucci 2019) reinforce this hypothesis. *Calyptaulax* had a facial suture (and therefore the eyes) near to the posterior border furrow and a vaulted cephalon (Clarkson & Tripp 1982). From these ancestral character states, phacopids developed from the Silurian onwards leading to an increase of the morphological disparity. Although the first phacopids *Acernaspis* exhibited a general morphology similar to *Calyptaulax*, the facial suture of phacopids are relatively close to the lateral margin in the Silurian. This was particularly the case for *Denckmannites*, *Lochkovella* and *Orygmatos*, the first reduced-eye phacopids (Chlupáč 1977; Sandford 2000; Crônier & Courville 2003). An eye reduction in trilobites could be linked to the migration and an adaptation to deeper environments (Feist et al. 2009; Feist 2019). While *Acernaspis* lived in shallow environments (Owen & Harper 2008), *Denckmannites*, *Lochkovella* and *Orygmatos* lived in a relatively deep environment. The observed morphological change seems to be related to the invasion of this environmental niche. However, *Calyptaulax* has proliferated in a deep environment (Owen & Parkes 2000; Carlucci & Westrop 2012), indicating that this large-eyed morphology is not inconsistent with the habitat of a basin environment. On its side, the pygidium of phacopids has lengthened compared to its ancestral morphology.

The morphological disparity curves, respectively corresponding to the cephalon and to the pygidium shapes, are partly uncorrelated. The constant increase of the morphological disparity from the Silurian until the Emsian observed in the cephalon is more irregular in the pygidium. Indeed, the pygidial disparity decreased in the Pragian. The diversity increase in the Lochkovian was associated with only a slight extension of the morphospace. This period

was more favourable to the origination of novelties in other trilobite families, such as proetids, scutelluids and dalmanitids than in phacopids (Chlupáč 1994). No important innovations occurred, the new morphologies remained close to those of the Silurian. Thus, the origination of new species brought morphologies close to those already existing.

During the Pragian-Emsian diversification, the taxonomic richness of phacopids increased, like many trilobite families (Feist 1991; Chlupáč 1994; Bault et al. 2021). This boost of diversity was linked to the increase in morphological disparity for both cephalata and pygidia. Again, no important novelties characterised the development of new phacopids. Only the blind genus *Afrops* exhibits a new cephalon morphology with a small cephalic shield without a genal angle (Alberti 1983). For pygidia, the main innovation involved the triangular shape as in *Rhinophacops schizoloma* (Kaneko 1990) or the elongated (tr.) pygidium as in *Morocops granulops* (Chatterton et al. 2006). Nevertheless, the Emsian was the age of the maximum disparity for the cephalata and was only exceeded in the Famennian for the pygidia. This morphological disparity peak occurred earlier than the maximum diversity, which followed in the Eifelian (Crônier & Courville 2003). Decoupling between morphological disparity and taxonomic diversity is common in the fossil record (Foote 1993) but it was often linked to extinctions (Bapst 2012; Hopkins 2013; Wan et al. 2021). Although Foote (1993) noted that the peak of morphological disparity occurred usually after the peak of diversity, especially for trilobites, it was the opposite in phacopids.

Another feature of the morphological diversification of this family is that its peak was reached in the late part of its evolutionary history. This was the opposite of the common trend among Palaeozoic clades, which often have a maximum of disparity early in their evolutionary history (Hughes et al. 2013). Hopkins & Smith (2015) argued evolutionary dynamics changed through time and were not necessarily higher in the first period of their existence. New ecological opportunities such as the Devonian ones could generate an increase of the evolutionary rate and thus, a disparity rise. On the other hand, the decrease of morphological disparity in the Eifelian was caused either by a loss of ecological habitats (Valentine 1995; Oyston 2015) or by an increase of developmental constraint (Gould 1991; Oyston 2015).

An important extinction phase occurred in the Givetian with a strong decrease of both diversity and morphological disparity. The sea-level changes and the anoxia of the Middle Devonian events (Walliser 1996; House 2002) affected all the trilobites (Chlupáč 1994; Lerosey-Aubril & Feist 2012). The phacopids did not escape these environmental events and lost more than 60% of their genera. The mid-Givetian Taghanic event was the most

devastating for them (Crônier & Courville 2003). This was a non-random extinction because it caused a collapse of the morphospace size (Ciampaglio et al. 2001). On the contrary, the density of the morphospace was not disturbed by these events, implying a marginal or lateral extinction (Korn et al. 2013). Interestingly, a lateral extinction affected the cephalon, and the morphospace shifted during the Middle Devonian, while the pygidium underwent a rather marginal extinction with no change in the morphospace range. The Taghanic extinction event led to the disappearance of genera with a cephalon characterised by an anterolateral facial suture. Consequently, during the end-Givetian all phacopids only had large eyes.

Nevertheless, reduced-eyed taxa still occurred in other families such as Tropidocoryphidae (Feist 2003). At the same time, two of the largest genera of the family appeared, it was *Drotops* and *Hypsipariops* Struve, 1982 (Struve 1995). The Early and the Middle Devonian were the time of giant organisms including trilobites (Klug et al., 2014). This trend was hardly explained by single environmental parameters, although a latitudinal influence cannot be excluded (Klug et al., 2014). *Drotops* and *Hypsipariops* lived in the mid-latitudes of Morocco (Struve, 1995), exactly the range of gigantism occurrences.

In the Frasnian, morphological disparity remained low, probably the lowest in phacopid history. However, this stagnation of morphological disparity was accompanied by important morphological changes. For cephalon, morphospace occupancy shifted to the area indicating the acquisition of an anterolateral facial suture, underlying the Late Devonian trend toward blindness (Feist 1995; 2019; Crônier & Courville 2003). This trend was also noticed in other families (Feist & Clarkson 1989; Lerosey-Aubril & Feist 2012; Schoenemann 2018). As for the Silurian, the existence of blind phacopids was associated with a life in deeper environments (Feist et al. 2009; Feist 2019). The successive transgressions and the long-term sea-level rise in the second part of the Devonian forced the trilobites to adapt to these new environments (Lerosey-Aubril & Feist 2012; Crônier & François 2014). Whatever the water depth, an endobenthic behaviour or a turbid environment with low luminosity implied also an eye-reduction (Feist et al. 2009). Concomitantly to the progressive modification of the eye and the displacement of the facial suture on the cephalon, the pygidium changed to a more elongated shape in phacopids. The morphological innovations still developed in the same direction in the Famennian. The combination of lateral facial sutures and elongated pygidium contributed to increase the morphological disparity, particularly for the pygidium. Subsequently to the disastrous Kellwasser events at the Frasnian-Famennian boundary (Buggisch 1991; Bond and Wignall 2008), trilobites recovered and invaded various habitats and areas (Crônier and François 2014). As the result of this dispersal, morphological disparity

increased, as was the case with the appearance of new niches in the Pragian. Some phacopids recolonized shallower environments and developed large eyes, such as *Omegops* (Crônier and François 2014).

The evolutionary history of phacopids stopped at the end of the Devonian with the disappearance of the whole order Phacopida (Lerosey-Aubril & Feist 2012). Their extinction was the consequence of the Hangenberg event consisting of sea-level changes, carbon cycle perturbation and temperature oscillations (Kaiser et al. 2016). All phacopids vanished regardless of their shapes, but the predominance of reduced-eyed and blind taxa inhabiting more distal environments probably doomed them. Indeed, this event was devastating for non-occulated and reduced-eyed trilobites, including Proetida (Lerosey-Aubril & Feist 2012).

5. Conclusion:

Phacopidae originated at the end of the Ordovician and diversified since the Silurian. They had a morphology close to their sister taxon Pterygometopidae, with a glabella broadening forward and a proparian facial suture. Some genera had an unusual morphology but most of them had rather a similar shape with minor morphological changes. The main morphological variations among phacopids were the position of the facial suture, the shape of the genal angle and the elongation of both cephalon and pygidium. For cephalae, most morphologies already existed in the Silurian but the morphological diversity increased in the Devonian. Innovations and novelties were particularly favoured by the colonisation of new habitats offered by the environmental changes in the Pragian. The maximum of morphological disparity occurred in the Eifelian, late in the evolutionary history of the phacopids. Their diversity peak occurred later, in the Eifelian. At this time, morphological disparity had already started to decrease. The Middle Devonian events strongly affected the phacopids, leading to a decrease of more than half of the morphological and taxonomical diversity in the Givetian. These extinctions were non-random, particularly affecting trilobites with reduced-eyes. Although morphological disparity remained low in the Frasnian, some morphological changes occurred. The facial suture migrated toward the anterolateral margins related to the eye-reduction and blindness and the pygidium elongated laterally. Eye reduction was achieved during environmental changes, especially sea-level changes. These trends continued in the Famennian, during which a recovery caused an increase in both diversity and morphological disparity. However, the Hangenberg event at the Devonian-Carboniferous boundary led to the disappearance of this representative family in trilobites during the Devonian.

Acknowledgements

The authors are grateful to the reviewers who greatly improved this work. Financial support was provided by the Région Hauts-de-France, the Ministère de l'Enseignement Supérieur et de la Recherche (CPER Climibio) and the project ECOS Sud-MINCYT A17A01 (Argentina).

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Supplemental figures

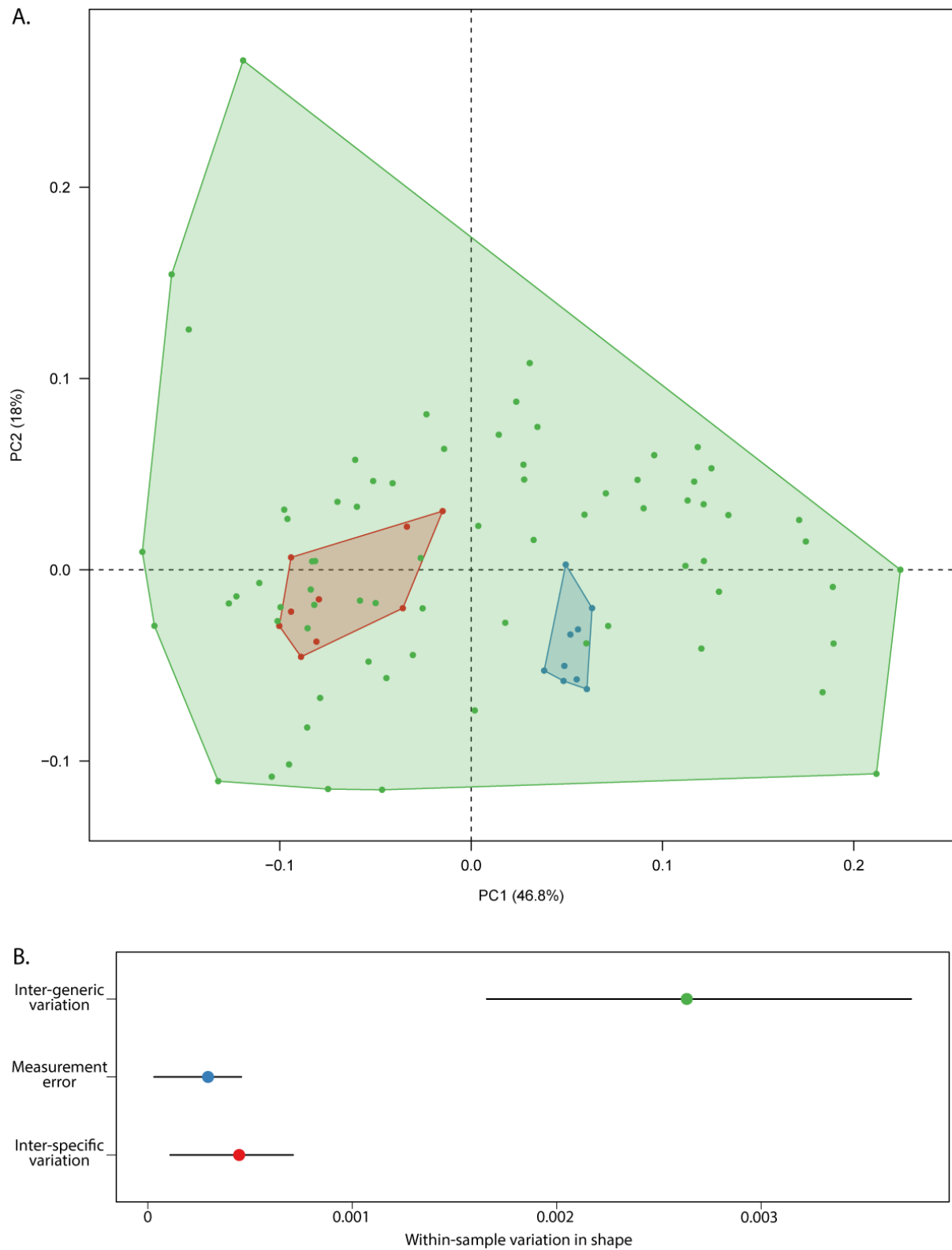


Figure S1: Evolution of the measurement process bias (blue) and the intra-generic variation (red). (A) phacopid cephalon morphospace and (B) phacopid pygidia are distributed along PC1 and PC2.

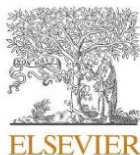
Chapitre 2. Diversité et la Disparité des trilobites du Dévonien d'Afrique du Nord

Les changements environnementaux et les faunes ne sont pas homogènes à l'échelle planétaire, c'est pourquoi un focus au niveau régional est nécessaire afin de mieux comprendre les relations entre les faunes et avec l'environnement. L'objectif est de comprendre les effets de l'environnement et d'identifier les périodes de diversification et d'extinction, à la fois en terme de diversité taxonomique (article 3) qu'en terme de disparité morphologique (article 4). La comparaison de ces deux métriques et l'identification d'un éventuel couplage permet également de mieux comprendre les phases de diversification et d'extinction (article 5). Enfin, dans l'optique d'analyser la composante spatiale de la biodiversité et le rôle de la géographie, une étude de la paléobiogéographie des trilobites du Maroc a été réalisée (article 6).

2.1. Tendances de la biodiversité des trilobites du Dévonien d'Afrique du Nord

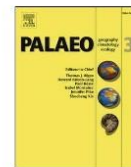
Article 2 : Trilobite biodiversity trends in the Devonian of North Africa

Article publié dans *Palaeogeography, Palaeoclimatology, Palaeoecology*



Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Trilobite biodiversity trends in the Devonian of North Africa

Valentin Bault, Catherine Crônier*, Ninon Allaire, Claude Monnet

Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

ARTICLE INFO

Keywords:

Arthropods
Palaeozoic
Morocco
Palaeobiodiversity
Extinction
Macroevolution

ABSTRACT

Taking advantage of the exceptional record of Devonian trilobites in North Africa, a new dataset was compiled in order to reveal their long-term evolutionary history leading to their extinction. This dataset comprises 1171 trilobite occurrences from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals (substage temporal scale), representing 556 species, 179 genera, and 15 families scattered among nine North African basins. The reconstructed palaeobiodiversity trajectories by means of various biodiversity estimators of taxonomic richness are consistent and highlight a progressive and continuous diversification throughout the Early Devonian to reach a maximum of diversity at the end of the Emsian. Most families encountered in North Africa contribute to this increase of diversity. This regional diversification shows the same trends as the global one. Thereafter, the trilobite diversity began to decline due to extinction rates higher than origination rates during the Eifelian (Middle Devonian). From the middle Givetian to the late Frasnian, the trilobite diversity remained low. After this major decline, and the Frasnian events, a faunal change occurred, especially in phacopid and proetid trilobites, which were the only two families crossing the Frasnian/Famennian boundary. Indeed, the Kellwasser Event impacted an already impoverished diversity leading to a major faunal renewal associated with quick taxonomic changes at the genus level. A larger proportion of deeper water and reduced-eye/blind trilobites who acted as opportunists characterized the Famennian recovery. Finally, these palaeobiodiversity trends are compared to those of ammonoids from the same area.

1. Introduction

During the Cambrian Explosion, trilobites diversified rapidly at a low taxonomic level to become a dominant macrobenthic fauna thanks to several novelties (Clarkson, 1975; Clarkson et al., 2006; Hughes, 2007; Esteve et al., 2018), which evolved during the 'Great Ordovician Biodiversification Event' (GOBE; Harper, 2006; Servais et al., 2010; Harper et al., 2015). They invaded both nektic and benthic zones (Fortey, 1985), shallow and deep waters (Fortey, 1975) and were present at many different latitudes (Cocks and Fortey, 1990; Adrain, 2013).

Whereas the diversity of trilobites have been well-studied and documented during the GOBE (Westrop and Adrain, 1998; Adrain et al., 2004; Adrain, 2013), much less attention has been accorded to their late evolutionary history; a period marked by important environmental changes, i.e., important temperature variations (Joachimski et al., 2009) and palaeogeographic changes causing volcanism (Ziegler et al., 1979). Only a few works (Feist, 1991; Leroosey-Aubril and Feist, 2012) focused on the diversity of Devonian trilobites and on the related events, which led to their decline from the Middle Devonian. Chlupáč (1994) identified

general trends in diversity for the Devonian as a whole.

The 'Devonian Nekton Revolution' (Klug et al., 2010) was an important event, which led to another major diversification of trilobites, especially during the Early Devonian. At the beginning of the Devonian, five orders and nearly eighteen families were present worldwide (Crônier and van Vierssen, 2007). They experienced a great diversification during the sea-level rise of the basal Pragian Event (House, 2002) and the related climate warming (Vacek, 2011). This sea-level rise probably contributed to the widening of shallow marine carbonate realms favourable for the development of trilobite communities (Chlupáč, 1994; Crônier and van Vierssen, 2007; Khaldi et al., 2016), and led to the maintenance of family-level diversity, which persisted with some minor changes until the early Eifelian. Their subsequent diversity decreased dramatically and high taxonomic levels disappeared due to a series of biological events (they were strongly affected by the Kacák and Taghanic events in the late Eifelian and the middle Givetian, respectively; Chlupáč, 1994; Leroosey-Aubril and Feist, 2012). These biotic events were associated with major rises in sea level and led to more widespread extinctions (Chlupáč, 1994; Crônier and van Vierssen, 2007;

* Corresponding author.

E-mail addresses: valentin.bault@univ-lille.fr (V. Bault), catherine.cronier@univ-lille.fr (C. Crônier), claudemonnet@univ-lille.fr (C. Monnet).<https://doi.org/10.1016/j.palaeo.2020.110208>

Received 16 September 2020; Received in revised form 24 December 2020; Accepted 24 December 2020

Available online 1 January 2021

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McKellar and Chatterton, 2009).

Devonian trilobites are especially well represented and diverse in North Africa (Fig. 1). Originally part of a regionally continuous Gondwana passive margin, the North African platform experienced an increase of epeirogenic activity during Devonian times, reflecting the initial collision between Gondwana and Euramerica and the progressive creation of Pangaea (Boote et al., 1998). During this episode, intracratonic basins were created, such as the Tindouf, Maider and Tafilalt basins of Morocco, and the Ougarta Basin of Algeria. In these basins, carbonate production led to carbonate-dominated facies and brought favourable conditions for the settlement and the development of trilobites (McKellar and Chatterton, 2009). Devonian outcrops are mainly composed of limestones with shale intercalations and correspond to a temperate platform environment of the Rheic Ocean. This platform was progressively flooded until the Givetian, which corresponds to the maximal transgression before the latest Devonian regression (Conrad et al., 1986; Hollard, 1967).

In this context, we focused our investigations on biodiversity

analyses of trilobite data gathered from this emblematic North African area, i.e., Morocco and Algeria, famous for their exceptional record of Silurian and Devonian trilobites, both qualitatively and quantitatively (Errami et al., 2015; Bonino and Kier, 2010). The aim of this study is to better understand the impact of the biological events occurring through the Devonian on macrobenthic organisms. Although the Silurian and Devonian trilobites from North Africa have been widely documented since the pioneer works of Richter and Richter (1943), Termier and Termier (1950), Alberti (1964, 1966a, 1966b, 1966c, 1967a, 1967b, 1969, 1970a, 1970b, 1981a, 1981b, 1982, 1983), and the subsequent studies of Morzadec (1997, 2001), Chatterton et al. (2006), McKellar and Chatterton (2009), Gibb and Chatterton (2010), van Viersen and Prescher (2011, 2014), van Viersen and Heising (2015), van Viersen et al. (2017), Johnson and Fortey (2012), Feist and Chatterton (2015), Feist et al. (2016), Khaldi et al. (2016), van Viersen and Holland (2016), Feist and Beika (2018), and Grönier et al. (2013, 2018a, 2018b), among others; but no analysis based on a substantial occurrence database has been performed at a regional scale for this area.

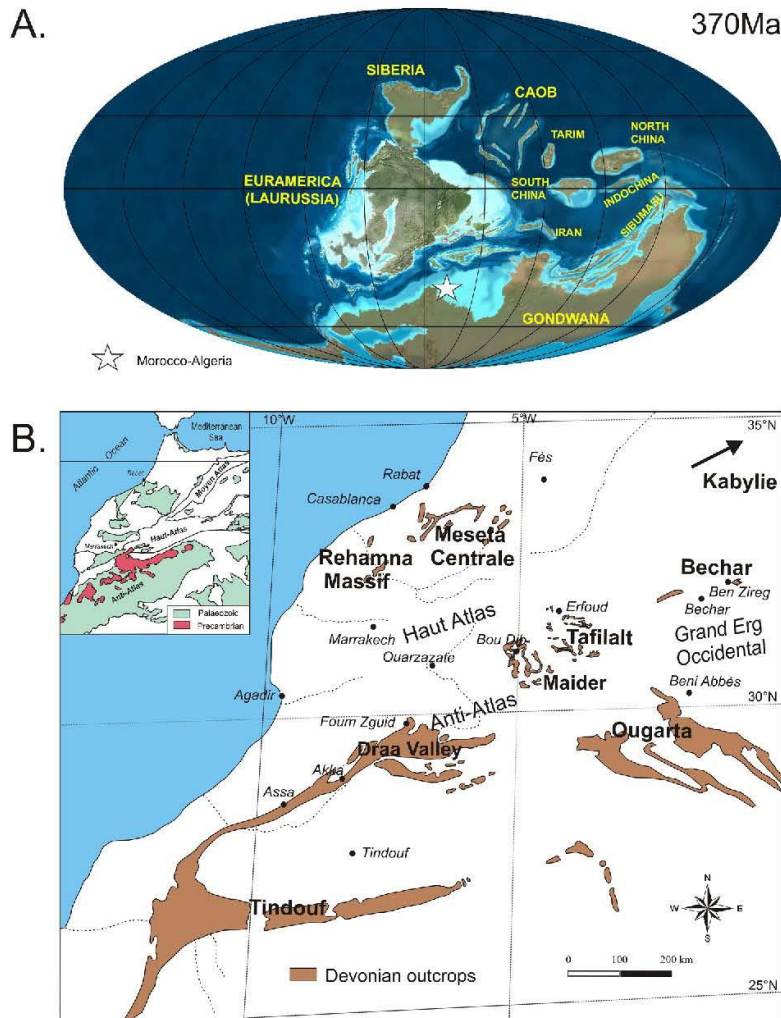


Fig. 1. (A) Location of Morocco and Algeria (white star) on a palaeogeographic map (modified from Blakey (2016), with continent positions and shapes for the Late Devonian modified from the tectonic data of Hara et al. (2010), Metcalfe (2011), and Xiao et al. (2010). (B) Geographical location of studied area with the nine studied basins (in bold; modified from Hollard, 1968).

A new dataset of trilobite occurrences is used and modern biodiversity metrics are applied to quantify the biodiversity fluctuations characterizing the evolution of trilobites throughout the Silurian and the Devonian, and to better document the Devonian extinction events in North Africa. Our investigations focus on the representative trilobite-bearing areas of Morocco and Algeria (North Africa) and on the taxonomic component of biodiversity (taxonomic richness, composition, and similarities), at the substage temporal scale. To understand their fluctuations in time and space, their distribution patterns are assessed thanks to diversity curves and by considering the palaeogeographic and palaeoenvironmental context.

2. Data

2.1. Occurrences

To analyse accurately the fluctuations in biodiversity, a dataset has been compiled to list all occurrences of Silurian and Devonian trilobites documented in Morocco, Algeria, Mauritania and Libya from the available literature (Appendix A). Only studies published after 1943 have been included, because the former publications either present an outdated taxonomy in need of revision, and/or a poor temporal resolution. This selection represents 98 publications (Appendix B) which cover the end of the Silurian and the Devonian from North Africa (Fig. Suppl. A). Our dataset contains all identified taxa at the species rank in a revised taxonomy and temporal framework, and is as much representative as possible of the current state of research concerning the knowledge of the Silurian and the Devonian trilobites from North Africa. All in all, this dataset (Appendix A) comprises 4324 trilobite specimens, i.e., 1171 trilobite bed-occurrences in total from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals from the Helderian to the Famennian. Only the highest number of either cephalon/cranidia, pygidia or complete exoskeletons per occurrence was kept to avoid duplicates. This number represents 556 species, 179 genera, and 15 families scattered among nine North African basins (Fig. Suppl. B). For each trilobite bed-occurrence, the dataset also contains the following information: source study (reference), location (locality, basin, country), stratigraphic position at different resolutions (stage and substage; their numerical ages are derived from the ICS International Chronostratigraphic Chart v2016/10; Cohen et al., 2013; updated), abundance, taxonomic information including the classification, taxonomic qualifiers (such as '?', 'cf.' and 'aff.') if relevant for genus and/or species, authorship, and original identification if it has been revised. In order to create a taxonomic framework reflecting the current state of research with as much consistency as possible, we relied on the identification and age-assignment in the original studies or subsequent published revisions and considered the intending synonymies. Without intention to validate or revise the taxonomy, the names used follow the last usage. Throughout our data compilation, genera and species were considered, but only the diversity fluctuations at the generic level are presented and discussed herein. The diversity changes at the specific level are presented in a supplemental figure (Fig. Suppl. F). The stratigraphic intervals or bins used in the database corresponds to the last three Silurian series and to the 18 Devonian substages. The duration of a substage varies from 1.6 Myr (lower and upper Pragian) to 8.6 Myr (lower Emsian) for a total duration of 68.5 ± 0.5 Myr.

2.2. Trilobite vision and palaeoenvironments

In order to highlight the potential environmental/ecological affinities or morphological adaptation of trilobites, two additional sets of information are recorded in the dataset. First, we considered the visual system of studied trilobites, which can be inferred directly from the eyes preserved as calcite lenses on a visual surface (Clarkson et al., 2006). Each taxon has been assigned to one of the three categories: blind, reduced-eye, or well-developed-eye. The diagnostic features related to

the eye size or to the number of lenses were considered to establish these categories.

Second, we considered the marine environment of studied trilobites, for which associations are well-known to reflect relatively precise palaeoenvironmental indicators of different depths across shelves (Fortey, 1975; Speyer and Brett, 1986; Turvey, 2005; Crónier and van Vierssen, 2007; Crónier and François, 2014). Four major environments can be recognized along a bathymetric profile: (1) the shoreface environment characterized by shallow, proximal and agitated deposits including trilobites as fragmented exoskeletons in sandstones; (2) the inner shelf environment characterized by mudstones intercalated with sandstones including trilobites as disarticulated and fragmented exoskeletons and/or as coquinas; (3) the middle shelf environment characterized by relatively deep deposits including moderately to highly diverse assemblages with trilobites with well-developed eyes, clumped or dispersed sclerites commonly articulated in mudstones; and (4) the outer shelf environment located below the effective storm wave-base including rare trilobites, as articulated exoskeletons, often blind or with reduced-eyes, in shales. Consequently, according to its depositional environment and to the observed faunal assemblages, each genus has been assigned to only one of these four categories. Trilobites considered to have habitat specificity are found almost exclusively in their specific environment.

Blind or reduced-eye trilobites often indicate a dark and relatively deep environment, i.e., outer shelf/external platform, near or below the photic zone (Clarkson, 1967; Feist, 1991). By contrast, trilobites with well-developed eyes often indicate a shallow (i.e., inner platform) or a mid-depth (i.e., middle shelf) environment. For example, it has been demonstrated that Late Devonian phacopid trilobites, in the context of a deepening ocean, were subject to such evolutionary changes, i.e., a gradual reduction of the visual complex leading to blindness (Crónier and Courville, 2003; Crónier et al., 2004, 2011; Crónier and François, 2014). Only, the state of preservation and/or the nature of sediments and the associated fauna allow us to determine roughly the palaeoenvironmental/palaeoecological position along a bathymetric profile.

3. Methods (biodiversity metrics)

The estimation of palaeobiodiversity and its variation through geological time is a major issue in macroevolution. Major biases (rock/fossil preservation, facies/ecology, sampling, ...) affect taxonomic richness reconstruction (Foote, 2000; Smith, 2001). For Morocco in particular, the biases concern also the issues due to the trade of valuable trilobites. Throughout the past decades, some beds that yield complete, articulated and well-preserved trilobites have often been the focus of investigations (e.g. Chatterton et al., 2006; van Vierssen and Holland, 2016; among others). Even if major biases exist, the last decades have seen substantial progress in the knowledge of the Phanerozoic biodiversity (Sepkoski Jr. et al., 1981; Benton, 1993; Alroy et al., 2008; Fan et al., 2020), notably thanks to the use of resampling methods (Alroy, 2010a; Chao et al., 2012, 2014; Close et al., 2018).

Palaeobiodiversity can be measured in different ways and for any taxonomic rank. To produce reliable biodiversity trajectories through time close to the true diversity of coexisting taxa at a given time (i.e., 'standing diversity', Cooper, 2004), taxonomic approaches based on the count of distinct names for a given taxonomic rank (species, genera, families) and known as 'taxonomic richness' indices were used. Taxonomic richness indices were calculated by computing traditional incidence-based binning approaches, as well as modern occurrence-based resampling methods.

Classical binning approaches estimate taxonomic richness according to different biostratigraphic categories (e.g., single-interval, ranging through, originating, and disappearing; see Foote, 2000) based on the synthetic incidence (i.e., binary presence) range of the taxa considered in a moving "window" covering three time bins (for additional details and discussion, see Foote, 2000; Alroy, 2010b; Nowak et al., 2015): the

sampled-in-bin diversity (SIB), which is the raw count of actually documented taxa; the range-through diversity (RT), which includes or excludes single-interval taxa, but interpolates discontinuous taxon ranges; the normalized diversity (NORM), which weights differently the various biostratigraphic categories; the boundary-crosser diversity (BC), which focuses at the chronostratigraphic limits and not within these time bins; and the single-interval diversity (SGL). All these traditional metrics can be biased by various effects such as heterogeneous sampling, but they are still useful in highlighting peculiarities in the dataset. Cooper (2004) evaluated the normalized diversity as a good approximation of the mean standing diversity. Additionally, the recent stochastic uniform-time-bin diversity (UTB) of Gibert and Escarguel (2017) has been applied: this approach is a back-transformation into a virtually continuous-time averaged time series of the time-discretized dataset constructed from the fossil record; the period of time under study was split into 2 Myr time bins, and each specimen was assigned multiple times at random to one of the bins between its maximum and minimum age brackets. This method has been shown to provide more accurate estimates of standing diversity than binning approaches, even when the origination and extinction are biased towards coinciding with the boundaries of bins (Gibert and Escarguel, 2017). Finally, origination and extinction rates are calculated based on range-through diversity excluding single-interval taxa. More precise and accurate methods of calculating origination/extinction rates such as the gap fillers method (Alroy, 2014, 2015) cannot be applied to our dataset because of the high proportion of taxa documented in less than four time intervals.

Although taxonomic richness is an intuitive measure of biodiversity, it is an elusive quantity to measure properly, because as more individuals are sampled, more species will be recorded (the so-called sampling intensity/effort problem) (Simpson, 1949; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001; Chao et al., 2014). Therefore, because the robustness of estimated curves of taxonomic richness depend on sample size, modern biodiversity metrics based on the resampling of abundance and/or collection data were also performed in this study: size-based rarefaction (CR) and coverage-based rarefaction (SQS), which are two interpolation methods, and richness estimated using a Poisson sampling model (TRiPS), which is an extrapolation approach (see Close et al., 2018). First, the conventional size-based rarefaction estimates taxonomic richness by repeated random down-sampling of data to a user-defined sample size (Sanders, 1968; Hurlbert, 1971; Foote, 1992; Shimadzu, 2018) to enable comparison of the time intervals considered at equal sampling effort. Second, the coverage-based rarefaction (shareholder quorum subsampling, SQS; Alroy, 2010a-b, Alroy, 2013) repeatedly randomly draws taxa from compiled in-bin occurrence lists, until a summed proportion of these taxa relative occurrence frequency reaches a certain 'quorum' to finally sum the taxa sampled. Coverage, as a measure of sampling quality, is defined as the proportion of the frequency distribution of taxa within a sample. In this study, diversity was estimated at various levels of coverage at intervals of 0.1 and by including dominant and single-interval taxa. Coverage-based rarefaction has been shown by both simulation studies and empirical data to be a robust method of correcting for preservation and sampling heterogeneity (Alroy, 2010a-b; Chao and Jost, 2012; Close et al., 2018). Finally, TRiPS (Starrfelt and Liow, 2016) aims to estimate true richness by modelling per-interval sampling rates (inferred by maximum likelihood using observed taxon occurrence frequencies and interval durations) for extinct lineages as a homogeneous Poisson process.

Additional insights on the biodiversity of the Devonian trilobite fauna from North Africa were completed by investigating their evenness component (Smith and Wilson, 1996; Tuomisto, 2012; Kvålseth, 2015). Taxonomic evenness ('equitability') refers to how equal in numbers (relative abundance) each taxon in a (space/time) bin is, and is typically derived by rescaling a diversity measure to the interval from 0 to 1. Two measures of evenness are here computed: the Simpson index of dominance (D; Simpson, 1949) and the Pielou's equitability (E; Pielou, 1966)

derived from the Shannon–Wiener index (Shannon and Weaver, 1949). Low values of dominance indicate taxa rather evenly represented, and conversely the index will be close to 1 if there is a single very dominant taxon. Inversely, values of equitability close to 0 reflect an overabundant taxon, while high values indicate almost equally distributed taxa.

In this work, the various biodiversity indices and methods were computed with the scientific environment R (version 3.5.2; R Core Team, 2019) using the package 'epaleo' (version 0.8.27; Monnet C., unpublished, University of Lille; for applications using this package, see e.g., Tétard et al., 2017; Shen et al., 2020), and with the software PAST (version 3.24; Hammer et al., 2001).

4. Results

4.1. Genus richness

The reconstructed biodiversity curves of the trilobite genera from North Africa during the Silurian and the Devonian substages are illustrated in Fig. 2 and Suppl. C and D, for both raw binning and collection resampling methods. As indicated by the various biodiversity estimates and notably the coverage-based rarefaction (SQS), the generic richness shows important fluctuations during the Silurian and the Devonian in North Africa (Fig. 2). The local diversity was characterised by low to moderate values from the Ludlow to the Lochkovian, followed by peaks of highest diversity in the second part of the Early Devonian and at the beginning of the Middle Devonian, i.e., from the Pragian to the Eifelian. This period constituted a plateau of high diversity. During this period, the diversity still fluctuated with a decrease of diversity in the early Emsian before the major peak at the late Emsian. After this high diversity period, the generic richness strongly decreased until the middle Givetian and stayed low until the late Frasnian. After a small diversification phase observed at the end of the Frasnian, there was a moderate decrease of diversity in the early Famennian, then, another small diversification phase occurred in the late Famennian (Fig. 2). However, the Late Devonian diversity remained low compared to the Early Devonian plateau.

The taxonomic richness evaluated by the boundary-crosser diversity (BC) shows similar trends to the SQS, such as the initial protracted increase of diversity from the Ludlow to the early Eifelian (Fig. 2). The major difference is the absence of a diversity decrease in the early Emsian. Next, a huge decrease took place and the diversity reached low values during the middle Givetian, and stayed relatively low until the end of the Famennian. The range-through diversity excluding single-interval taxa (RTexS) shows as the boundary crosser diversity, a continuous Early Devonian diversification from the Lochkovian to the Emsian (Fig. 2). This period is followed by a relatively regular decrease of the diversity until the early Famennian. No increase was spotted in the late Frasnian contrary to the SQS method. Then, an increase happened in the middle and late Famennian as shown by the SQS curve. The sampled-in-bin diversity (SIB) and the uniform-time-bin diversity (UTB) show the same trends as the SQS diversity (Figs. 2, Suppl. C and D). This method also suggests a slight increase of the generic richness throughout the Frasnian. Most discrepancies observed between these various biodiversity estimates were due to episodic increases of single-interval taxa (e.g., late Pragian, late Emsian, late Frasnian and early Famennian; Fig. Suppl. D) or to increases of virtual ranges (e.g., early Emsian), depending on the importance given to these parameters by each index.

The size-based rarefaction (CR, Fig. Suppl. E2) analysis shows that some substages are under-sampled and require a higher number of individuals to achieve robust diversity estimates. Therefore, additional studies and fieldworks are required to complete the knowledge of trilobites especially for the early Lochkovian, the Givetian and the Frasnian. Nevertheless, the size-based rarefaction analysis confirms the trends observed with the other indices: a high diversity from the late Pragian to the late Emsian followed by a decrease during the Eifelian.

4.2. Origination and extinction

With regard to taxonomic changes, i.e., extinctions (E_{RT}) and originations (O_{RT}) (Fig. 3), the observed evolutionary pattern shows a global increase of the number of originations with moderately high values from the late Lochkovian to the late Emsian, interrupted by two major decreases occurring during the early Pragian and the early Emsian. Then, the number of originations decreased drastically during the Eifelian and the early Givetian. Thereafter, a small peak of originations occurred during the early and the middle Famennian (Fig. 3).

Concerning extinctions, the evolutionary pattern shows a major increase during the Early Devonian, with a maximum reached in the early Eifelian. This peak of extinction followed the high origination period observed during the Early Devonian. During the Middle and Late Devonian, four other moderate extinction peaks occurred (early and late Givetian, late Frasnian and late Famennian; Fig. 3).

4.3. Evenness and dominance

In North Africa, the dominance was generally low (less than 0.3) during the Early and Middle Devonian (Fig. 4). Only the Ludlow, the early Lochkovian and the late Givetian were characterized by a dominance above 0.4, and the middle Givetian was characterized by a dominant taxon ($D = 1$) in a very depauperate assemblage (Fig. 4). Throughout this period, a relatively high evenness (more than 0.4) is recorded except for the Emsian. The transition from the late Frasnian to the late Famennian was characterized by a sharp decrease of evenness (from 0.82 to 0.23) and a distinct increase of dominance (from 0.23 to 0.72). After these important changes, the evenness increased gradually during the Famennian to reach high values, and conversely, the dominance decreased until the late Famennian before a slight increase at the end of the Devonian.

4.4. Richness per family

Six orders of trilobites (Trinucleida, Lichida, Harpetida, Corynexochida, Proetida, Phacopida) are documented in North Africa from the Ludlow to the latest Famennian (Fig. 5). Trinucleida (see Bignon et al., 2020) did not reach the Devonian, Corynexochida disappeared in the Middle Devonian, and Lichida and Harpetida did not cross the Frasnian/Famennian Boundary. Only Proetida and Phacopida were present until the Famennian.

Sixteen families are documented in North Africa during the studied period (Fig. 5). The Raphiophoridae (Trinucleida) were only present during the end of the Silurian. Among Phacopida, Calmoniidae, Calymenidae, Cheiruridae, Dalmanitidae and Homalonotidae did not cross the Early Devonian. During the maximum diversity period characterizing the late Emsian, 12 families coexisted in North Africa. After the major decrease of the diversity observed during the Eifelian, the middle Givetian records the presence of only one family (Proetidae). In comparison to the Emsian and Eifelian stages, the Frasnian is relatively poor in both phacopids and proetids. The odontopleurids and the harpetids were present until the late Frasnian, where they are both represented by only one genus. Then, only two families managed to survive the Kellwasser Crisis, proetids and phacopids, which experienced a new diversification in the Famennian.

4.5. Vision of trilobites and palaeoenvironments

The variations of the relative genus diversity according to the visual capabilities (blind, reduced-eye or well-developed-eye taxa) and to the living environment (shoreface, inner shelf, middle shelf, outer shelf) are reported in Fig. 6. Three time intervals were marked by peaks of presence of reduced-eye and blind taxa: the Pragian, the late Emsian and the Famennian (Fig. 6A). Compared to the total taxonomic richness, the early Famennian was characterized by the greatest proportion of

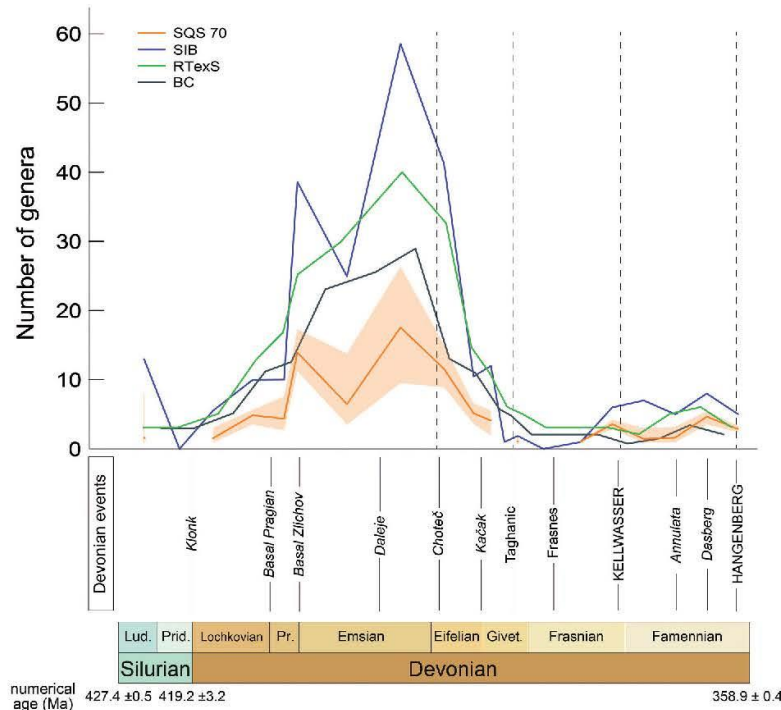


Fig. 2. Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Shareholder Quorum Subsampling (SQS) diversity, estimation for a quorum of 70; Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Range-through diversity excluding single-interval taxa (RTextS), which estimates diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Boundary-Crosser diversity (BC), count of all taxa present in two successive intervals. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

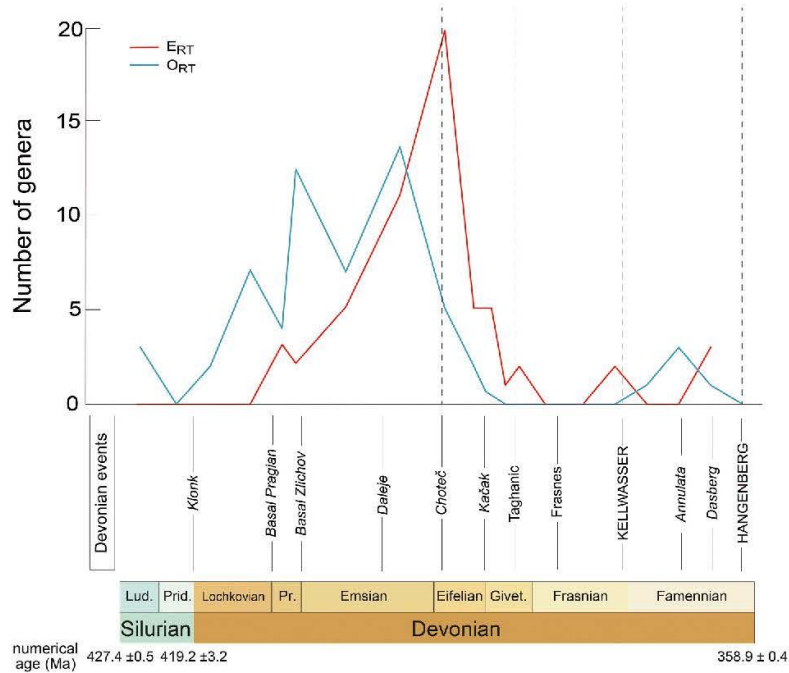


Fig. 3. Fluctuations of the number of extinctions (E_{RT}) and originations (O_{RT}) of trilobites from North Africa during the Silurian and the Devonian, at the generic level. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

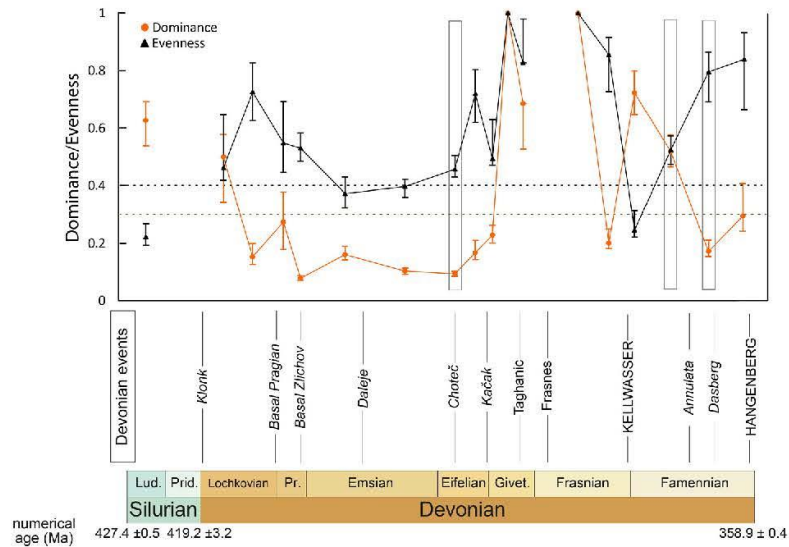


Fig. 4. Variations of two diversity indices (dominance and evenness) during the Silurian and the Devonian, computed for the trilobites from North Africa at the generic level. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

reduced-eye or blind taxa. The Pragian showed a relatively substantial number of reduced-eye and blind trilobites. The increase of trilobites with a reduced vision in the late Emsian corresponded to a global and regional diversity peak, whereas the two other peaks of reduced-eye taxa

occurred in the Famennian were associated to low diversity values (Fig. 6A).

Regarding the depositional environments and faunal assemblages, trilobites encountered in shallow environments (shoreface) were present

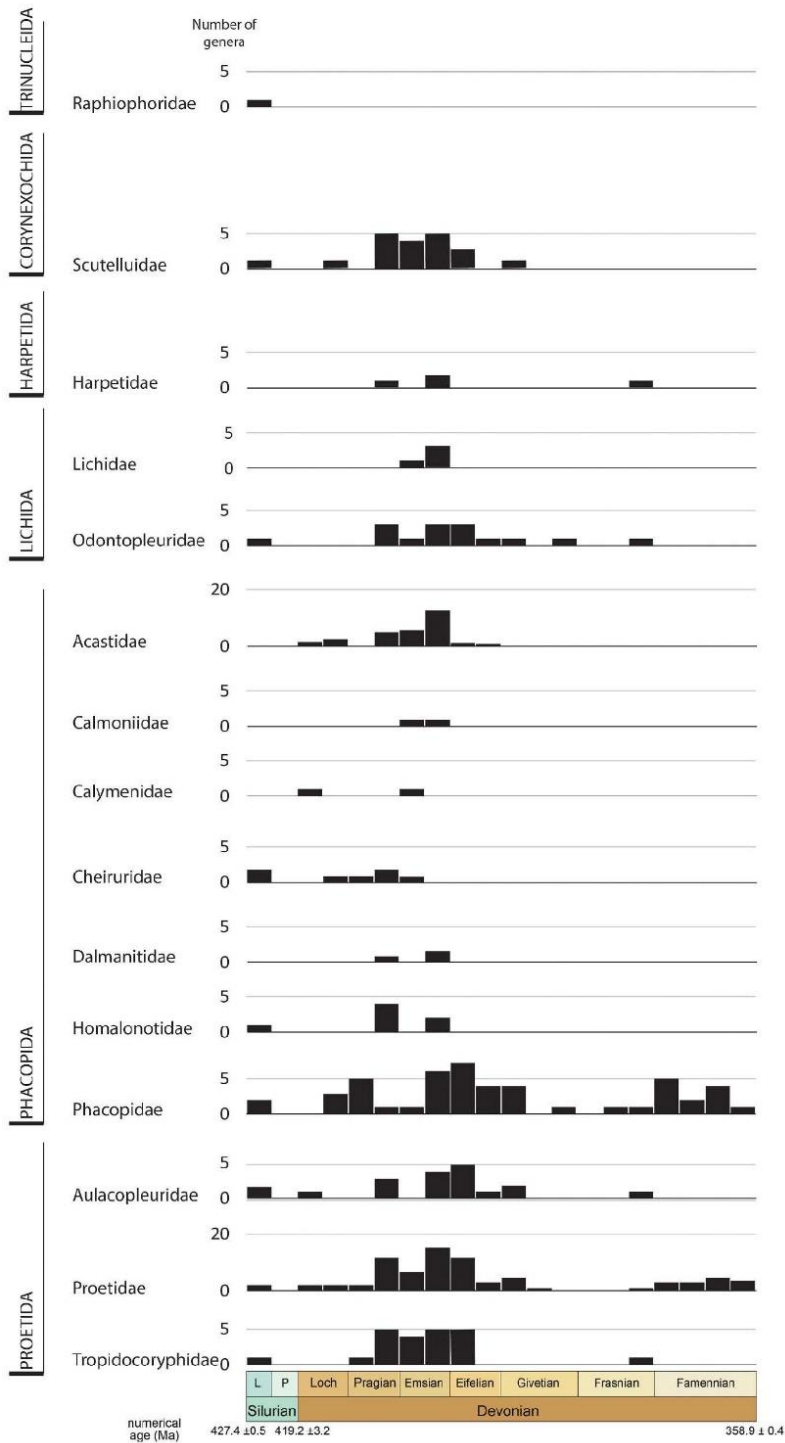


Fig. 5. Number of genera for each trilobite family during the Silurian and the Devonian in North Africa. Families are ordered by order. Ages from Cohen et al. (2013, updated).

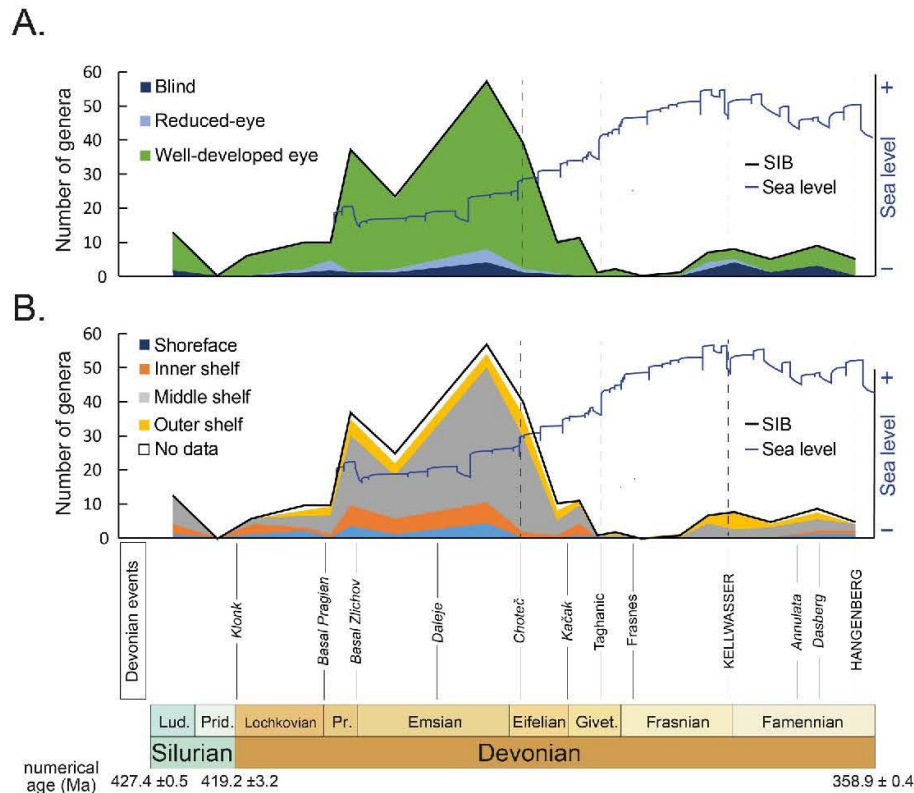


Fig. 6. Fluctuations of the relative genus diversity of trilobites from North Africa during the Silurian and the Devonian, according to (A) three visual capabilities (blind, reduced-eye or well-developed-eye taxa), and (B) four depositional environments, i.e., bathymetric depth (shoreface; upper offshore or inner shelf; median offshore or middle shelf; lower offshore or outer shelf located below effective storm wave-base environments; and not allocated or ubiquitous genera). Each genus is attributed to its main environment even if it could live in other environment. Sea level from Johnson et al. (1985). Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

especially during medium to high diversity periods, i.e., during the entire Early Devonian, the early Givetian and the latest Famennian (Fig. 6B). In contrast, the trilobites encountered in deeper environments (outer shelf) were present throughout the Devonian but in higher proportion in the late Frasnian and the Famennian.

5. Discussion

The palaeobiodiversity trends of the North African trilobites reconstructed using various biodiversity indices are consistent and highlight significant diversity changes throughout the end of the Silurian and the Devonian. In summary (Fig. 2), North African trilobites were characterised by a low diversity, slightly increasing during the Lochkovian. A sharp increase was recorded during the Pragian, leading to a plateau of maximum diversity during the Emsian and the early Eifelian. An abrupt diversity decrease occurred subsequently during the late Eifelian, from which the diversity stayed low until the end of the Devonian, with only small changes observed.

5.1. End of the Silurian and Lochkovian

The comparison of the regional diversity with the global diversity patterns described in the literature shows marked similarities and differences. At the global scale, the trilobite diversity that is characterized by numerous genera that belongs to conservative and long-ranging genera, was documented from the Silurian to the Lochkovian with few

changes due to only minor extinctions (Chlupáč, 1994). A decrease of diversity occurred in the Ludlow and the Pridoli in some places (e.g., Prague Basin; Manda and Frýda, 2014) and especially in North Africa. The Lau Event (Jeppsson and Aldridge, 2000) which took place during this interval with faunal changes concerning conodonts and graptolites among others, at the global scale. This event was not clearly identified in North Africa but could be associated to this decrease. No trilobites are found in the shale and black limestone deposits of the eastern Anti-Atlas because of the deep-water conditions, which are not favourable to the development of benthic fauna (Morzadec, 2001). Thus, in North Africa, a low trilobite diversity was documented from the Silurian to the Lochkovian. Only few trilobite taxa dominated these communities as shown by the high dominance index in the Ludlow and the Lochkovian (Fig. 4).

5.2. Pragian and Emsian

At a global scale, the major regressive Basal Pragian Event (Chlupáč and Kukal, 1986) contributed to the widening of shallow marine environments with carbonate sedimentation favourable for trilobites, and led to an increase of the genus diversity (Chlupáč, 1994) associated with the proliferation of many benthic species on the continental shelves (Morzadec, 2001). There was a protracted diversification throughout the Early Devonian, with a diversity maximum recorded during the late Emsian. Meanwhile, the long-term gradual transgressive Daleje Event occurring at the beginning of the late Emsian (House, 1985; García-

Alcade, 1997; Becker et al., 2018) contributed to the installation of siliciclastic environments and led to strengthening the trilobite diversity increase. As a result of the preceding Daleje Event, offshore trilobites also proliferated worldwide, with numerous blind and reduced-eyes taxa (Chlupáč, 1994). The fauna composed of *Plagiolaria* associated with other small-eyed or blind trilobites (*Piriproetus*, *Leonaspis*) encountered in the Pragian, represents a specialized group of trilobites inhabiting a muddy and rather deep water environment (Chlupáč, 1977, 1983). Hence, the generic richness reached its maximum level (Adrain, 2008).

In North Africa, the Pragian diversification is also documented (Hollard, 1967; Morzadec, 2001; Ouali Mehadji et al., 2011). However, whereas the peak of diversity was recorded in the early Pragian at the global scale (Chlupáč, 1994), the African regional diversity showed a peak rather in the late Pragian. This difference can be explained by the fact that most studies concerning Pragian trilobites from North Africa

lack enough chronostratigraphic resolution to be included in our analysis. However, our study is the only one with a substage chronostratigraphic resolution, contrary to previous ones with a stage chronostratigraphic resolution. The increase of diversity is not explained by the proliferation of a few genera but corresponds to a general trend: the diversification (Fig. 6) is also observed at the family level (Fig. 5). The majority of Pragian genera persisted through the Emsian, both in North Africa (Fig. 2, see BC curve) and at the global scale, therefore, contributing to the richest interval, i.e., the Emsian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012).

A decrease of diversity occurred in the early Emsian. However, the poor preservation of trilobites with no commercial opportunities limits their sampling and their subsequent analyses despite the notified presence of dalmanitids (odontochilines) for instance in the Draa valley (Becker et al., 2004). After this decrease of diversity, the transgressive

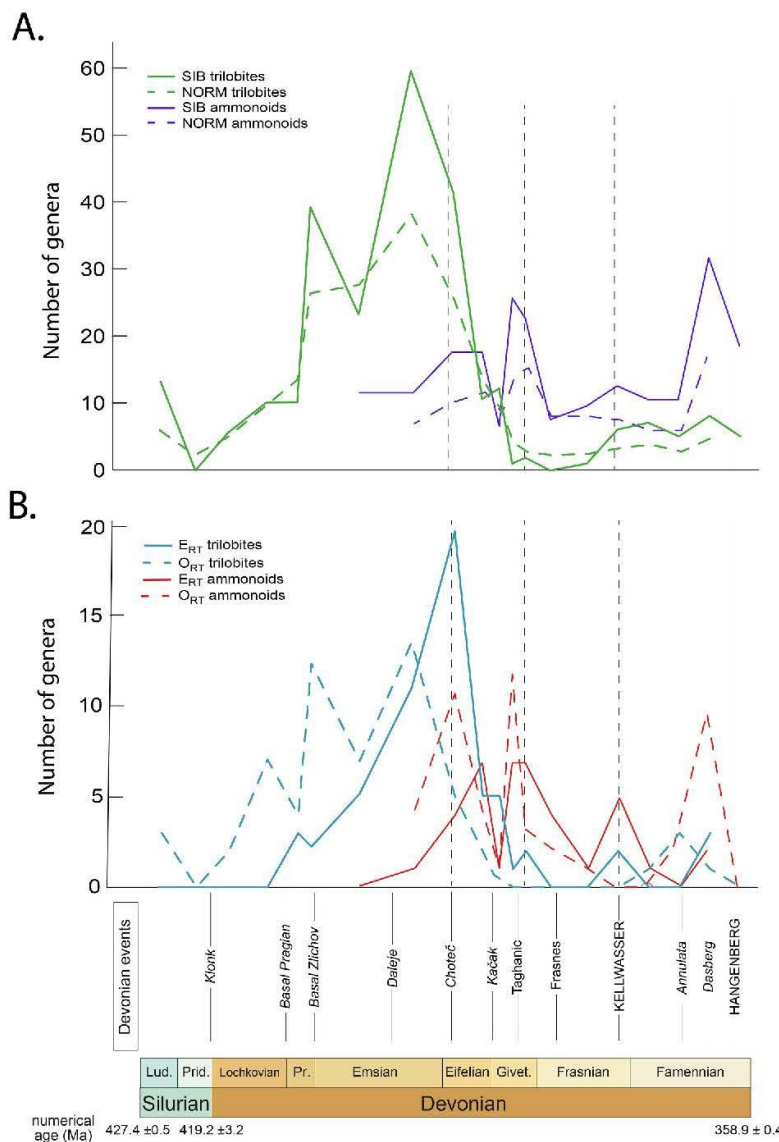


Fig. 7. Diversity dynamics of trilobites from North Africa and ammonoids from Morocco during the Silurian and the Devonian, at the generic level. See text for the definition of indices. Data for trilobites: this study; data for ammonoids from Allaire (2017, unpublished PhD). (A) Taxonomic richness: Sampled-in-Bin diversity (SIB) and normalized diversity (NORM). (B) Extinctions (E_{RT}) and Originations (O_{RT}). Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

Daleje Event led to an increase of the abundance of trilobites encountered in deeper environments in North Africa (Fig 6). Blind and reduced-eye trilobite genera were better adapted to live in this environment and become more numerous in the late Emsian (Fig 6). Additionally, trilobite taxa from shallow siliciclastic environments such as asteropygins were also well diversified in Morocco (Morzadec, 2001). All these diversification phases led to the Devonian peak of diversity recorded in the late Emsian (Fig. 2) in North Africa but also at the global scale (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). The evenness decreased with the Early Devonian diversification to reach a minimum in the late Emsian, which corresponds to the substage with the highest diversity (Fig 4). This decrease shows that even if no genera dominate the community, some of them took advantage of the environment (e.g., proetids, acastids and phacopids; Fig 5).

In the context of the progressive colonization of the water column by predators during the 'Devonian Nekton Revolution' (Klug et al., 2010, 2017), potential connections especially with ammonoids can be evaluated. Indeed, the ammonoids which appeared during the early Emsian worldwide, were efficient nektonic predators during the Devonian, as the jawed fishes (Klug et al., 2017). A comparison with the ammonoids from Morocco (data from Allaire, 2017, unpublished PhD; the same methods as those used in this study were performed to obtain these data) has been done in order to evaluate differences and similarities between trends. Evolutionary novelties within the trilobites may be a direct response of the development of passive morphological defences (as spinose skeletons) or active behavioural defences (as infaunal moulting or other cryptic behaviours) against durophagous predators such as nektonic ammonoids. During the Devonian, the highly diverse Emsian and Eifelian trilobites from Morocco and from North America show a high frequency of spinose genera in several lineages (Brett and Walker, 2002). Such spinose skeletons may have had a selective advantage against durophagous predators (Brett and Walker, 2002). The ammonoids from Morocco showed a relatively low diversity during the Emsian, while the trilobites were characterized by a very high diversity (Fig. 7A). This trend suggests a nekton-benthos decoupling as proposed by Ebbighausen et al. (2011) for the Draa Valley in Morocco. These low diversity values represent the first step of the Nekton Revolution (Klug et al., 2010) which is underway and has not yet reached its acme. The subsequent increase of the ammonoid diversity (see following section) could be a consequence of the development of benthos such as trilobites in oxic zones.

5.3. Eifelian and Givetian

In contrast to the Silurian and Early Devonian, the diversity patterns observed during the Middle Devonian were somewhat different considering regional and global scales. Lerosey-Aubril and Feist (2012) noted a global diversity loss from the Eifelian to the Frasnian, but without an examination at a substage resolution. Trilobite faunas were rather diverse and locally abundant, and often distributed in geographically restricted biofacies. As underlined by Lerosey-Aubril and Feist (2012), this period was affected repeatedly by environmental disturbances generating large restructuring within marine ecosystems at a global scale (Walliser, 1996).

Although only a small faunal turnover occurred at the global scale during the Chotec Event (Barnes et al., 1996), a sharp decrease of the diversity occurred at the regional scale in North Africa in the early Eifelian. Indeed, a transgression occurred in the Western Sahara Platform (Ouali Mehadji et al., 2004) leading to biotic and abiotic changes. These changes were not favourable for trilobites and led to extinctions such as the genus *Paralejurus*, which disappeared both at the regional and global scales (Chlupáč, 1994). Additionally, this event strongly affected the Proetida with the regional extinction of some representatives of the Proetidae and Aulacopleuridae. Morzadec (2001) noted that because of the high sea level, trilobites living in shallow environments such as Asteropyginae remained scarce even if, at a global scale, they

were able to adapt in deep environments (Bignon and Crônier, 2015). In North Africa, numerous taxa were impacted by this event; after the crisis, the diversity and the evenness remained relatively low and the dominance index suggests the presence of barely dominant taxa (Fig. 4).

The Chotec Event, which particularly affected trilobites in North Africa, did not affect all organisms in the same way. Indeed, as pelagic and nektonic organisms, the ammonoids were less impacted by this transgressive event than the trilobites. The generic richness of the Moroccan ammonoids showed a progressive increase from the late Emsian to the late Eifelian; no drop down is recorded after the Chotec Event (Fig. 7A; Allaire, 2017, unpublished PhD).

The Kacák and Taghanic events (late Eifelian and middle Givetian, respectively) mark the end of the sharp decrease of the trilobite diversity already underway at all taxonomic ranks, and lead to a stepwise diversity drop (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). The major transgressive Taghanic Event initiated in the middle Givetian led to a worldwide development of a deep-sea/pelagic cephalopod environment (Johnson, 1970; House, 1985) not favourable for trilobites; the disappearance of numerous families is observed (Calmoniidae, Cheiruridae, Lichidae) due to the disappearance of the near-shore neritic and perireefal environments. Only, a few taxa survived this worldwide deepening and successfully adapted to deeper and more homogeneous environmental conditions which characterise the late Givetian. The surviving faunas exhibited a pronounced reduction in generic and specific diversity concomitant with an increasing cosmopolitanism (Lerosey-Aubril and Feist, 2012).

At the regional scale, the Kacák Event was underlined by an increasing number of extinctions in trilobites. As the Chotec Event, the Kacák Event corresponds to a global eustatic rise combined to oxygenated-depleted conditions in benthic environments (Lerosey-Aubril and Feist, 2012) not favourable to trilobites (Fig. 6A). This deepening (House, 1985) affected the North African faunas (Beika et al., 1999). The low trilobite diversity recorded after the Kacák Event corresponds to assemblages dominated by one genus (i.e., *Gerastos*).

For ammonoids, the early Givetian is poorly documented in the literature; only a few genera have been reported in Morocco. Consequently, the ammonoid diversity characterising the early Givetian is certainly underestimated (Fig. 7B) and so the impact of the Kacák Event is difficult to evaluate. Aboussalam and Becker (2011) noted a remarkable near absence of trilobites (and also brachiopods) in south-eastern Tafilalt in comparison to the similar reefal environments observed in Germany for the middle Givetian. Kaufmann (1998) highlighted that significant faunal and lithological changes affected the eastern Anti-Atlas from the early Eifelian to the early Givetian, and documented the replacement of benthic faunas (trilobites) by pelagic ones (ammonoids). Our results seem to confirm such patterns: for trilobites, the diversity continues to decrease dramatically, while for ammonoids, the diversity reaches high values and the number of originations significantly increases during the Givetian (Fig. 7B).

After the Chotec and Kacák events, the trilobite diversity remained very low in North Africa and the middle Givetian Taghanic Event (Johnson, 1970; House, 1985) impacted already impoverished trilobite faunas. Aboussalam and Becker (2011) noted that the Taghanic Event affected trilobites, in particular those of the Tafilalt basin and the Draa Valley; this extinction phase is immediately followed by a radiation in the Tafilalt basin only. They reported only the presence of phacopids and proetids in the Givetian of Morocco. Moreover, McKellar et al. (2012) reported an exceptional occurrence of *Pedinopariops* (*Hypsipariops*) in the Givetian coarsely siliciclastic facies from Libya. Such occurrence suggest a shift away from carbonate environment in which phacopids prospered during much of the Lower to early Middle Devonian.

For ammonoids, the Taghanic Event seems to have not sharply affected the communities: the late Givetian record high diversity values (Fig. 7A). However, when regarding the fluctuations at a higher time resolution (i.e., biozone temporal scale), the diversity recorded through the Taghanic interval is particularly low and the impact of the Taghanic

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Event in ammonoids can be seen (Allaire, 2017, unpublished PhD). Thus, the Taghanic Event seems to have more impacted nekitic organisms as ammonoids.

As it was demonstrated in the Ardenne Massif (Belgium) by Bignon and Crónier (2015) during the Middle Devonian, the trilobite biodiversity was more influenced by the global events than the local environmental changes. However, due to regional peculiarities, the global events may have different consequences at the local scale compared to the global scale.

5.4. Frasnian

At a global scale, the trilobite diversity was low during the early Frasnian and the Frasnian Event (sensu House, 1985), called also the *Manticoceras* Event (sensu Walliser, 1985), was marked by few extinctions of trilobites, and showed the appearance of two subfamilies, the Pteropariinae and Drevermanniinae (Feist, 1991).

During the late Frasnian, the pronounced eustatic deepening became maximal just before the upper Kellwasser event (Girard et al., 2005), leading to the development of pelagic and euxinic facies. The Kellwasser Event, leading to one of the five major extinctions (Raup, 1986; Raup and Sepkoski, 1982), was characterized by an eustatic instability and hypoxic/anoxic depositional conditions in the deeper outer-shelf environment, affecting especially benthic trilobites adapted to life in deep environments. In these offshore depositional environments beyond the light penetration limit, the visual complex regression leading to blindness in trilobites was an evolutionary trend observed in various independent lineages (phacopids and proetids). This evolutionary trend may result from an 'opportunistic' and adaptive strategy correlative with environmental constraints, insofar as it leads to a good match between organisms and their environment (Crónier, 1999; Crónier and Courville, 2003). However, such a link led them to a subsequent evolutionary impasse resulting in their extinction. Moreover, the late Frasnian *Acuticryphops* showed a morphological intra-specific drift inducing a variability of the visual complex (Crónier et al., 2004; Feist et al., 2009), which would be located at speciation boundaries. These disturbances that occurred during the development seem to be linked to environmental stress, which can be induced by the rapid sea-level fluctuations recorded at the end-Frasnian (Feist and Schindler, 1994). The Kellwasser Event led also to the extinction of almost all reefs and their associated trilobite faunas (Odontopleuridae), and to a significant decrease of diversity for other trilobite taxa (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Otherwise, the late Frasnian trilobites from shallow/near-shore deposits remain poorly known (Lerosey-Aubril and Feist, 2012). Only few data are available; they concern the trilobite faunas from the Canning Basin in Australia (Feist et al., 2009), where well-oxygenated conditions prevailed throughout the Frasnian-Famennian transition (George and Chow, 2002).

In North Africa, only four trilobite orders (Fig. 5) were present during the Frasnian (Lichida represented by Odontopleuridae, Harpetida, Phacopida, and Proetida). For phacopids, among the seven genera known during the Frasnian at the global scale (Crónier et al., 2013; Crónier and François, 2014; van Viersen and Vanherle, 2018), only two were present in North Africa (*Chlupacops* originated in the middle Frasnian and *Acuticryphops* in the late Frasnian; Fig. 8). Phacopids were also rare elsewhere and only one genus (i.e., *Eldredgeops*) was reported so far in North America for example (Crónier and François, 2014). No Proetida were present during the early and the middle Frasnian (Fig. 8). The Drevermanniinae (*Palpebralia*) appeared in the late Frasnian at the same time as other genera (Fig. 8), implying an increase in diversity (Fig. 2). Additionally, the low dominance and the high evenness observed during the late Frasnian suggest a balanced ecosystem for benthic trilobite faunas for this period (Fig. 4).

Unlike trilobites, ammonoids experienced a severe extinction during the Frasnian Event, both in North Africa (Fig. 7) and at the global scale (Walliser, 1996). The generic richness of the Moroccan ammonoids

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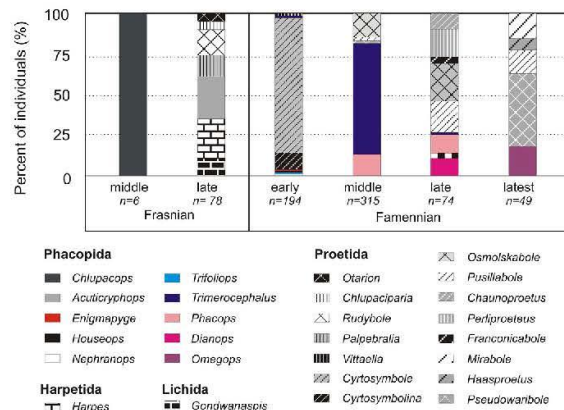


Fig. 8. Relative diversity of trilobite genera in percent of individuals, for the Late Devonian in North Africa.

shows a sharp decrease around the Givetian-Frasnian boundary, and the values stayed low throughout the Frasnian. Although the ammonoids diversity shows low values during this stage, their diversity was significantly higher than the trilobite diversity (Fig. 7A). This difference reflects a global trend. In the Frasnian deposits, the trilobites as well as the majority of the benthic faunas remain scattered, the nekitic and planktic faunas were more widespread (Wendt and Beika, 1991).

For the North African trilobites, the impact of the Late Devonian mass extinction remains elusive because the taxonomic richness is already low during the Frasnian (Fig. 2). Nevertheless, the coverage-based rarefaction and the boundary-crosser diversities show a small decrease during this event (Fig. 2). For the Moroccan ammonoids, an increasing number of extinctions was recorded and no origination has so far been reported (Fig. 7B; Allaire, 2017; unpublished PhD). However, this interval needs to be better documented to assess robust and precise conclusion concerning the impact of the Frasnian-Famennian biocrisis on the ammonoids from Morocco.

5.5. Famennian

The Famennian was punctuated by several global events (i.e., the Condruz-Enkeberg events in the early Famennian, the *annulata* event in the middle Famennian, and the Dasberg and Hangenberg events in the late Famennian), which impacted the trilobite diversity (Walliser, 1996; Lerosey-Aubril and Feist, 2012). Of the five orders present during the Frasnian (Corynexochida, Harpetida, Lichida, Phacopida, and Proetida), only the Phacopida and Proetida persisted into the Famennian (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) by surviving to the Kellwasser Event. The post-Kellwasser recovery was slow, and no trilobite was found in the first Famennian conodont zone (Lerosey-Aubril and Feist, 2012). The earliest Famennian trilobite encountered was a blind phacopid (*Nephranops*) from European offshore environments and in North Africa, the oculated phacopid (*Houseops*), earlier than the reappearance of proetids (Lerosey-Aubril and Feist, 2012). The recovery occurring during the early Famennian was due to the development of blind phacopids. At the global scale, they even have the highest origination rate (Feist, 2019). Apart from these blind phacopids, the other taxa present in the Famennian were mainly blind or small eyed, both in North Africa (Fig. 6) and at a global scale (Feist, 1991; Becker et al., 2016a); except in the Americas where no phacopid are reported (Chlupáč, 1975; Lerosey-Aubril and Feist, 2012; Crónier and François, 2014) and in the Central Asian Orogenic Belt where phacopids have well-developed eyes (Crónier et al., 2020). A new turnover occurred during the late Famennian (Crónier et al., 2013) and the late

Famennian Dasberg Event witnessed a major diversification of both phacopids and proetids at the global scale (Lerosey-Aubril and Feist, 2012). Phacopids originated and diversified in the deeper offshore environments and were mostly blind or reduced-eyed, reflecting the ultimate evolutionary step of the visual complex regression leading to blindness. On the shallow carbonate platforms, the phacopids *Omegops*, *Rabienops*, and *Phacops sensu lato* and the proetids *Pseudowaribole* and *Perliproetus*, which were oculate taxa, were widely distributed, exhibiting a high degree of cosmopolitanism (from eastern to western of the North Peri-Gondwanan margin), except in the Americas and in Australia (Lerosey-Aubril and Feist, 2012; Crônier et al., 2013; Crônier and François, 2014). The global Hangenberg Crisis which was caused by a complex pattern of palaeoenvironmental changes (Kaiser et al., 2015) seriously impacted the diversity of pelagic and hemipelagic environments (Walliser, 1996) including trilobites. The disappearance of Phacopida strongly impoverished and several genera of Proetida including all reduced-eyed and blind taxa suggests a significant eustatic lowering (Lerosey-Aubril and Feist, 2012). The reason why the widespread phacopids died out in the neritic environments whilst the associated brachymetopids managed to survive remains unexplained (Kaiser et al., 2015).

In North Africa, the very high dominance and the low evenness (Fig. 4) show that the Kellwasser Event had an impact on the trilobite community and a few opportunistic taxa such as Cyrtosymbolinae took advantage of the extinction event and became dominant during the early Famennian (Fig. 4). Thus, the post-Kellwasser recovery marked a new step for biodiversity and occurred during the middle Famennian leading to a new turnover. A relative increase in taxonomic richness is observed for trilobites, linked to increasing origination (Fig. 7). This pattern is also observed at the global scale in trilobites (Lerosey-Aubril and Feist, 2012) and largely results of the diversification of Cyrtosymbolinae fostered by the development of shallow outer-shelf in northern Gondwanan margins (Feist, 1991; Wendt, 1993). Proetida and Phacopida remained the only trilobite component in the Famennian (Fig. 5). For proetids, of the 11 genera present in North Africa, all were new and dominated by two Cyrtosymbolinae: *Cyrtosymbolina* and *Cyrtosymbola*, which represent 100% of the proetids and 95% of all the trilobites (Fig. 8). Apart from these well-developed eye proetids, other taxa present in the Famennian were mainly blind or small eyed taxa both in North Africa (Figs. 6, 8) and at a global scale (Feist, 1991; Becker et al., 2016a). For phacopids, of the eight genera present in North Africa, seven were new and dominated by the blind *Trimeroccephalus* taxa until the middle Famennian; *Trimeroccephalus* represented almost 70% of the phacopid generic diversity during the middle Famennian (Fig. 8). The development of blind and reduced-eye trilobites after the Frasnian–Famennian crisis partially explain the rise of the diversity during the Famennian. Another peak of blind trilobites occurred, after their diversity decrease in the middle Famennian. Two blind phacopid genera, i.e., *Dianops* and *Trifollops*, occurred and persisted during the late Famennian (Fig. 8). No reduced-eyed phacopid taxa has so far been encountered in North Africa (but newly sampled in the Famennian of the Saoura Valley, a work in progress). From the middle to the latest Famennian in North Africa, the reappearance of trilobites inhabiting shallow habitats (*Omegops*, *Phacops*, *Pusillabole*, *Osmolskabole*) in north-west Gondwana is coherent with the wide distribution of well-developed-eyed phacopids and proetids in contemporaneous shallow shoal environments (Lerosey-Aubril and Feist, 2012; Crônier and François, 2014). *Omegops*, a well-developed-eyed taxon replaced another well-developed-eyed taxon, i.e., ‘*Phacops*’. *Phacops* known in the Early and Middle Devonian were different from those known in the Late Devonian such as ‘*Phacops*’ *granulatus* widely distributed geographically all around the world (Crônier and François, 2014). In North Africa, this diversification initiated during the Dasberg Event (late Famennian) was followed by a decrease of the diversity which led to the lower values recorded during the latest Famennian (Fig. 2). The same pattern affected the ammonoids. Throughout the Famennian, the evenness increased and

the dominance decreased and tended to reach the late Frasnian values, symbol of a balanced community. Finally, at the Devonian–Carboniferous boundary, the rise of the sea-level trapped the deep sea trilobites and for this reason, blind taxa and/or outer shelf trilobites almost disappeared. Phacopida died out without leaving any Carboniferous descendants.

6. Conclusions

Based on a substantial compilation of published data on North African trilobites during the end of the Silurian and throughout the Devonian, the taxonomic diversity of these organisms has been accurately estimated at the genus level.

The reconstructed regional diversity follows the patterns observed at a global scale, except an important diversification in the Early Devonian (from the Lochkovian to the Emsian) in North Africa. The sharp decrease of the trilobite diversity observed through the Middle Devonian at a global scale, occurred earlier in North Africa (Eifelian) than in other localities where this important decrease was generally recorded during the Givetian. In North Africa, the diversity remained very low in the Givetian and the early Frasnian before a slight increase in the late Frasnian. Then, the well-known Kellwasser Event (one of the big five mass extinction) at the Frasnian–Famennian boundary also affected the North African trilobites with a decrease in diversity which is associated to an increasing number of extinctions. Only two orders crossed this limit: Phacopida and Proetida. Then, the trilobites recovered in the early Famennian thanks to the development of opportunistic taxa. This recovery was accompanied by morphological and habits changes. Indeed, a high fraction of blind, reduced eyes and/or deep-water trilobite genera proliferated after the Kellwasser Crisis. Afterward, another increase of diversity occurred in the late Famennian, then, the diversity decreased again, at the end of the Devonian. This decrease in diversity is followed by the occurrence of the Hangenberg Event, which led to the disappearance of the Phacopida. All these diversity fluctuations through the Devonian seems to reflect the rapid reaction of trilobites facing abrupt sea level changes and hypoxic/anoxic events. This review concerning a famous region for its trilobites highlights a lack of data for the Lochkovian, Givetian and Frasnian stages, for which more studies will help to better estimate the regional diversity of North African trilobites.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.110208>.

Declaration of Competing Interest

For our manuscript entitled “Trilobite biodiversity trends in the Devonian of North Africa” by Bault, Allaire, Monnet and myself that we wish to submit for publication in the Palaeogeography, Palaeoclimatology, Palaeoecology, there is no conflict of interest.

Acknowledgments

The authors thank the reviewers A. van Viersen (Netherlands), B. Pratt (Canada) and A. Bignon (Argentina) and the editor for their valuable and constructive comments improving the original manuscript. This work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic timescale’, to the ECOS Sud-MINCYT (Argentina) A17A01, and to the French CNRS UMR 8198 Evo-Eco-Paleo. The authors thank the Région Hauts-de-France, and the Ministère de l’Enseignement Supérieur et de la Recherche (CPER Climibio) for their financial support.

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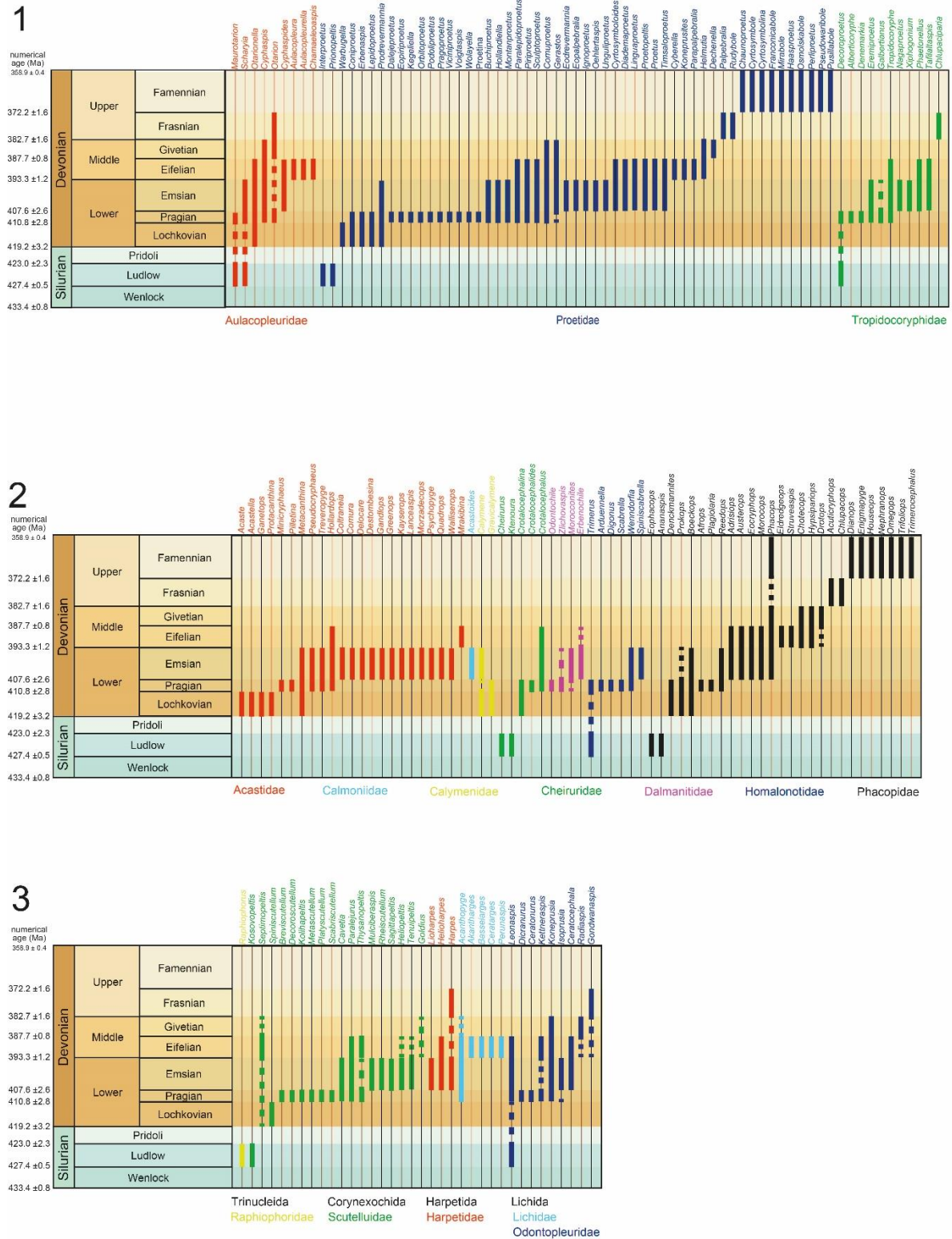


Figure B. Synthetic occurrence range chart; genera are ordered by family. (1) Proetida. (2) Phacopida. (3) Other orders.

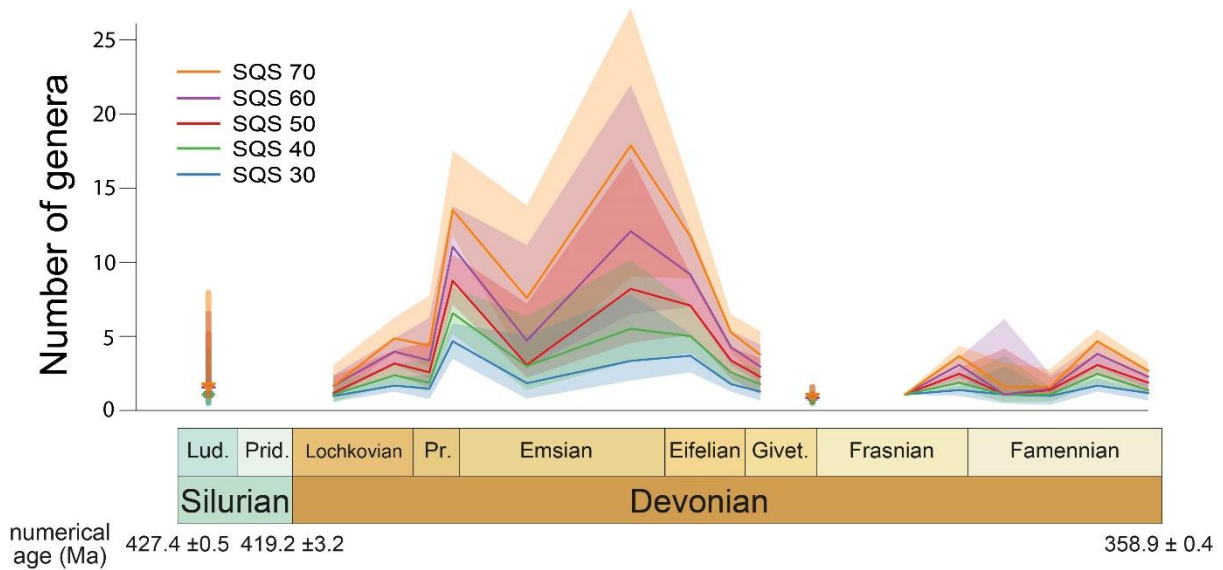


Figure C. Fluctuations of the Shareholder Quorum Subsampling (SQS) diversity of trilobites from North Africa during the Silurian and the Devonian, computed at the generic level (estimations for quorums of 30, 40, 50, 60 and 70). See text for the definition of indices. Ages from *Cohen et al. (2013, updated)*.

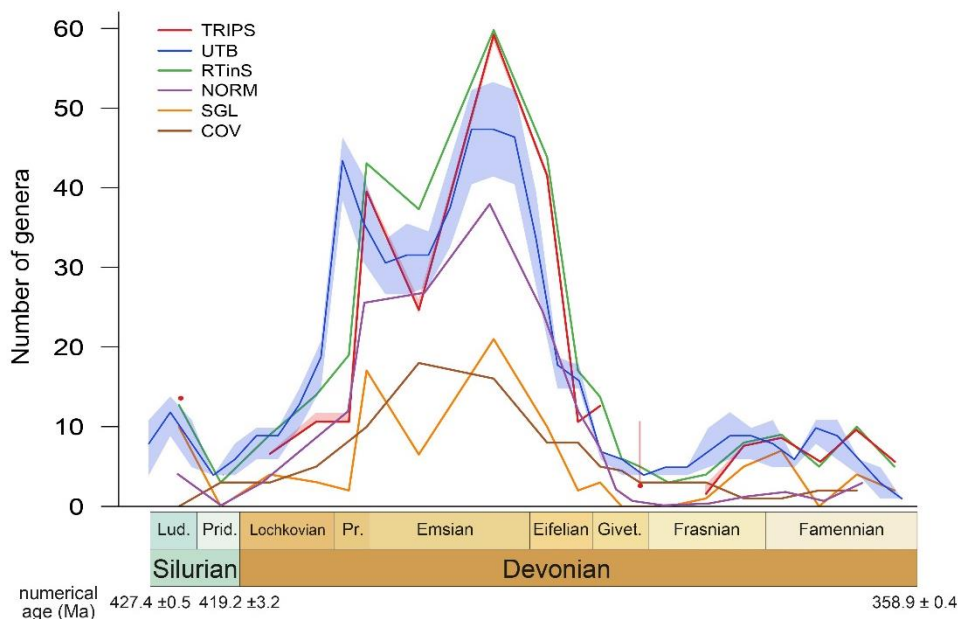


Figure D. Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Poisson-based resampling diversity (TRiPS), computes the approach of ‘true richness estimation using Poisson sampling’ based on an abundance range chart and a time; Uniform time bin diversity (UTB), quantifies the length of uniform time bins to reconstruct time series by using the mean time interval duration; Range-through diversity including single-interval taxa (RTinS; aka. total diversity), estimates the diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Normalized diversity (NORM), corresponds to the number of taxa ranging from the interval below to the interval above, plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself; Single-interval diversity (SGL), corresponds to the number of single-interval taxa known from only one bin; Crossover diversity (COV), counts the number of taxa known before and after the considered stratigraphic interval. Ages from *Cohen et al. (2013, updated)*.

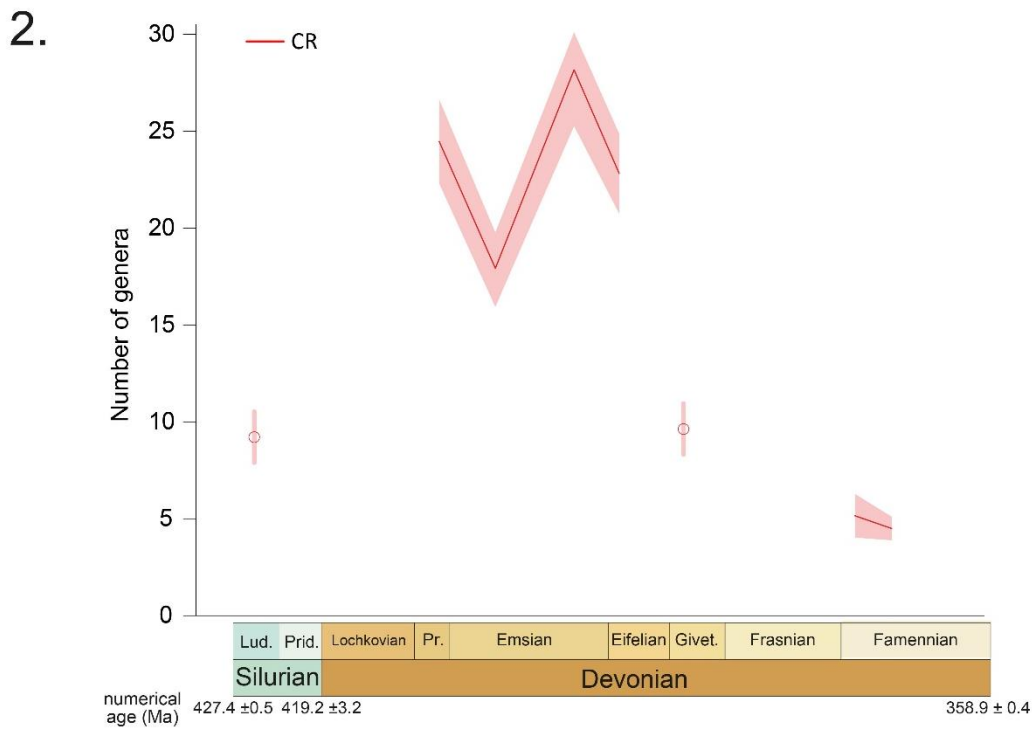
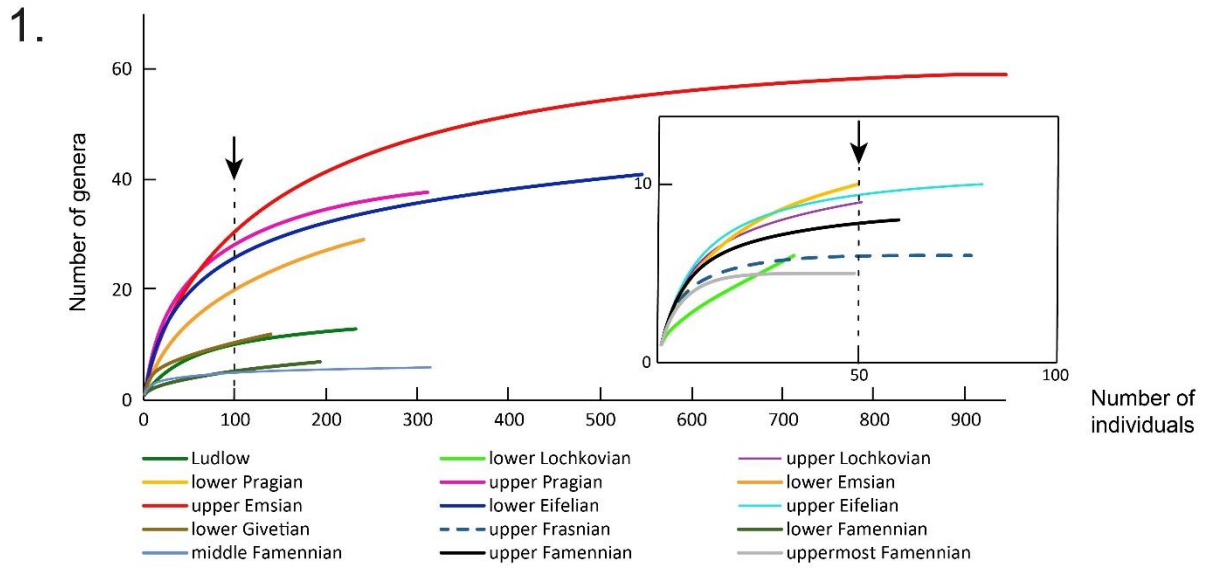


Figure E. Rarefaction methods. (1) Rarefaction curves per substages. Arrows indicate the comparative individual number for substages of same size (50 or 100). (2) Size-based rarefaction (CR). Ages from *Cohen et al. (2013, updated)*.

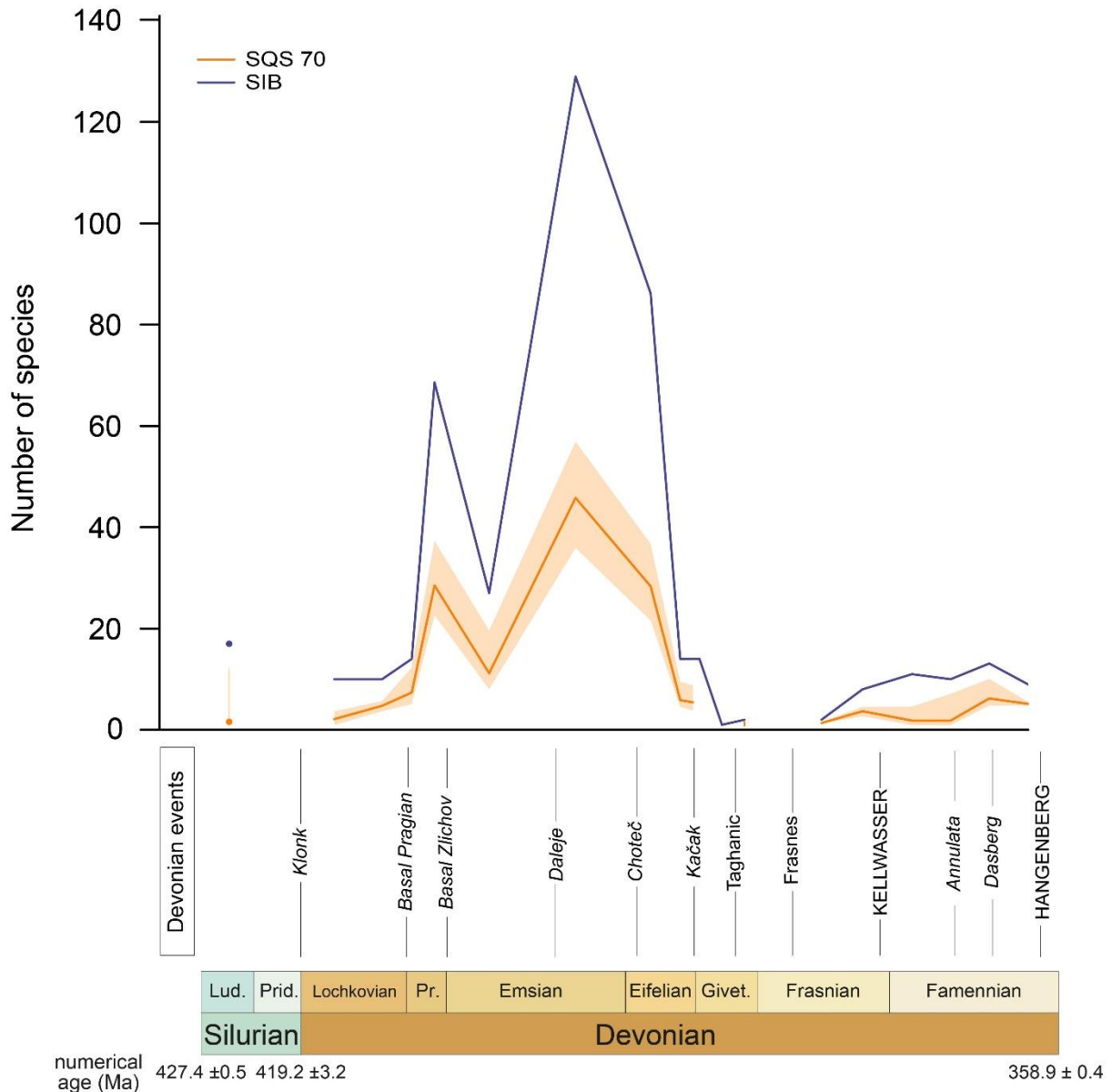


Figure F. Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the specific level per substages. Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Normalized diversity (NORM), number of taxa ranging from the interval below to the interval above, plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself. Stratigraphic position of the extinction events according to [Becker et al. \(2016b\)](#); first-order events in capital, second-order events in bold and third-order events in italic. Ages from [Cohen et al. \(2013, updated\)](#).

2.2. Tendances de la disparité morphologique des trilobites du Dévonien d'Afrique du Nord

Article 4 : Morphological disparity trends of Devonian trilobites from North Africa

Article accepté avec revisions par Palaeontology

MORPHOLOGICAL DISPARITY TRENDS OF DEVONIAN TRILOBITES FROM NORTH AFRICA

by VALENTIN BAULT^{1*}, CATHERINE CRÔNIER¹, *and* CLAUDE MONNET¹

¹Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France; valentin.bault@univ-lille.fr, catherine.cronier@univ-lille.fr, claude.monnet@univ-lille.fr

* Corresponding author

ORCID:

Valentin Bault <https://orcid.org/0000-0002-9225-5195>

Catherine Crônier <http://orcid.org/0000-0002-7606-0822>

Claude Monnet <http://orcid.org/0000-0002-0899-8392>

Abstract:

The Devonian was a time of drastic environmental changes that shaped the morphology of trilobites. This study aims to investigate their morphological evolution and to show the influence of some abiotic and biotic factors (bathymetry, feeding habits and visual abilities) on their shape. A dataset was compiled to investigate the shape of three structures (cephalon as a whole, cranidium and pygidium) of Devonian trilobites from North Africa, using a geometric morphometric approach. Based on empirical morphospaces, the morphological changes were quantified through the Devonian stages. The results reveal significant variation in the morphological disparity of the glabella shape, the facial suture location, the pygidial length and the presence of spines. In the Lochkovian, morphological disparity was low, but it subsequently increased in the Pragian with numerous innovations, and reached a maximum in the Emsian. If the morphospace occupancy persisted until the Eifelian, a severe loss of disparity occurred in the Givetian, a time known for important environmental changes. Disparity then remained low in the Late Devonian. The shapes inherited from the Silurian persisted throughout the Devonian whereas Pragian novelties were most affected by morphological losses. These persistent shapes were more versatile for environmental adaptation, helping those trilobites to survive environmental events. Similarly, the trilobite orders that survived Devonian events had a wide morphological spectrum and were better adapted to withstand environmental change.

Key words: Trilobites, North Africa, Devonian, Morphological disparity, Morphometrics, Evolution, environmental changes

INTRODUCTION

Appearing as early as the Cambrian Explosion, trilobites diversified quickly to reach their maximum diversity at the end of the Cambrian (Westrop & Aldrain 1998) and then underwent an irregular decline until the end of the Permian (Sepkoski & Sheehan 1983; Foote 1993; Fan *et al.* 2020). Especially, the Devonian marked an important step of this decline. Despite an important diversity increase in the Early Devonian, a protracted decrease at all taxonomic ranks (family, genus, species) occurred during the Middle Devonian up to the disappearance of three of the five orders (i.e., Odontopleurida, Harpetida and Corynexochida using Adrain (2011) classification updated by Lamsdell & Selden (2015) concerning the superfamily Aulacopleuroidea) in the Late Devonian during the Kellwasser events (Feist 1991; Chlupáč 1994; Crônier & vanViersen 2007; Lerosey-Aubril & Feist 2012; Bault *et al.* 2021). In addition

to these diversity losses, the visual abilities and the life environments were modified in trilobites, and especially after the Frasnian/Famennian boundary (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Therefore, the Devonian is a critical period in the evolutionary history of trilobites. This interval of time is also well known to record major biotic and abiotic changes, such as the Devonian Nekton Revolution (Klug *et al.* 2010), the development of vascular land plants (Pawlik *et al.* 2020), exceptional sea-level highstands, widespread epicontinental shallow seas, greenhouse climates (Tinn *et al.* 2020) and several anoxic/hypoxic events and rapid sea level fluctuations (House 2002; Becker *et al.* 2016).

Another important morphological indicator of evolutionary success or failure is disparity, as measured by the occupancy of a morphospace (Foote 1997; Wills 2001; Erwin 2007, Minelli 2016, Guillerme *et al.* 2020). Success in diversity does not necessarily go together with success in disparity. Many taxa show high diversity with low disparity, while others are highly diverse but also exhibit high disparity (Minelli 2016). Taxonomic richness and morphological disparity are two complementary metrics, which can be decoupled (Foote 1991a, 1991b, 1993). Such decoupled changes in taxonomic diversity and morphological disparity can suggest different proxies for understanding the ecological effect of an extinction event for example (Wan *et al.* 2021). Morphological disparity of trilobites has been extensively documented in the Cambrian and the Ordovician (Foote 1991a; Smith & Lieberman 1999; Webster 2007; Hopkins 2013; Jacobs & Carlucci 2019). On the contrary, Devonian studies are rare and often dedicated to developmental and ontogenetic topics exploring the intrinsic factors of morphological changes (e.g. Crônier *et al.* 1998; Crônier 2013; Oudot *et al.* 2019). However, if biotic and abiotic factors are known to contribute to diversification, they also contributed to the morphological disparity (Crônier *et al.* 2004; Hopkins & Gerber 2017). Some relationships have been noticed or demonstrated between trilobite shapes and ecological affinities such as bathymetric conditions (Hopkins 2014), feeding habits (Fortey & Owens 1999) or life habits (Fortey 2014). Although the environmental influence on morphological disparity was rarely evaluated, Hopkins (2014) emphasized the effect of bathymetry, substrate and latitude on the trilobite shape for the entire Palaeozoic. As the result of these environmental effects, morphological disparity can be dependant of the geographical location of populations through time (Hopkins & Webster 2009; Abe & Liebermann 2012; Esteve *et al.* 2017). These recent studies have been done at the global or focusing on only one family. Nevertheless, for Devonian trilobites, no studies have been performed on the total richness available throughout a span time for a relatively well-constrained area.

During the Devonian, the environmental and ecological changes were particularly well exhibited in North Africa wherein trilobites were especially well represented and diverse (Lebrun 2018; Bault *et al.* 2021). This area is one of the richest in terms of Devonian trilobites with five orders and 15 families (Bault *et al.* 2021), corresponding to all known worldwide Devonian orders and the majority of families (Crônier & van Viersen 2007). In addition to its fossil record, this area is also particularly well known for its stratigraphy and its palaeoenvironmental context (Massa 1965; Hollard 1967; Wendt & Belka 1991; Becker *et al.* 2004; Abbache *et al.* 2019; among others). It allows establishing the relationship between the trilobites characterized by their shape and their habits and their palaeoenvironmental affinities. Moreover, the Devonian events were all spotted in this area (Kaufmann 1998).

In the context of a period of diversity changes (Bault *et al.* 2021), analysing the morphological changes through time for a relatively well-constrained area, helps to better understand the impact of the Devonian biological events on benthic faunas. We focused our investigations on the Devonian trilobites gathered from the North African area. To understand the fluctuations in time and space, the disparity patterns are assessed through morphological space in a stratigraphic and palaeoenvironmental framework. First, we investigated the evolution of the trilobite morphospace to identify the different morphotypes and to explore the presence of evolutionary key innovations in lineages for each stage. Then, we investigated how the morphological shape may be linked to different palaeoenvironmental and/or palaeoecological factors (such as bathymetry, feeding habits and visual ability) and detecting which factors contribute most to the observed patterns.

MATERIAL AND METHODS

Trilobite data and frameworks

We compiled a dataset to investigate the morphology of Silurian and Devonian trilobites from Morocco and Algeria (Fig. 1). This area was situated on the continental margin of the Gondwana at a latitude between 30° and 45°S (Scotese & Golonka 1992; Golonka 2002). It was a favourable place for the settlement of benthic communities such as trilobites (Morzadec 2001; McKellar & Chatterton 2009). All figures of specimens illustrated over the last 80 years with a sufficient quality have been exploited for shape analyses (Appendix S1). Morphology of trilobites is here quantified by focusing on their most important structures, i.e., cephalon, cranidia and pygidia (Fig. 2). The cranidium is a subset of the cephalon, which is actually composed by

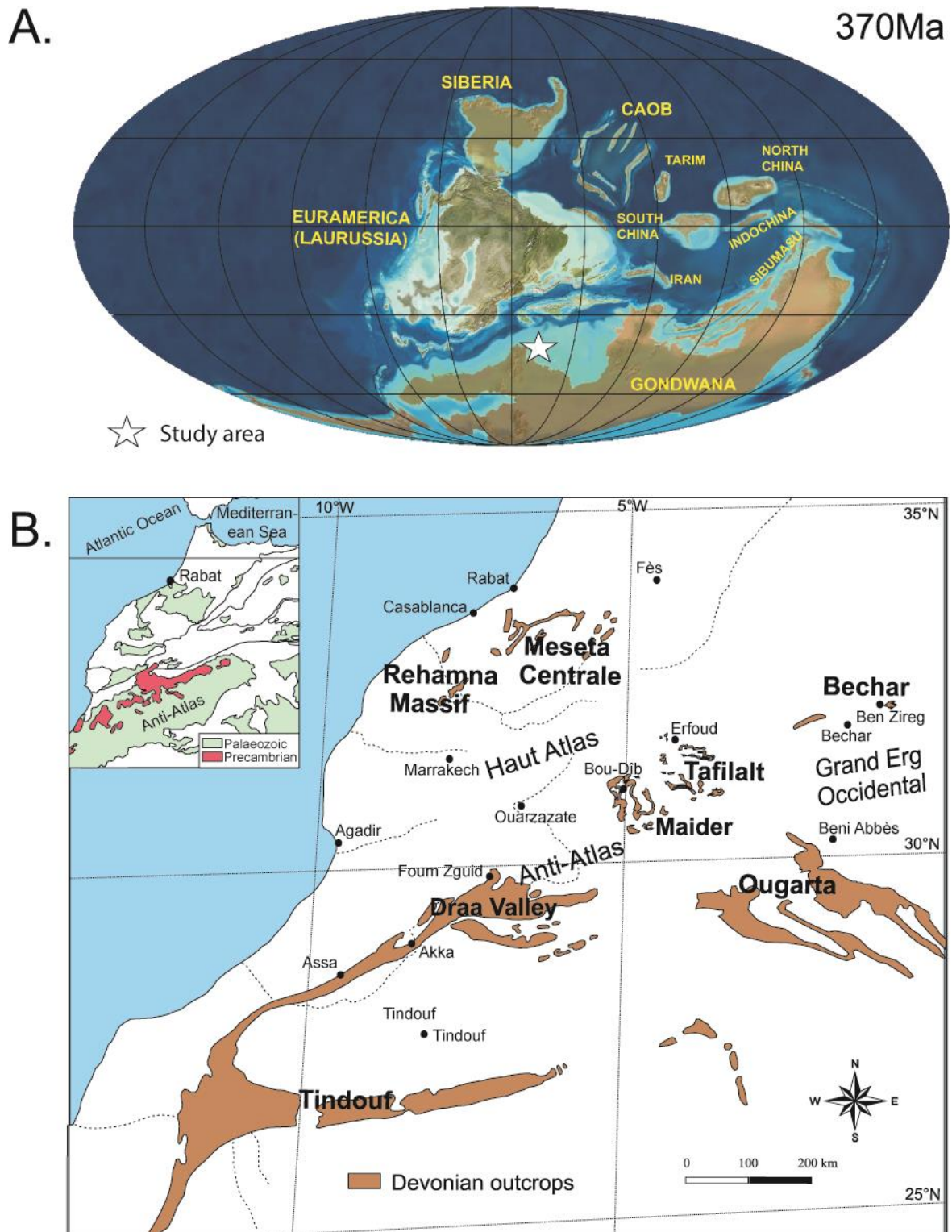


Figure 1. (A) Location of Morocco and Algeria (white star) on a palinspastic map (modified from Blakey (2016), with continent positions and shapes for the Upper Devonian modified from the tectonic data of Hara *et al.* (2010), Metcalfe (2011), and Xiao *et al.* (2010)). (B) Geographical location of studied area with the Devonian outcrops (in bold; modified from Hollard 1968).

two modules: the cranidium (fixigena) and the free cheeks (librigena). For morphological analyses the cephalon is studied as a whole, including the cranidium landmarks.

A first dataset contains 328 complete cephalon, 959 complete cranidia and 605 complete pygidia; each structure being studied independently. This dataset includes all well-preserved and illustrated specimens during the last 80 years from 65 publications (Appendix S2). Only dorsal views were used and the right-side from each structure was selected except if the left-side was more completed; mirror images were used to correspond to the right side. A second dataset contains 30 complete specimens of 30 different species for which both the cephalon and the pygidium were simultaneously preserved.

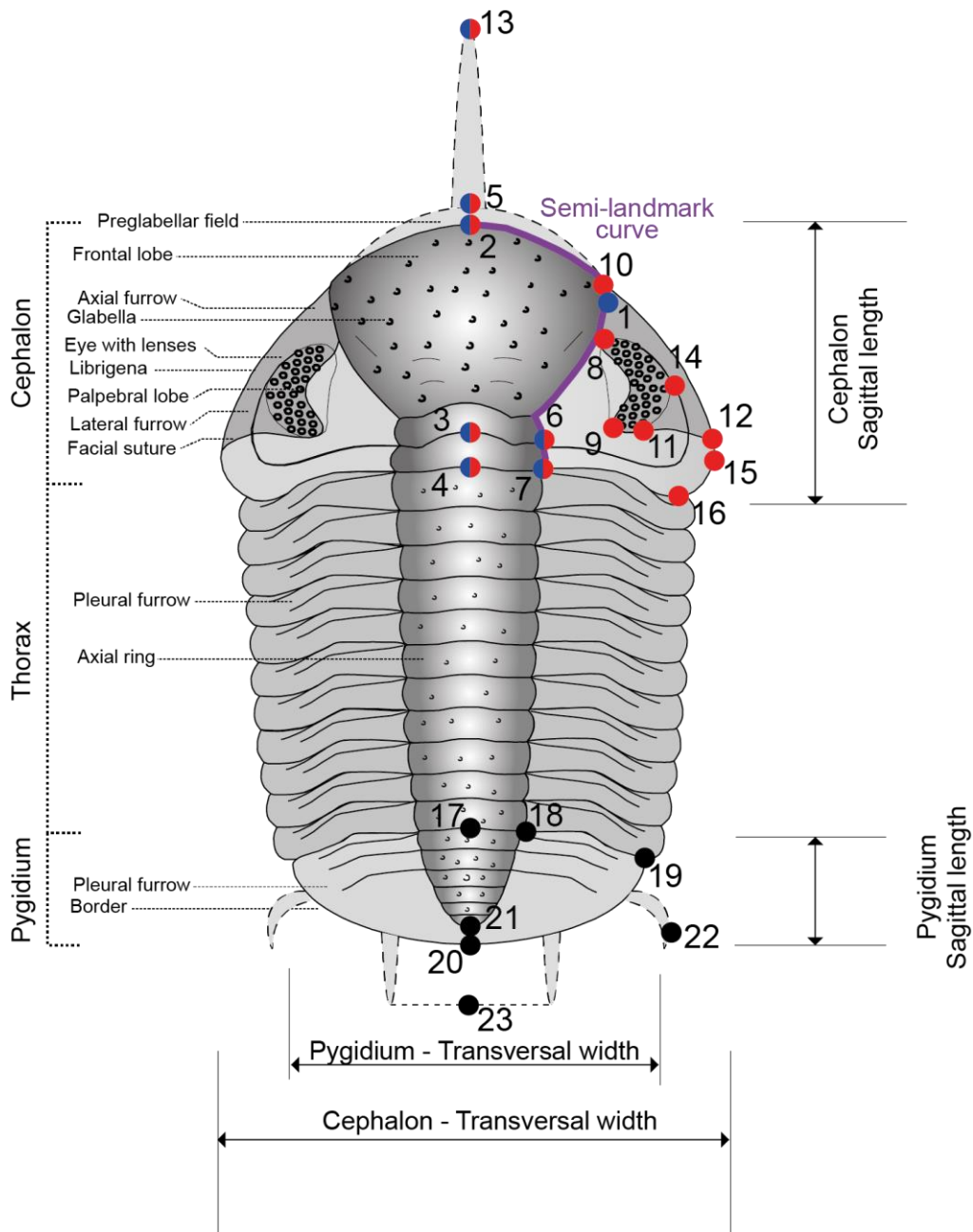


Figure 2. Complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight landmarks for cephalon (in red), plus eight for cranidium (in blue), and seven for pygidium; and some linear measurements. Modified from Crônier (2013).

For each specimen, taxonomy, age (stage) as well as ecological characteristics were also included in the dataset. Firstly, genera were classified by environmental affinities, i.e., by water depth conditions (Fortey 1975; Turvey 2005; Crônier & vanViersen 2007). Bathymetrical affinity for each genus was determined as the environment where it mainly occurred. Because these data were not available for each occurrence, we interpolated it with the data from other papers with the same stratigraphic context or from genera with the same affinity. Four categories are identified along the bathymetric profile: (1) the shoreface environment characterized by shallow and proximal conditions; (2) the upper offshore or inner shelf environment characterized by relatively shallow waters; (3) the median offshore or middle shelf environment characterized by relatively deep deposits; and (4) the lower offshore or outer shelf environment located below effective storm wave base. It is important to note that depth categories were based on sedimentological evidence and not from trilobite shapes to avoid analysis biases.

Secondly, genera were classified by their diet. We referred to Fortey and Owens (1999) to determine the feeding habits of genera based on hypostome features. Three diet categories are recognized in our database: ‘Predator/Scavenger’, which ingested small prey, ‘Particle feeding’, which fed on nutrients and ‘Filter chamber’, which brought sedimentary material into suspension before selecting out edible particles (Fortey & Owens 1999). It should be noted that the estimates of feeding habits are only assumptions and the evidence in the fossil record is rare. For instance, only two examples confirmed as particle feeders are known (Zhu *et al.* 2014; Gutiérrez-Marco *et al.* 2017). Feeding habits are still an ongoing debate and advances in biomechanics (Bicknell *et al.* 2018, 2021) will help refine the trilobite diets.

Third, genera were classified by their eyes, preserved as calcite lenses on a visual surface (Clarkson *et al.* 2006). Each taxon has been assigned to one of the three categories: blind, reduced-eye, or well-developed-eye. The diagnostic features related to the eye size or to the number of lenses were considered to establish these categories. In trilobites, the visual ability has often been linked to environment or life habits (Clarkson 1967; Feist 1991). For this last analysis, blind cephalae were not considered because of the lack of three landmarks (i.e., landmarks 8, 9 and 14; Fig. 2).

Landmark data

The 2D shape of studied trilobites is here quantified by a geometric morphometric approach, which is now a standard set of techniques for quantifying shape independently of size by using homologous points (landmarks) on the surface of a series of objects (Bookstein 1991; Rohlf &

Marcus 1993; Rohlf 1999; Adams *et al.* 2004, 2013; Mitteroecker & Gunz 2009; Zelditch *et al.* 2012). This method preserves the geometry of the landmark configurations throughout the analysis and thus permits representation of analytical results as actual shapes or forms. It is routinely used in biological and palaeontological studies.

The shape of cephalia is here described by a set of 15 landmarks and one curve of 24 equally spaced semilandmarks between landmark 2 and landmark 7 (Fig. 2, Table 1). For cranidia (i.e., cephalia without free cheeks), seven landmarks plus the semi-landmark curve have been digitized (Fig. 2, Table 1). Similarly, seven landmarks were digitized for pygidia (Fig. 2, Table 1). Landmarks were positioned in key locations to summarize the complexity of morphologies. The semi-landmarks were used as landmarks and were not transformed into a curve. Specimens with missing landmarks were excluded. The *x*- and *y*- coordinates of 2D landmarks and semilandmarks were digitized (Fig. 2) with TPSdig 2.32 (Rohlf 2010, 2015). The landmark 2D coordinates were then exported in the standard TPS file format (Rohlf 2012).

Structure	Landmark	Definition
Cranidium only	1	Maximum transversal glabellar width
Cephalon (including cranidium)	2	Anterior most point of sagitta cephalic length without spine
	3	Anterior most point of sagittal glabellar length
	4	Intersection between sagittal axis and occipital furrow
	5	Posterior most point of sagittal cephalic length
	6	Intersection between occipital furrow and dorsal furrow
	7	Intersection between posterior border and dorsal furrow
	8	Anterior most end of eye
	9	Posterior most end of eye
	10	Intersection between anterior facial suture and anterior lateral border
	11	Intersection between posterior branch of facial suture and posterior or lateral border furrow
	12	Intersection between posterior branch of facial suture and posterior or lateral border
	13	Anterior most point of sagittal (or ex -sagittal) cephalic length with spine
	14	Lateral external most point of eye
	15	Maximum transversal cephalic width
	16	Extremity of genal angle or spine
Pygidium	17	Anterior most point of sagittal pygidial length
	18	Intersection between anterior pygidial border and dorsal
	19	Maximum transversal pygidial width without spines
	20	Posterior most point of sagittal pygidial length without spines
	21	Posterior most point of sagittal pygidial axis length
	22	Maximum transversal pygidial width with or without spines
	23	Posterior most point of sagittal or ex-sagittal pygidial length (with spines)

Table 1. Description of landmarks.

Because we analysed specimens from different lineages, shapes can be different with extreme landmark locations and thus, geometric morphometric methods could not be applied (Zelditch *et al.* 2012). In our case this issue concerns only the cephalo where landmarks 10, 11 and 12 can exhibit topological changes compared to relative position to other landmarks (Fig. 2, Table 1). The Pinocchio effect (Chapman 1990; Thulman 2019) can also affect landmarks 13 and 16 (Fig. 2, Table 1). In order to assess the impact of these issues, we removed them to see if the morphospace is affected by these *biases* or not. We also performed a correlation circle of landmarks to identify if some of them strongly affected the morphospace, emphasizing a topological issue rather than a morphological pattern. Our morphospaces are not determined by topological issues or a Pinocchio effect: the potential problematic landmarks (11, 12, 13, and 16) due to their extreme location among individuals did not influence the morphospace more than the other landmarks (Fig. S1).

Shape analyses

Standardization of the landmark data (superimposition) to remove variability due to differences of size, placement, and orientation was performed by means of a generalized Procrustes analysis (GPA), which minimizes the sum of square distances between equivalent landmarks (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O’Higgins 2000; Zelditch *et al.* 2012). The superimposed landmarks are projected to a linear tangent space at the full Procrustes mean (Rohlf 1999; Kendall 1984).

For each of the three studied structures (i.e., cephalo, cranidia and pygidia), we performed a principal components analysis (PCA; Ringnér 2008; Abdi & Williams 2010) to reduce the high-dimensionality of the superimposed landmarks to fewer variables (eigenvectors), along which the shape variation is maximal. Each specimen can be represented by relatively few variables and can be plotted in a PCA-space (morphospace) defined by principal component axes (PCs), which are ordered by decreasing percentage of the total shape variance. The morphospace is centred on the average shape (consensus) and where each point represents a specimen shape and its position reflects the relative shape similarities and differences between specimens. Finally, among the studied specimens, series of virtual shapes were reconstructed by doing a back transformation from the PC scores for PC1 and PC2 to illustrate the largest shape changes over the morphospace. Shape analyses have been computed with the R scientific environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>) and the packages ‘geomorph’ (v. 3.2.1; Adams & Otárola-Castillo 2013) and ‘epaleo’ (v. 0.8.41; Monnet, unpub.), as well as the software PAST (version 3.24; Hammer *et al.* 2001). Figures from R outputs.

To identify some morphological clusters or morphotypes (Fig. S2), we performed a Hierarchical Cluster Analysis (HCA) with the package ‘epaleo’ on the Principal Component scores by using the Euclidean distance measure and Ward’s linkage algorithm. See [Everitt *et al.* \(2011\)](#) or [Murtagh & Contreras \(2012\)](#) for more details on methods.

Morphospace analyses

Morphospaces were established for the complete data set of all specimens independently for cephalia, cranidia and pygidia. They were explored to evaluate the morphospace occupation first by the previously defined morphotypes, and then by the orders (using [Adrain \(2011\)](#) classification updated by [Lamsdell & Selden \(2015\)](#) concerning Proetida). Moreover, to investigate trilobite shape changes through time, individuals for each structure were categorized by stages on their respective morphospace. This allows visualizing how the different groups are distributed in the morphospace, to identify which morphotypes or orders are impacted by morphological changes and how, and to identify key morphologies among trilobites for a given stage for a successful diversification or disappearance.

Additionally, the morphospace was explored according to the inference of the potential influence on morphospace variation of three different factors related to life modes known to be changing with Devonian events: bathymetry, feeding habits and visual ability ([Chlupáč 1994](#); [Lerosey-Aubril & Feist 2012](#)). Effect of eye reduction was investigated for all the structures, including those without eyes (i.e. cranidium and pygidium). This analysis was done by mapping each factor of each individual onto the morphospace. We computed a one-side nonparametric, permutational ANOVA on the PC axes to test statistically if a shape difference exists according to these three palaeoenvironmental and palaeoecological different factors (i.e., bathymetry, feeding habits and visual ability). Procrustes ANOVA with permutation procedures are performed using the Wilks’lambda test to quantify the amount of shape variation allocated to factors in a linear model and to estimate the probability of this variation for a null model ([Collyer & Adams 2018](#)). Statistical analyses based on PCA axes are advocated instead of original Procrustes coordinates because the scores of each axis are uncorrelated and the number of dimensions corresponds to the degree of freedom ([Rohlf 1993](#); [Polly 2017](#)). Then, to assess how the shape is distributed according to these factors, we highlighted the different categories of our factors on PCA. Morphospace analyses have been also computed with R 3.6.2 and PAST 3.24.

RESULTS

Global morphological space

For cephalata, the PCA yields 78 principal components (PCs), five of which explained 84.2% of the variance in shape of the studied trilobites: PC1, 48.7%; PC2, 15.2%; PC3, 11.6%; PC4, 4.6%; and PC5, 4.1%. The remaining components accounted for less than 4% each. The morphological interpretation of the shape changes associated with PC1 and PC2 is depicted by overlying reconstructed shapes at various locations of the morphospace (Fig. 3A). PC1 depicts the presence or absence of genal spines and a sagittal spine, the shape change of the glabella and the postero-lateral position (i.e., opistoparian, proparian or gonatoparian; Fig. 2) of the facial suture. Negative scores of PC1 show the presence of long genal or sagittal spines, a wide transversal (tr.) glabella at its base and an opistoparian facial suture with its terminal end to the posterior border (Fig. 3A). At the opposite, positive scores of PC1 show cephalata without spines, a wide (tr.) glabella at the frontal lobe and a proparian facial suture with its terminal end to the lateral border. PC2 depicts the presence or absence of spines and the postero-lateral position of the facial suture too (Fig. 3A). However, the main shape change seems to be depicted by the shape of the occipital ring. High scores of PC2 show a wide (tr.) occipital ring, while low scores of PC2 show a narrow (tr.) occipital ring. PC3 contrasts two different morphologies with spines (Fig. S3A). Negative scores of PC3 show a long sagittal spine without a genal spine, while positive scores of PC3 show genal spines without a sagittal spine. Finally, positive scores of PC4 indicate a narrow (tr.) librigena, while negative scores show a wide (tr.) librigena.

The set of individuals are grouped into five morphotypes, along the first two principal component axes, with only few individuals between them (Fig. S2A, Fig. 3A). HCA shows five main morphologies corresponding to five main morphotypes (Fig. S2). The most common shapes are depicted by positive PC1 and null PC2 scores (Fig. 3A). These shapes assigned to Morphotype 1 (MCp1) correspond to cephalata without sagittal and genal spines, with a wide frontal lobe (tr.) and a proparian facial suture (Fig. 3A). MCp1 spread to similar glabellar shape and facial suture position but with presence of genal spines, i.e., MCp3, and of a sagittal spine, i.e., MCp2, depicted by negative PC1 and PC2 scores. Other morphologies are depicted by slightly positive PC1 and PC2 scores (i.e., MCp5) to negative PC1 and positive PC2 scores (i.e., MCp4). These two morphotypes 4 and 5 correspond to cephalata with a proparian or opistoparian facial suture, with a frontal lobe narrower (tr.) than in the other morphotypes, such as the basal part of the glabella is wider (tr.). The main difference between MCp4 and MCp5 is

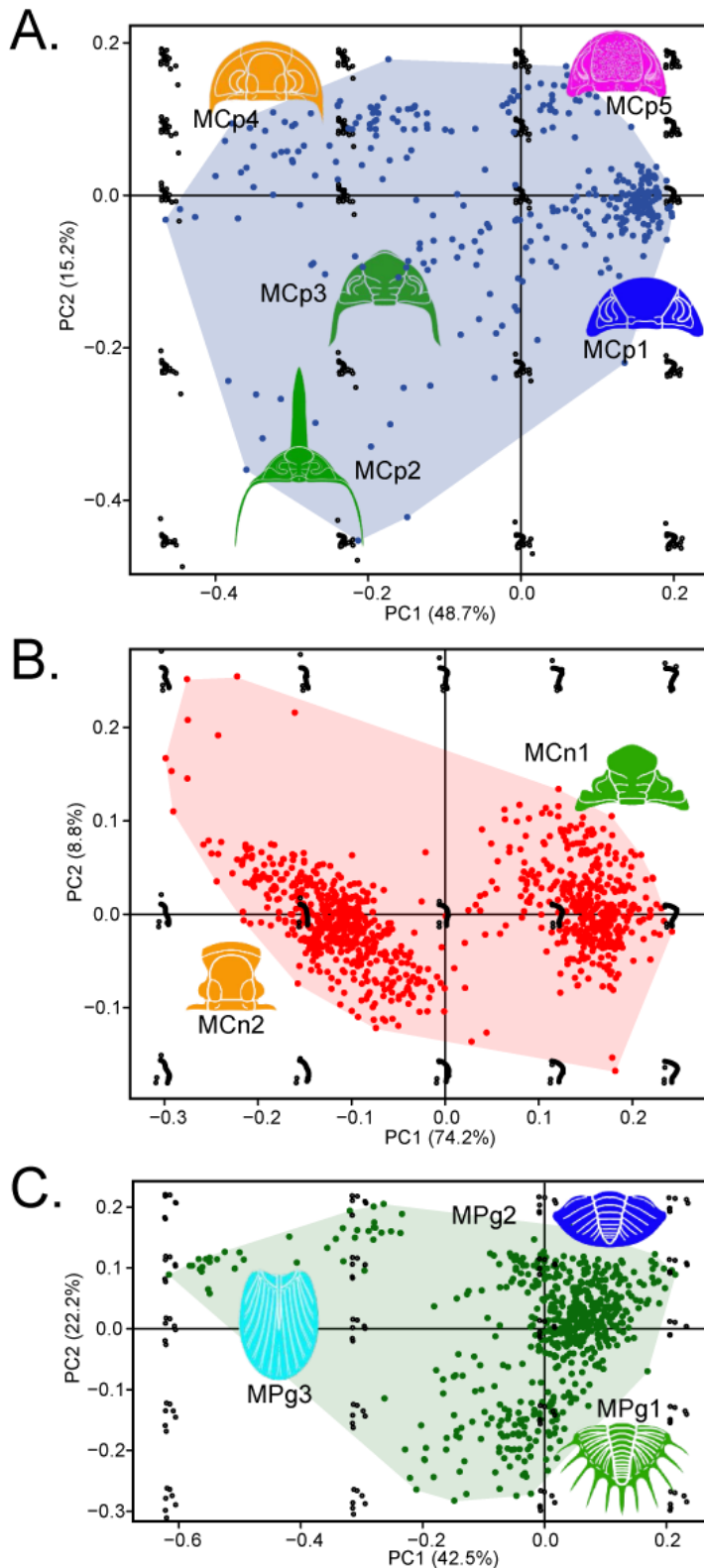


Figure 3. Location of: A, 328 cephalons; B, 959 cranidia; and C, 605 pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals. Black dots represent the reconstructed virtual shape, see Fig. S8 for more details. Coloured representative morphotypes are displayed.

the presence of genal spines in MCp4. For all types of glabella (i.e., wide or narrow frontal lobe (tr.), MCp1 and MCp5), cephalons can exhibit spines but it requires narrower (tr.) glabellar furrows without an inflated frontal lobe (Morphotypes 2, 3 and 4).

For cranidia, the PCA yields 62 PCs, two of which explained 83% of the variance in shape of the studied trilobites: PC1, 74.2%; PC2, 8.8%. The remaining components accounted for less

than 6% each. PC1 depicts the variation in glabellar shape. Positive PC1 scores depict individuals with a wide (tr.) frontal lobe compared to the glabellar base and without a preglabellar field anteriorly (Fig. 3B). Negative PC1 scores depict individuals with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B). Rare intermediate shapes show a frontal lobe just slightly wider (tr.) than the glabellar base. Shapes with very narrow (tr.) or very wide (tr.) occipital and preoccipital rings do not exist. PC2 depicts the presence or absence of a preglabellar field and the width (tr.) of glabellar lobes.

The set of individuals are grouped into two morphotypes (MCn1 and MCn2; Fig. S2B), mainly along the first principal component axis PC1 (Fig. 3B). Positive PC1 and null PC2 scores depict a common shape (Fig. 3B). This shape assigned to MCn1 corresponds to cranidia with a wide (tr.) frontal lobe compared to the glabellar base and without a preglabellar field anteriorly (Fig. 3B). Negative PC1 and null PC2 scores depict another common shape (Fig. 3B). This shape assigned to MCn2 corresponds to cranidia with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B).

For pygidia, the PCA yields 14 PCs, four of which explained 89.9% of the variance in shape of the studied trilobites: PC1, 42.5%; PC2, 22.2%; PC3, 14.2%, and PC4, 11.0%. The remaining components accounted for less than 5% each. PC1 (Fig. 3C) shows that the main shape change contrasts narrow (tr.) pygidia (negative scores) to wide (tr.) pygidia (positive scores). PC2 depicts the sagittal (sag.) length of the pygidial axis, PC3 depicts the presence of lateral and sagittal spines and PC4 depicts the curve of the pygidial border (Fig. S3B). Along PC3 and PC4, most of the shapes show individuals with no spines. Only a few individuals located in the negative PC3 scores have small pygidial spines. These pygidial spines are generally short and never longer (sag.) than the pygidium itself. Positive scores on PC4 indicate a maximal (tr.) length below the anterior most point of sagittal pygidial length and conversely negative scores indicate a maximal (tr.) length above the anterior most point of sagittal pygidial length (Fig. S3B). No pygidia are present in the area of the morphospace that depicts pygidia with a very narrow (tr.) and a long (sag.) pygidial axis (i.e., negative PC1 and PC2 scores).

The set of individuals are grouped into three morphotypes (Fig. S2C). The most common shapes assigned to MPg1 and MPg2 are depicted by rather null scores of PC1 (Fig. 3C). These shapes correspond to pygidia with a medium size and with either a long (i.e., MPg1) or a medium length of the pygidial axis (i.e., MPg2). MPg3 is depicted by negative PC1 and positive PC2 scores (Fig. 3C). The shapes associated with this cluster correspond to pygidia with a narrow (tr.) and a short (sag.) axis (i.e., MPg3).

Morphospace occupation by time

The changes in occupancy/filling of the morphospaces (i.e., the morphological disparity) through time are illustrated in figure 4 for the three structures. For cephalata, the morphological space was characterized by a reduced occupation from the Ludlow to the Lochkovian, followed by widespread occupation in the second part of the Early Devonian. During the Ludlow, the filling of morphological space was narrow (Fig. 4A) and was restricted to MCp1 and MCp5. The location of morphotypes through time is given in figure S4A. Then, morphological disparity remained reduced in the Lochkovian and restricted to only one cephalon assigned to a new morphotype (i.e., MCp4) in the early Lochkovian and three cephalata to MCp1 in the late Lochkovian. After this low disparity period, the disparity in the Pragian covered almost all the morphospace, with the only exception of some cephalata with sagittal spines i.e., MCp2 (Fig. 4A, Fig. S4A). This morphology appeared during the Emsian when the morphospace reached its maximal coverage.

The transition to the Middle Devonian (Fig. 4A, Fig. S4A) did not coincide with an important loss of morphological disparity for the cranidium and the pygidium but the cephalon was more affected with the disappearance of MCp2. Only cephalata characterized by low PC2 scores disappeared. These cephalata exhibit sagittal spines. However, morphotypes 2, 3 and 4 disappeared from North Africa in the late Eifelian (Fig. 4A, Fig. S4A). These morphotypes correspond to cephalata with spines. Although MCp1 and MCp5 were maintained in the early Givetian, MCp1 disappeared in the middle Givetian and MCp5 in the late Givetian. In the Late Devonian, only MCp1 reappeared.

As for cephalata, the morphospace occupation for cranidia was narrow from the Ludlow to the Lochkovian, but largely extended during the Pragian toward shapes with wide sagittal (sag.) preglabellar field and wide (tr.) occipital ring. The morphospace occupation remained constant during the Emsian and the Eifelian but collapsed during the Givetian (Fig. 4B, Fig. S4B). This collapse concerned both density and expansion, with the disappearance of shapes with a wide (tr.) frontal lobe in both morphotypes. This disappearance led to a morphospace occupation comparable to the Lochkovian one. During the Frasnian, the morphological expansion increased to specimens with a wide (sag.) preglabellar field and a wide (tr.) occipital ring despite the decrease of specimen density. Finally, the morphospace collapsed again during the Famennian to achieve a similar morphospace occupation as the Lochkovian or the Givetian (Fig. 4B, Fig. S4B).

As for cephalata and cranidia, the morphological space for pygidia was characterized by a broad occupation of shapes during the late Early Devonian (Fig. 4C, Fig. S4C). From the

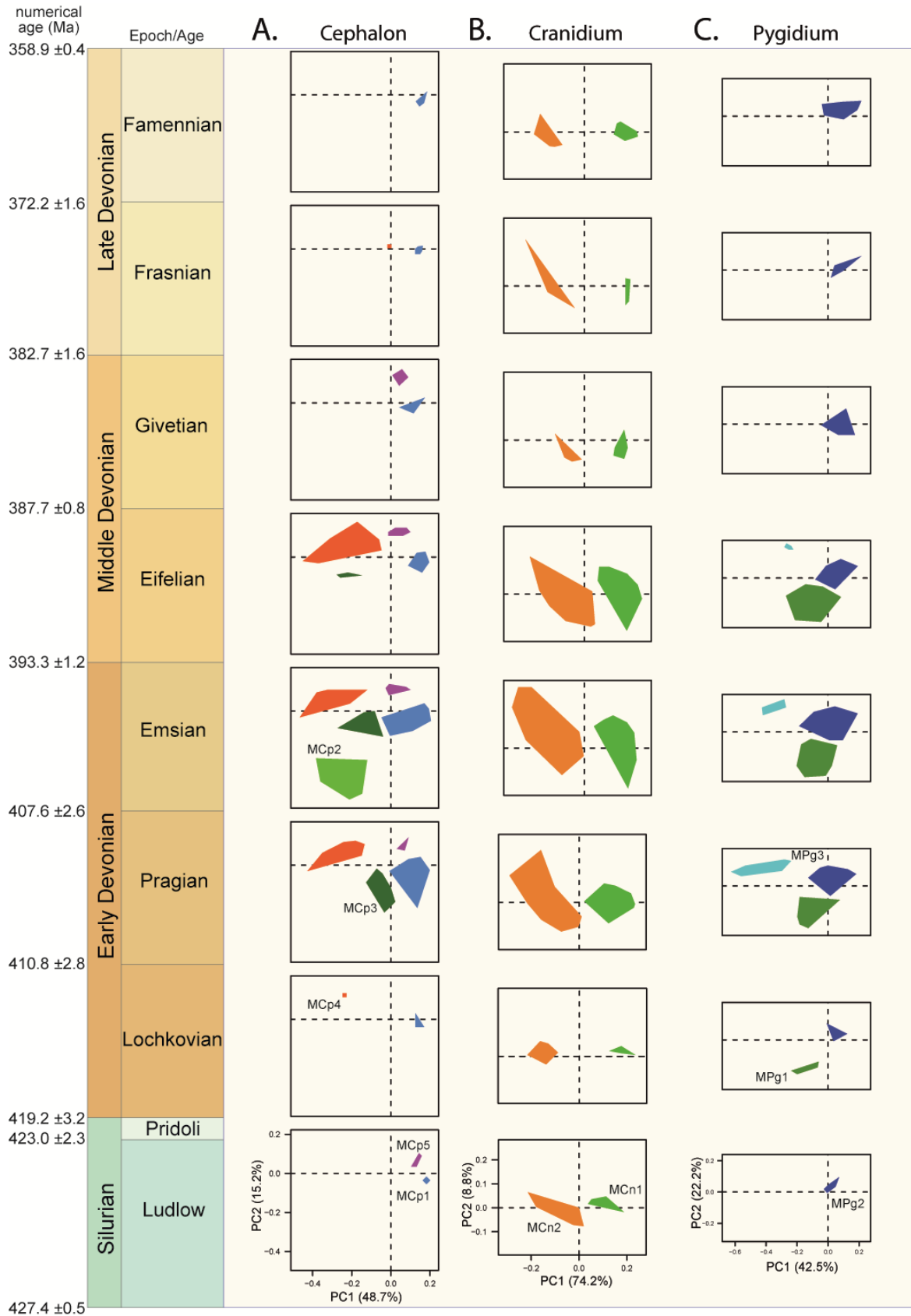


Figure 4. Location of the morphotypes of: A, cephalon; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals, represented for each Devonian stage. Coloured morphotypes according to Figure 3. Ages from *Cohen et al. (2013, updated with the version of 3/2020)*.

Ludlow to the Lochkovian, the morphological space slightly increased by the appearance of MPg1 which is characterized by a long (sag.) pygidial axis (Fig. 4C, Fig. S4C). After this low disparity period, the morphological space reached a maximal occupation by maintaining the previous morphologies but also by developing a new one, i.e., MPg3 (negative PC1 scores) with narrow (tr.) pygidia from the Pragian to the Emsian (Fig. 4C, Fig. S4C). In this morphological space, MPg1 with a long (sag.) pygidial axis developed but without co-occurring with pygidia with a long (sag.) axis and a narrow (tr.) outline. Morphologies with spines and a curved pygidial border were also developed (negatives PC3 and PC4 scores). Narrowest (tr.) pygidia occurred only in the Pragian, never again.

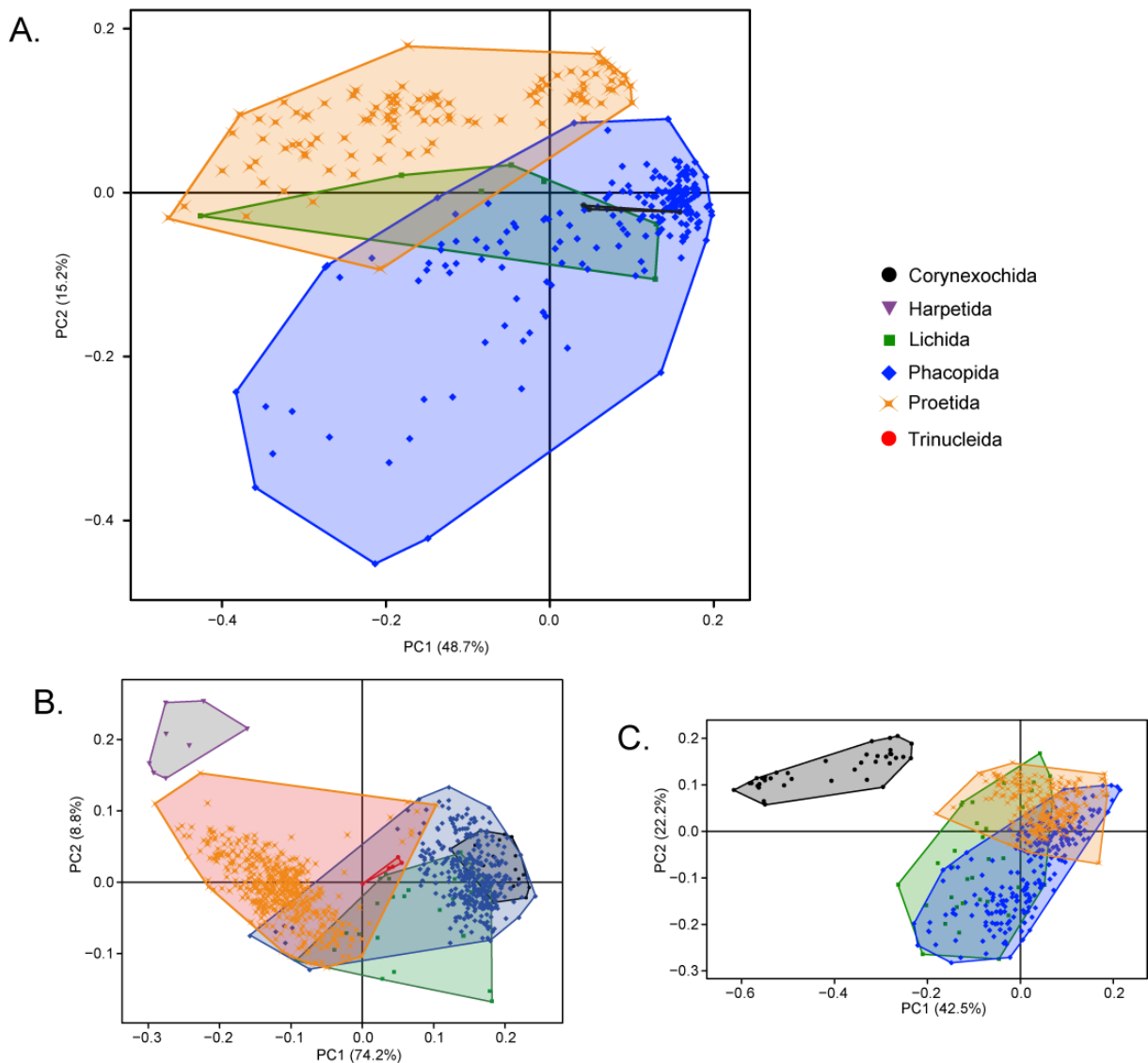


Figure 5. Location of: A, cephalae; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for each order.

The transition to the Middle Devonian did not coincide with a loss of morphological disparity; the three main morphotypes remain present (Fig. 4C, Fig. S4C). The reduction of the morphological space occurred during the late Eifelian. All the extreme shapes disappeared: narrow (MPg3) and wide (tr.) pygidia disappeared as well as long (MPg1) and short (sag.) pygidial axis and pygidia with a curved pygidial border (Fig. 4C, Fig. S4C). Although the pygidia with spines were maintained in the Eifelian, they disappeared in the Givetian with the collapse of the morphospace; only one pygidium morphotype is encountered, i.e., MPg2. A slight expansion of the morphological space occurred during the Frasnian but remained relatively restricted compared to the Early Devonian. Only wide (tr.) pygidia were present. During the Famennian, the morphological space was a little bit more widespread and not so scarce but remained in the same occupation ranges until the latest Famennian where a reduction of the morphological space occurred. Only MPg2 was maintained in the Late Devonian (Fig. 4C, Fig. S4C).

Morphospace occupation by taxonomic orders

For cephalia, the morphospace shows a reduced overlap between Phacopida and Proetida, two orders that occupied respectively a vast area (Fig. 5A). Lichida appeared somewhat an intermediate Order (Fig. 5A). Corynexochida is the only Order with a restricted area (Fig. 5A). The main cephalic shape differences between these lineages are related to the position of the facial suture and the relative width (tr.) of the frontal lobe. Proetida were distinguished by an opistoparian facial suture and a wide (tr.) glabellar lobe equal to the frontal lobe (MCp4 and MCp5). Proetida have no sagittal spines and no or short genal spines (according to PC3 scores close to zero, Fig. Fig. S3A). At the opposite, Phacopida are distinguished by a wide (tr.) frontal lobe (according to positive scores of PC2) and mainly without spines assigned to morphotypes 1, 2 and 3 (according to positive scores of PC1). All of the Phacopida specimens have a proparian facial suture and no genal spines but some of them are characterized by the presence of sagittal spines. Corynexochida are distinguished by a prominent frontal lobe and no long (sag.) spines (MCp1). Finally, Lichida are characterized by a wide (tr.) frontal lobe as in Phacopida and an opistoparian facial suture as in Proetida. Like Proetida and Corynexochida, Lichida have no sagittal spines and no or short (sag.) genal spines (according to PC3 scores close to zero).

For cranidia, six orders are documented (Fig. 5B). The morphospace shows important overlap between Trinucleida, Phacopida, Proetida, Corynexochida, and Lichida (Fig. 5B). Phacopida and Proetida remain two orders that occupied respectively a vast area sharing a

moderate overlap (Fig. 5B). Proetida are characterized mainly by MCn2 with a wide (tr.) preoccipital and occipital rings, while Phacopida are characterized mainly by MCn1. Corynexochida are characterized only by MCn1 with a wide (tr.) frontal lobe and no prelabellar field. Trinucleida are characterized by an intermediate morphology between wide (tr.) frontal lobe (i.e., MCn1) and wide (tr.) preoccipital and occipital rings (i.e., MCn2). Lichida is another order with a vast area but sharing an important overlap with Phacopida (Fig. 5B). As for cephalo, Lichida are characterized by various morphologies corresponding to both MCn1 and MCn2 excluding the morphologies with a prelabellar field. Harpetida is the only Order with an isolated area with no overlap. They are characterized by narrow (tr.) cranidia with a broad prelabellar field.

For pygidia, the morphospace shows a large overlap of most orders. However, Phacopida and Corynexochida are quite separate (Fig. 5C). The main pygidial shape differences between lineages are related to the width (tr.) of pygidia and the length of the pygidial axis. Proetida are distinguished by a wide (tr.) pygidium with a medium-size axis (MPg2). As for Proetida, Phacopida can have a wide (tr.) pygidium with a medium-size axis (MPg1). However, most of them have a wide (tr.) pygidium with a long (sag.) axis (MPg1). Corynexochida is the only order with a narrow (tr.) pygidia (MPg3) with a small axis. Lichida order is characterized by a relatively important shape variation despite its low number of specimens where the pygidial axis length or the pygidial (tr.) width seem to be not discriminant (MPg1, MPg2 and MPg3).

Morphospace occupation by bathymetry

For cephalo, cranidia and pygidia, all habitat groups related to the depth/bathymetry show a very large overlap (Fig. 6A-C). Nevertheless, the results of the ANOVA (Table 2) show significant p -values ($p < 0.05$) suggesting a shape difference between all habitat groups according to bathymetry with some exceptions. These exceptions mainly concerned cephalo from deep environments or with major difference in water depth affinities (i.e., shallow vs. middle shelf). These datasets (i.e., cephalo, cranidia, pygidia) reveal a differentiation between bathymetry-related groups. For cephalo, MCp1 and MCp4 were present at every bathymetric level, unlike other morphotypes (Fig. 6A). MCp2 gathers mainly trilobites that lived in the middle shelf. Some trilobites from shallow environments have also this morphotype but they are rare and this trend never concerns the extreme shapes with long (sag.) spines (according to the lowest PC2 scores). Almost all the trilobites that lived in the inner shelf correspond to MCp5. Two specimens from the middle shelf correspond to MCp5. MCp4 is dominated by trilobites from the middle shelf but trilobites with other bathymetrical affinities could also have

this morphology. Finally, trilobites from shallow to middle shelf environments could have cephalons attributed to MCp3, but are never encountered in the deep environment. All cranium morphologies were present at different depths except crania with a large (sag.) preglabellar field (Fig. 6B). For pygidia, morphological differences related to bathymetry affinities affect only the MPg3 which was absent from shallow and deep environments. MPg1 and MPg2 encountered at every bathymetric depth were present in the deep environment (Fig. 6C).

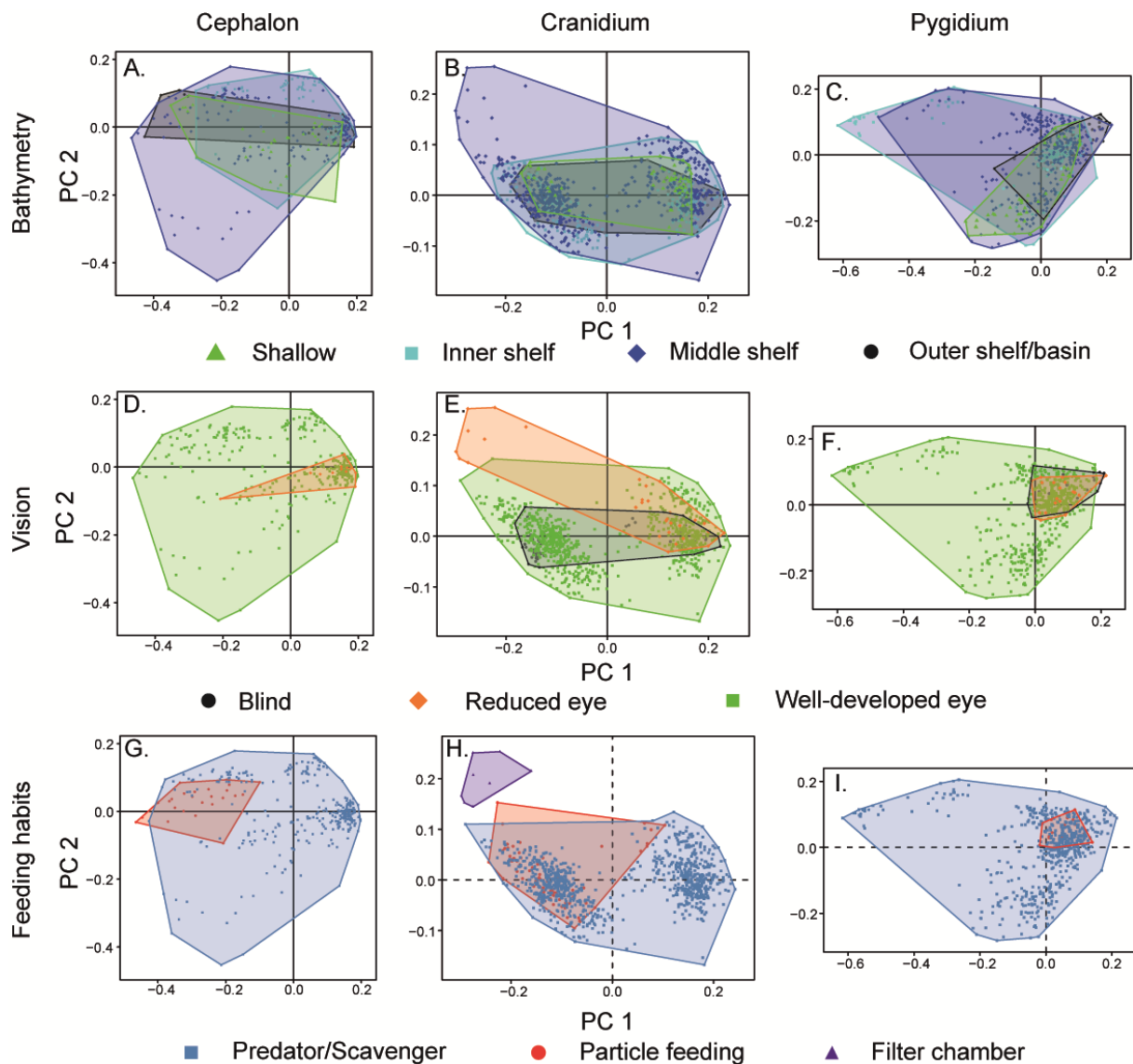


Figure 6. Location of: A, D, G, cephalons; B, E, H, crania; and C, F, I, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for three factors: (A-C) bathymetry; (D-F) visual abilities and (G-I) feeding habits. See supplementary figures S5, S6 and S7 for more details.

Morphospace occupation by vision

	Cephalon			Cranidium			Pygidium		
Total	0.001			0.001			0.001		
Bathymetry	Shallow	Inner shelf	Middle shelf	Shallow	Inner shelf	Middle shelf	Shallow	Inner shelf	Middle shelf
Inner shelf	0.001			0.001			0.001		
Middle shelf	0.254	0.001		0.001	0.005		0.001	0.001	
Deep	0.059	0.050	0.057	0.020	0.192	0.063	0.001	0.001	0.001

	Cephalon		Cranidium		Pygidium	
Total	0.009		0.022		0.001	
Vision	Reduced-eyes	Blind	Reduced-eyes	Blind	Reduced-eyes	Blind
Blind			0.001		0.268	
Well-dev. eyes	0.022		0.001	0.001	0.034	0.001

	Cephalon		Cranidium		Pygidium	
Total	0.001		0.001		0.012	
Diet	Particle feeding	Filter	Particle feeding	Filter	Particle feeding	Filter
Filter			0.001			
Predator/Scav.	0.001		0.001	0.001	0.012	

Table 2. *p*-values of the Procrustes ANOVA with permutation procedures to assess shape covariation according to bathymetry, visual abilities and feeding habits as factors.

For cephalata, cranidia and pygidia (Fig. 6D-F), the morphospace shows a widespread area for large-eyed trilobites, while reduced-eye trilobites show a more restricted area. Blind trilobites show a restricted area (Fig. 6E-F). Nevertheless, the results of the ANOVA (Table 2) show significant *p*-values ($p < 0.05$), suggesting a shape difference between all vision groups according to visual abilities except between two compared groups of pygidia represented by reduced-eyed and blind taxa. These datasets (i.e., cephalata, cranidia, pygidia) reveal a differentiation between visual abilities. For cephalata, reduced-eyes trilobites are not represented in MCp2, MCp4 and MCp5 and they are characterized by shape without spines or with very small spines. For cranidia, both blind and reduced-eye trilobites are represented by both MCn1 and MCn2. However, for MCn2, reduced-eye trilobites did not constitute a subset of the large-eyed trilobites but had their own unique morphology with a wide (sag.) preglabellar field contrary to MCn1 for which they showed no new morphology (Fig. 6E). For pygidia, only MPg2 corresponds to blind or reduced-eyes trilobites, while all other morphotypes show large eyes.

Morphospace occupation by feeding habits

For cephalia as for cranidia and pygidia (Fig. 6G-I), the morphospace shows a widespread area for one group, i.e., predator/scavenger habits, while particle feeding and filter chamber habits show a restricted area. The results of the ANOVA (Table 2) show significant p-values ($p < 0.001$) suggesting a shape difference between all diet groups according to feeding habits; only two compared groups of pygidia represented by particle feeding and predator/scavenger taxa show a p-value $p < 0.05$. For cephalia, particle-feeding trilobites were mainly restricted to MCp4 characterized by no genal spines except one specimen within MCp3 (Fig. 6G). In terms of morphology, predators and/or scavengers were distinguished from particle feeding trilobites, although these differences could be minor as for MCp4 where the facial suture was slightly different between both diet categories. For cranidia, particle-feeding trilobites were also characterized by narrow (tr.) frontal lobes occurring mainly in MCn2 (Fig. 6H). At the opposite, Predator/Scavenger trilobites occupied all the morphospace. The greatest number of cranidia allows having the repartition of filter chambers, which had very large preglabellar field and narrow (tr.) frontal lobes. For pygidia, particle-feeding trilobites show only MPg2 (Fig. 6I). They also have no spines occupying only the centre of the PC3-PC4 morphospace.

DISCUSSION*Relationships between morphological spaces and proxies*

The maximum morphological disparity in trilobites with many different morphologies for both cephalia and pygidia was documented in the Ordovician but remained important in the Devonian (Foote 1993; Webster 2007). During this Devonian time interval, and according to our results, the overall dispersion of taxa in the morphospace shows (1) cephalia with spines or not, visual surfaces or not, proparian or opistoparian facial sutures, glabella with wide or narrow (tr.) anterior frontal lobes, and (2) pygidia with spines, wide or narrow (tr.) outlines and different lengths (sag.) of the pygidial axis. The type of sutures was already an important criterion to segregate the trilobite morphologies in the Early Palaeozoic (Foote 1991a) although their ecological or life-history-strategy significance is uncertain (Hopkins 2014). The position of facial sutures corresponded to a trade-off between burrowing and moulting and could be an advantage to develop an infaunal lifestyle (Esteve *et al.* 2021). The presence of spines is identified as a contributor to overall morphological variation for pygidia too, for which elongation (sag.) is a major axis of shape variation.

The three studied morphospaces are characterized by the presence of morphological clusters. The palaeoecology, measured here as the bathymetry and the diet factors, has only a weak effect

on the trilobite morphology because different categories overlapped, and cannot explain such identified morphotypes (Fig. 6, Table 2). Hopkins (2014) already noticed a weak bathymetric influence on trilobite morphology except during the Ordovician and the Late Devonian when Proetida lived in shallow environments and Phacopida in deeper ones. The absence of real links between the trilobite morphologies and the water depth contrasts with the structure of the morphological disparity in ammonoids (Neige *et al.* 1997). As nektonic organisms, the ammonoids colonized the water column from the platform to the basin with typical morphologies related to the pressure, which is not the case for benthic trilobites found only on the sea floor of the platform.

The diet influenced on the shape of trilobites as it contributed to morphological variations in modern arthropods (Lunardi *et al.* 2017). The distinct glabellar shapes recognized in our analyses (Fig. 6) are already identified in previous studies and are interpreted as an indicator of feeding habits (Fortey & Owens 1999). The expanded glabella anteriorly with wide frontal lobes observed in our study was interpreted as predator feeding habits, which are associated with the ingestion of bulky food (Fortey & Owen 1999). However, some predator/scavenger taxa showed a glabellar shape with narrower anterior frontal lobes, a morphology attributed to particle feeding trilobites. Difference of feeding habits for a same dorsal morphology is explained by the fact that morphological changes in connection with diet mostly concerned especially the ventral structure, i.e., the hypostome (Fortey & Owens 1999). Filter chamber feeding trilobites needed a large cephalic shield to filter suspension particles in the water. Consequently, these trilobites presented the larger preglabellar field (Fig. 6). However, a large cephalic shield can also be used to avoid sinking into the mud (Richter 1920) and would not be related to feeding habits. Although pygidium shape did not play a role in trilobite feeding, particle feeding trilobites occupied only a small area of the morphospace.

The visual abilities, estimated here from the shape of the visual surfaces, have an important effect on the global trilobite morphology. Devonian trilobites with well-developed eyes occupied the global morphospace whereas blind and reduced-eye trilobites occupied only a small part of this morphospace (Fig. 6). Moreover, blind and reduced-eye trilobites occupied the same small part of the morphospace, except for taxa with narrow frontal lobes anteriorly (Fig. 6, Table 2). During the Devonian, paedomorphic evolutionary trends have been observed in Late Devonian taxa showing progressive eye reduction between closely related species that eventually leads to blindness (Feist & Clarkson 1989; Feist 1995; Crônier & Courville 2003; Schoenemann 2018). Such eye reduction implies morphological changes such as the enlargement of fixigenae observed among Proetida or the 'displacement' of the facial suture

towards the outer margins observed among Phacopida (Feist 1995; Crônier & Courville 2003). Consequently, Phacopida with reduced eyes are mainly confined to the part of the morphospace characterized by a suture closer to the lateral border (i.e., higher PC1 values, Fig. 6D).

In addition to diets and habitats, the trilobite morphologies are known to be influenced by their lifestyle, such as living in low-oxygen habitats (Fortey 2004) or the enrolment type (Suárez & Esteve 2021). In the same way, competition between species is also a driver of diversification recognized in arthropods (Eberle *et al.* 2014).

Morphological evolution through time

The trilobite morphospace occupation evolved during the Devonian in North Africa. A minimum occupancy in the morphospace occurred at the beginning of the Early Devonian, inherited from the end of the Silurian (Fig. 4). Only one cephalic and pygidial morphotype and two cranidial morphotypes were encountered; the difference between cephalia and cranidia being due to a lack of cephalic record. These morphologies were adapted to all depth/bathymetry and vision abilities but not to a particle feeding behaviour. Despite a reduced shape variability, trilobites were not restricted to any depth or type of vision. These morphologies coincided with the expansion of Phacopida disparity (Fig. 5A) and their dominance during the Lochkovian in North Africa (Bault *et al.* 2021).

During the Pragian, morphological disparity increased and new morphologies were explored, i.e., cephalia with an opistoparian facial suture and a narrow (tr.) frontal lobe. These new morphologies are assigned to Proetida (Fig. 5A) which developed in North Africa (Bault *et al.* 2021) and exhibited their maximal dispersion at the global at this time (Foote 1993). Moreover, exoskeletons with spines proliferated, i.e., pygidia with spines developed as well as cephalia with genal spines, which became more diverse and extended towards shapes with very long genal spines. Pygidia with a narrow (tr.) outline assigned to Corynexochida appeared too (Fig. 5C). Cephalia with a wide preglabellar field appeared in both Proetida and Phacopida morphologies without a link to environmental depth (Fig. 6A-C) contrary to the Ordovician (Fortey & Wilmot 1991). Genal spines and a preglabellar field appeared at the same time in different lineages showing a common trajectory in morphospace through time. However, Phacopida explored morphologies with sagittal spines but not Proetida, suggesting that different causes could influence different lineages. The diversification of morphologies with the appearance of novelties in the Pragian coincided with new ecological opportunities due to the sea-level fall (Chlupáč 1994). The extension of the carbonate platform toward offshore environments offered new habitats leading to the morphospace expansion toward the middle

shelf and to a trilobite radiation. Similarly, the predator/scavenger trilobites showed an increasing morphospace occupation possibly linked to a food partitioning and to an interspecific competition (Schluter 2000; Grant & Grant 2006). The increase of enrolment type in the Devonian was also a source of morphological disparity (Suárez & Esteve 2021). More generally, the diversification phases could be partly attributed to interspecies competition in arthropods (Eberle *et al.* 2014). The diversification of many clades in the Early Devonian (Alroy *et al.* 2008; Klug *et al.* 2010; Fan *et al.* 2020), may have an influence on the predator morphology with the arrival of new prey (Cattau *et al.* 2017). This advantageous feeding strategy could induce a radiation of predator/scavenger trilobites and at the opposite, particle feeding trilobites decreased maybe because of an increasing competition of more efficient organisms. Despite new morphologies explored in the Pragian, those already present during the Lochkovian remained the majority.

During the Emsian, all the main morphologies maintained with the maximum dispersion in the morphospace with the development of cephalons with long genal spines and especially with a wide (tr.) frontal lobe (Fig. 3). Only shape losses regarding the narrowest (tr.) pygidia occurred. In trilobites, spinose exoskeletons were interpreted as passive morphological defences by some authors (Fortey 2004; Pates & Bicknell 2019). In a context of the Devonian Nekton Revolution (Klug *et al.* 2010), the emergence of morphologies with spines can be interpreted as a new answer to an increase of the predation. However, this hypothesis seems unlikely because some potential predators appeared only from the Emsian like ammonoids or chondrichthyans (Becker *et al.* 2019) or developed in the end of the Devonian like fishes (Derycke 2017). In addition, the morphologies with spines disappeared in the Middle Devonian and Frasnian, contrary to other shapes, which remained in the Famennian (Fig. 4). Nevertheless, these disappearances could be attributed to the inefficiency of spines against the large-jawed predators of the Late Devonian (Brett 2003). The diversification of morphologies in the Early Devonian could be partly related to novel feeding habits, i.e., particle feeding habits with the appearance of glabella with a short (sag.) preglabellar field (Fortey 2014). In addition, only exoskeletons with genal spines were attributed to this diet as well as in North Africa during the Devonian as in other areas and at other times (Fortey & Owens 1999). In their evolutionary history during the Early Devonian, trilobites explored morphospace with much of the subsequent variation in their cephalic features compared to their pygidial features. Accordingly, the pygidial characters display much overlap of taxonomic groups in the morphospace, while the cephalic characters show more distinct morphospace occupation at the order level.

The morphospace was maintained during the Eifelian with all the cephalic, cranidial and pygidial morphotypes despite environmental changes implying sea-level and oxic condition changes (Kaufmann 1998). Only the morphologies appeared during the Pragian were rarer, especially MCp2 for cephalia and MPg3 for pygidia (Fig. 4).

The Givetian was characterized by an important loss of morphology. The disappearance of some orders, i.e., Lichida and Corynexochida (Bault *et al.* 2021) led respectively to the loss of exoskeletons (i.e., cephalia and pygidia as well) with spines or the loss of cephalia with a long (sag.) glabella and of pygidia with a long (sag.) axis. However, Corynexochida was known in the lower Givetian of North Africa (Feist & Orth 2000) but only represented by a single pygidium; thus, the loss of the cephalic morphology occurred later although it is not possible to observe this in the morphospace. Between the different lineages, a common pattern of disappearance seems to exist and in particular, for both Proetida and Phacopida, which showed that the most affected trilobites were those with morphologies with protuberance like spines and preglabellar field implying a common origin of disappearance. The Givetian is known to be a period marked by a series of anoxic/hypoxic events associated with sea-level rise (Kaufman 1996; House 2002; Becker *et al.* 2016) and to have an important impact on trilobite diversity (Feist 1991; Chlupáč 1994; Lerosey-Aubril & Feist 2012). The morphospace was reduced probably due to marginal or lateral extinctions (Foote 1991b; Korn *et al.* 2013). Morphologies with the lowest bathymetric extent such as the MCp2 and MCp3 for cephalia and MPg3 for pygidia were the most impacted and they disappeared (Fig. 6A-C). Indeed, these morphologies have never been encountered in a deep environment, which could be a disadvantage in a context of rising sea level. In addition, the morphologies that remained were versatile and exhibited different vision abilities (Fig. 6). Accordingly, these morphologies were more adapted to environmental changes. The morphologies maintained during the Givetian corresponded to morphologies already present in the Ludlow and represent persistent morphologies.

The dispersion in the morphospace decreased in the Frasnian to reach only one morphotype for cephalia (MCp1) and for pygidia (MPg2). Nevertheless, the absence of additional morphotypes (i.e., MCp3 and MCp4 without spines or short genal spines) for cephalia in Proetida is due to the lack of sampled specimens in our dataset. Some Proetida were encountered in the upper Frasnian of North Africa (Feist 2002). The Frasnian is marked by the reappearance of morphologies with numerous spines. These morphologies occurred within the dark-grey hypoxic limestone levels of the Kellwasser deposits related to relative deep-sea conditions (Feist 2002). Trilobite morphologies did not show significant shape losses and seem to have been little affected by the Kellwasser Events that occurred at the Frasnian/Famennian

boundary and was one of five major extinction events in the history of life on Earth (McGhee 1988, 1996; Racki 2005, 2020). The main shape change was the disappearance of morphologies with spines except genal spines in Cyrtosymbolinae (Proetida). Unfortunately, only the cranidia and the pygidia for the Famennian Proetida are available in North Africa and they are therefore not included in the cephalic morphospace. As for the Givetian and the Frasnian, only the versatile morphologies related to depth conditions and vision abilities were maintained during the Famennian. Only Proetida and Phacopida crossed the Frasnian-Famennian boundary both at the global and at the North Africa regional (Chlupáč 1994; Lerosey-Aubril & Feist 2012; Bault *et al.* 2021). These two orders are characterized by the maximal morphological variation in the Devonian morphospace in North Africa (Fig. 4). Such variability is known to be helpful to cope the environmental changes in other clades (Kolbe *et al.* 2011; González-Suárez & Revilla 2012; Huang *et al.* 2015; Austin & Dunlap 2019). Across all these events, from the Eifelian to the Famennian, there were progressive shape losses among trilobites but no extensive morphological innovation occurred after mass extinctions despite potential availability of the ecospace (Erwin 2015).

The notable extinction at the end of the Famennian, i.e., the Hangenberg event led to the demise of Phacopida whereas Proetida survived (Feist 1991; Lerosey-Aubril & Feist 2012; Bault *et al.* 2021). During this event, a severe but selective shape loss occurred which only affected Phacopida and their cephalia. Such selective patterns were previously identified in other organisms such as ammonoids where the morphology of clymeniids was more affected than that of goniatitids (Korn *et al.* 2013). If Phacopida and Proetida showed different morphologies of cephalia, they exhibited similar morphologies of pygidia, suggesting that the pygidia were the structures with the less extinction selectivity contrary to the cephalia.

Morphospace divergence in the light of morphological constraints

Location of cephalia, cranidia and pygidia in the morphospaces showed a different relative distribution of specimens: for instance, Corynexochida and Phacopida that occupied the same part of the cranidium morphospace occupied distinct parts of the pygidium morphospace (Fig. 5B-C). This is explained by the relatively independence of the evolution of the studied structures known as tagmata (Hughes 2003) even if some covariations between these different structures exist due to enrolment (Oudot *et al.* 2019). Functional morphology, consequently functional modularity, explains why some orders showed overlapping morphologies for cephalia or pygidia but different shapes for other structures. Modularity was implied in the developmental process of trilobites indicating a developmental constraint on the morphology.

Not all combination of characters were possible due to intrinsic constraints that channel the morphological evolution like physical or developmental constraints (Arnold 1992; Gould 2002; Gerber 2014; Briggs 2017). For trilobites from the Devonian of North Africa, it was not possible to develop a sagittal spine without genal spines in the cephalon (high PC1 and low PC2 scores; Fig. 3A). Ontogenetic studies underlined a progressive enlargement (tr.) of the glabella during the development, especially in Phacopida due to a change in the food niche (Crônier & Feist 1997; Crônier & Fortey 2006; Jacobs & Carlucci 2019). Thus, feeding constraints during development probably led to the absence of trilobites with a very narrow (tr.) glabella at an adult stage (high PC2 scores; Fig. 3B) in our dataset.

Some taxa exhibit intermediate morphologies between the morphotypes indicating that physical constraints did not hamper the existence of these morphologies (Fig. 3). The density distribution of morphologies in morphospace can reflect the positions of clusters with high-fitness interpreted as an ‘adaptive peak’, separated by ‘valleys’ with few morphologies, driven by competition, trophic specialization or behaviour (McGhee 2007; Polly 2017). The trade-offs between different tasks led to an adaptive landscape and therefore to phenotypic clusters (Shoval *et al.* 2012; Tandler *et al.* 2015). Thus, the overall dispersion of taxa was restricted to some areas of the morphospace with some empty areas and with a heterogeneous distribution for the Devonian time slice. This explains why some morphologies were absent during the Devonian such as a narrow (tr.) pygidium associated with a long (sag.) axis while such morphologies were present during the Cambrian, in the genus *Balcoracania* for example (Pocock 1970). Consequently, intrinsic factors alone cannot explain the absence of these morphologies and two other factors can be identified: the environmental conditions were not favourable to these morphologies or these morphological areas were simply never explored again after their disappearance. In the case of *Balcoracania*, this genus was found in very shallow environments, like lagoon or estuaries, during the Cambrian (Paterson *et al.* 2007) but trilobites deserted this environment during the Devonian of North Africa, suggesting an environmental explanation for the absence of a narrow (tr.) pygidium. The evolution of such parameters may be a trade-off between selection on factors such as function, ecology/environment, or development.

Our study shows some trends of covariation of different characteristics and the most obvious covariation concerns the cephalon, for which a common pattern of morphological changes occurred. For both Proetida and Phacopida, some arrangements of the cephalon were needed to develop spines: the glabellar shape became less curved with a narrow (tr.) frontal lobe (lower PC1 and PC2 scores, Fig. 3A). Morphological covariations are known in trilobites and were

mainly due to physical and developmental constraints (Hughes 2003; Crônier & Feist 1997; Gerber & Hopkins 2011; Webster & Zelditch 2011; Oudot *et al.* 2019).

CONCLUSION

In the Devonian, North African trilobites showed substantial morphological variation in their cephalata, cranidia and pygidia. The morphological disparity concerned the width (tr.) of the glabella, the location of facial sutures, the elongation (sag.) of pygidia and the presence of spines. Both abiotic and biotic factors such as depth of water conditions, feeding habits and visual abilities seem to have only a weak effect on the global trilobite morphology. Trilobites with well-developed eyes occupied the global morphospace whereas blind and reduced-eye trilobites occupied only a small part of this morphospace.

North African trilobites experienced significant morphological fluctuations from the Early to the Late Devonian. During the Devonian, the trilobites exhibited cases/examples of convergence in the visual surfaces or and spines and, a development of ‘rare’ morphologies such as the very spiny shapes of the Pragian-Emsian. The morphological disparity was low at the end of the Silurian and the Lochkovian. The trilobites occupied a relatively small part of the morphospace. Subsequently, the disparity increased considerably in the Pragian with the appearance of several new morphologies. Then, the disparity reached a maximum in the Emsian. The trilobites occupied the global morphospace and exhibited additional new morphologies, although some areas of the morphospace remained empty because some morphologies did not develop in the Devonian. The morphological disparity maintained until the Eifelian, decreased considerably in the Givetian, and reached a minimum in the Late Devonian with a density more important for the Famennian than for the Frasnian. The trilobites developed no novelties anymore. This significant decrease in the morphological disparity occurred during a period characterized by numerous environmental events implying habitat changes with sea-level fluctuations and anoxic/hypoxic conditions. Some taxa (i.e., morphologies) were more resilient to these environmental changes and persisted during the Devonian because of their adaptation to different bathymetry and their visual ability. Similarly, Phacopida and Proetida survived most of the events thanks to their large morphospace occupation, and they were characterized by an evolutionary trend toward a progressive eye reduction leading to blindness.

ACKNOWLEDGEMENTS

This work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic time’, to

the project ECOS Sud-MINCYT A17A01 (Argentina), and to the French CNRS UMR 8198 Evo-Eco-Paleo. The authors thank the Région Hauts-de-France, and the Ministère de l'Enseignement Supérieur et de la Recherche (CPER Climibio) for their financial support.

AUTHOR CONTRIBUTION

Conceptualization C. Crônier, V. Bault, C. Monnet **Data Curation** **Formal Analysis**
Funding acquisition C. Crônier **Investigation** V. Bault **Methodology** **Project administration**
Resources **Softwares** C. Monnet **Supervision** C. Crônier **Validation** **Vizualisation** V. Bault
Writing-Original V. Bault, C. Crônier, C. Monnet **Draft Preparation** V. Bault **Writing –**
Review & Editing V. Bault, C. Crônier, C. Monnet

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SUPPLEMENTAL FIGURES

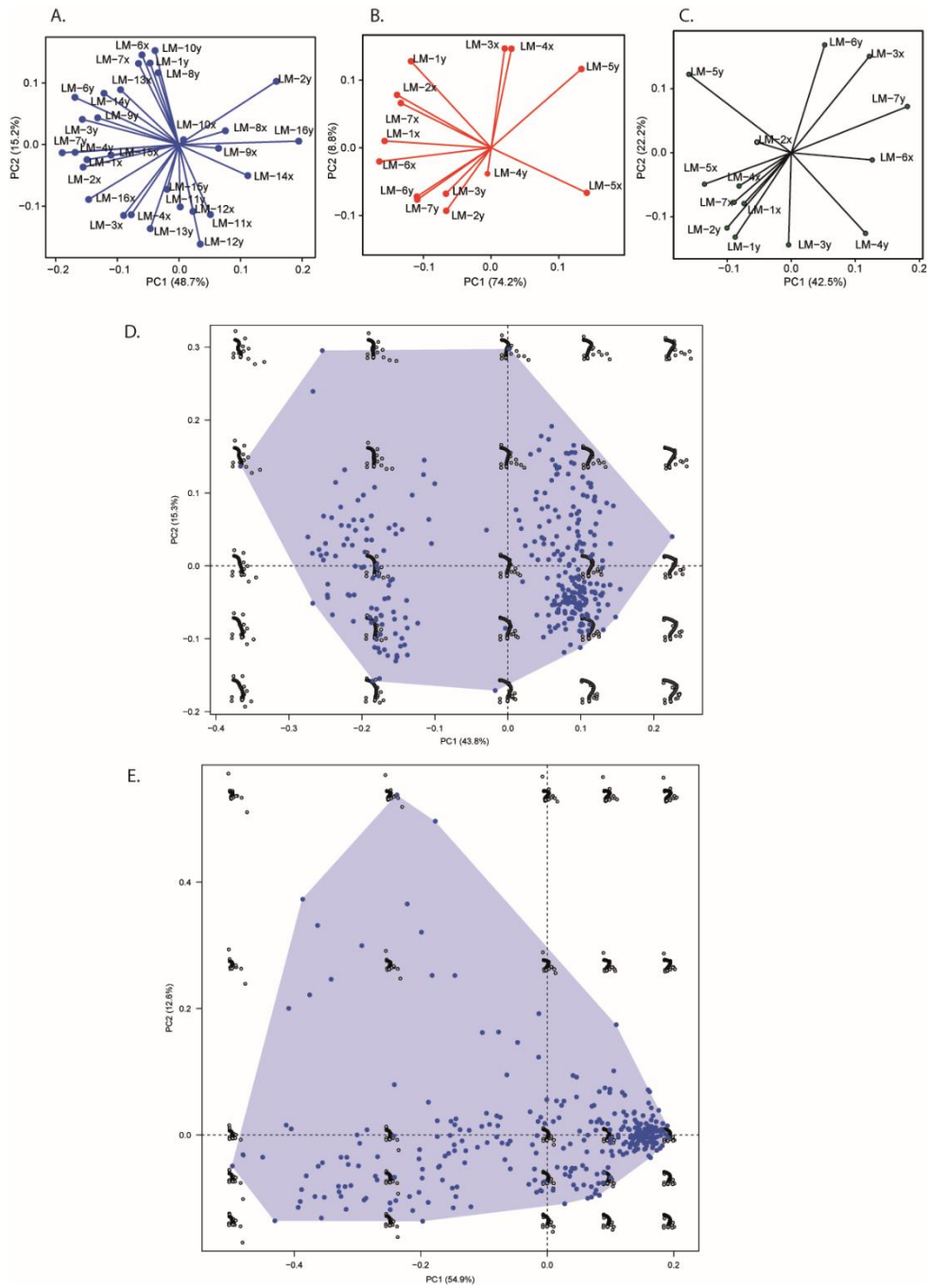


Figure S1. Results of analyses performed to verify if topological issues occurred with our set of landmarks. Correlation circles of landmarks showing the most contributing variables for: A, cephalon; B, crania; and C, pygidia. Morphospace defined according to the two first principal component axes performed on Procrustes residuals using cephalon specimens without landmarks 13 and 16 (D) and landmarks 10 and 12 (E).

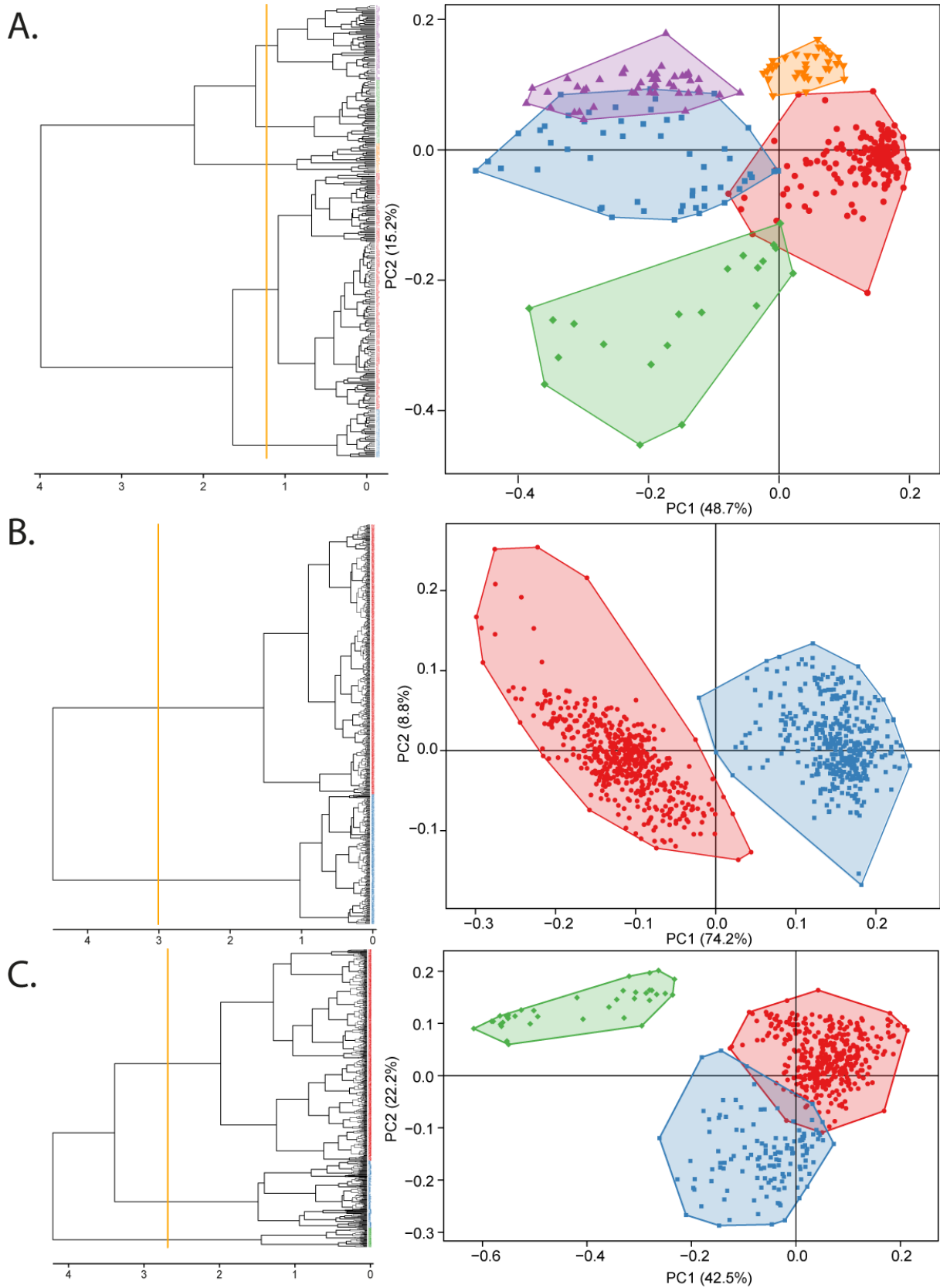


Figure S2. Clusters identify by a Hierarchical Cluster Analysis (HCA) performed with the Euclidian distance measure and Ward's linkage algorithm on the PC's scores for all specimens, and the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for: A, cephalia; B, cranidia; and C, pygidia.

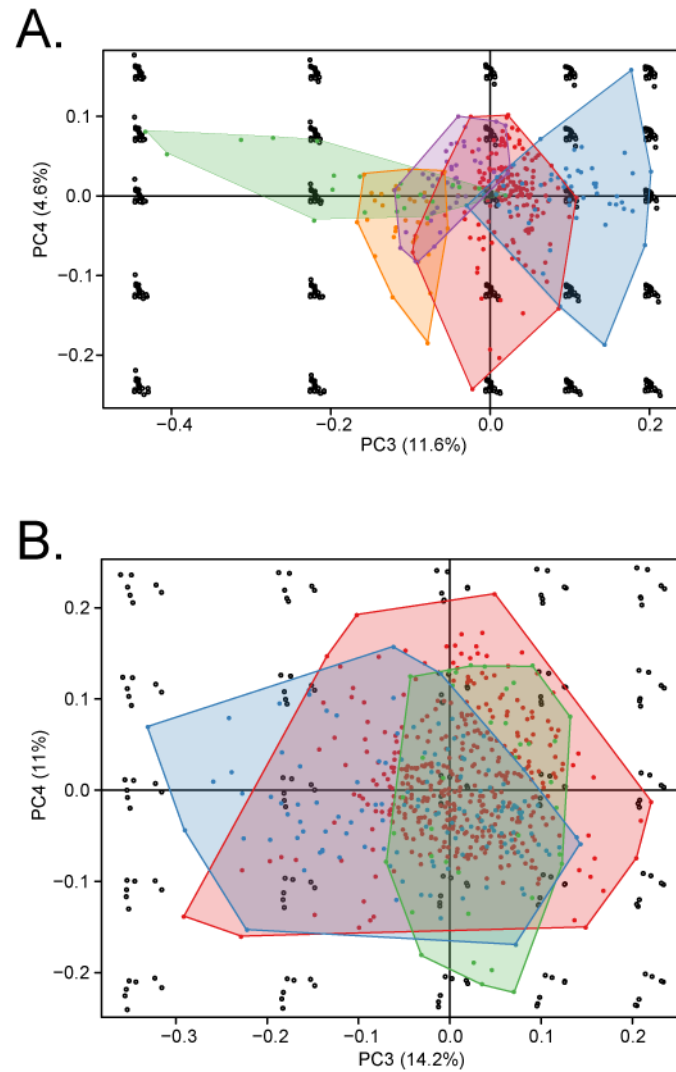


Figure S3. Location of: A, 328 cephalons; and B, 605 pygidia from the Devonian of North Africa in the global morphospace defined according to the third and the fourth principal component axes performed on Procrustes residuals.

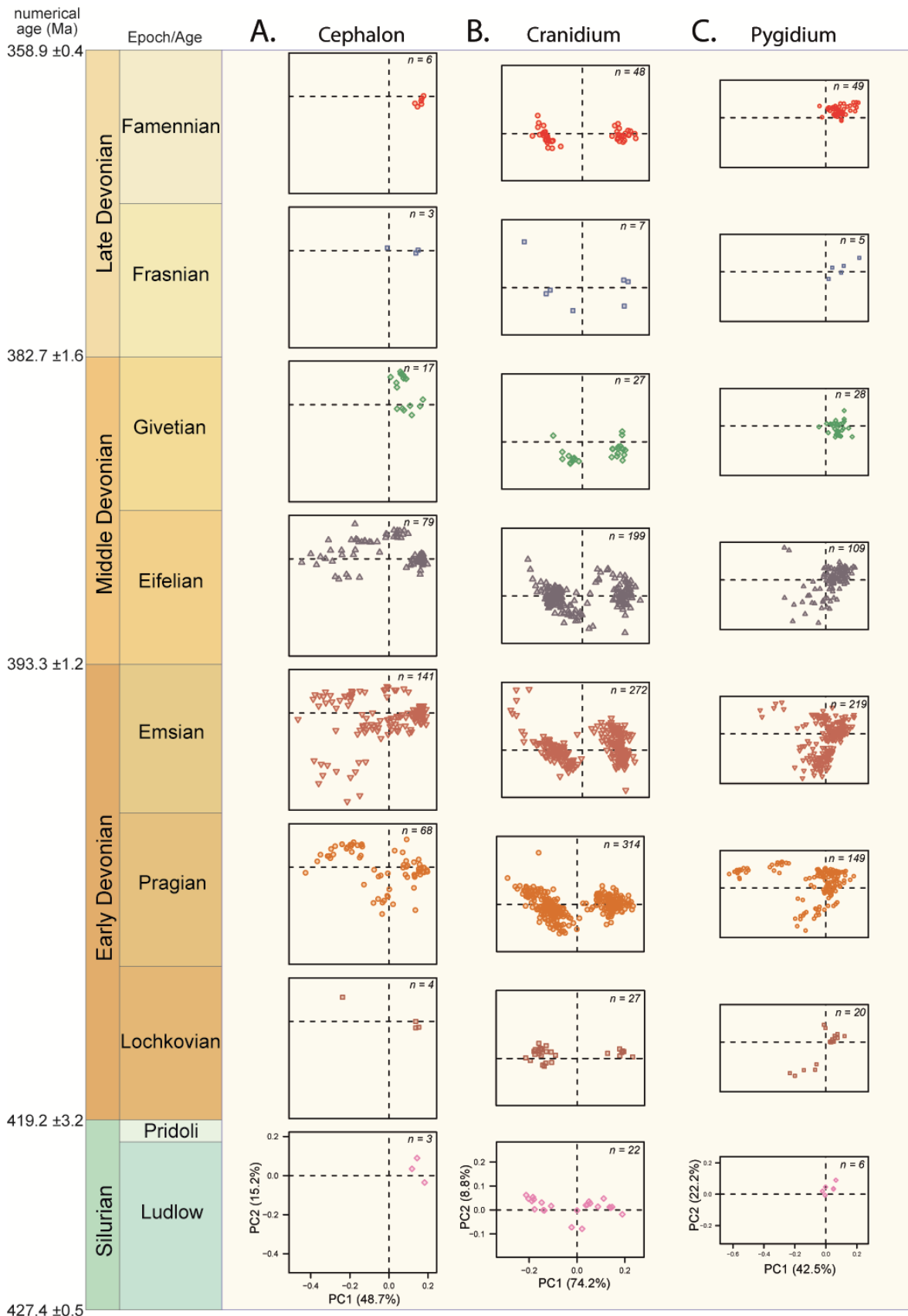


Figure S4. Location of: A, cephalons; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals, represented for each Devonian stage. The number of specimens is indicated for each stage. Ages from Cohen et al. (2013, updated with the version of 3/2020).

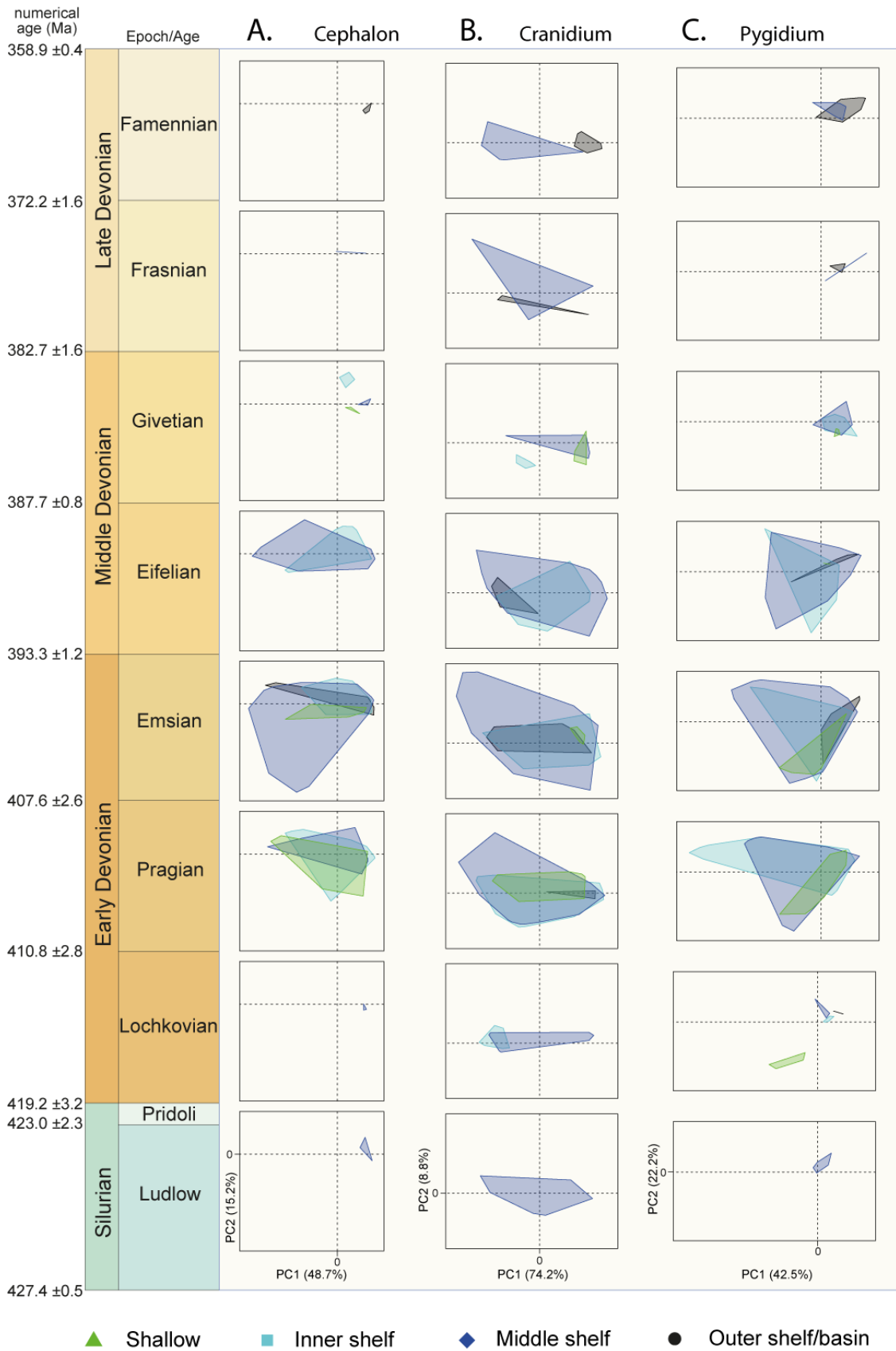


Figure S5. Location of the morphotypes of: A, cephalon; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for bathymetry. Ages from *Cohen et al. (2013, updated with the version of 3/2020)*.

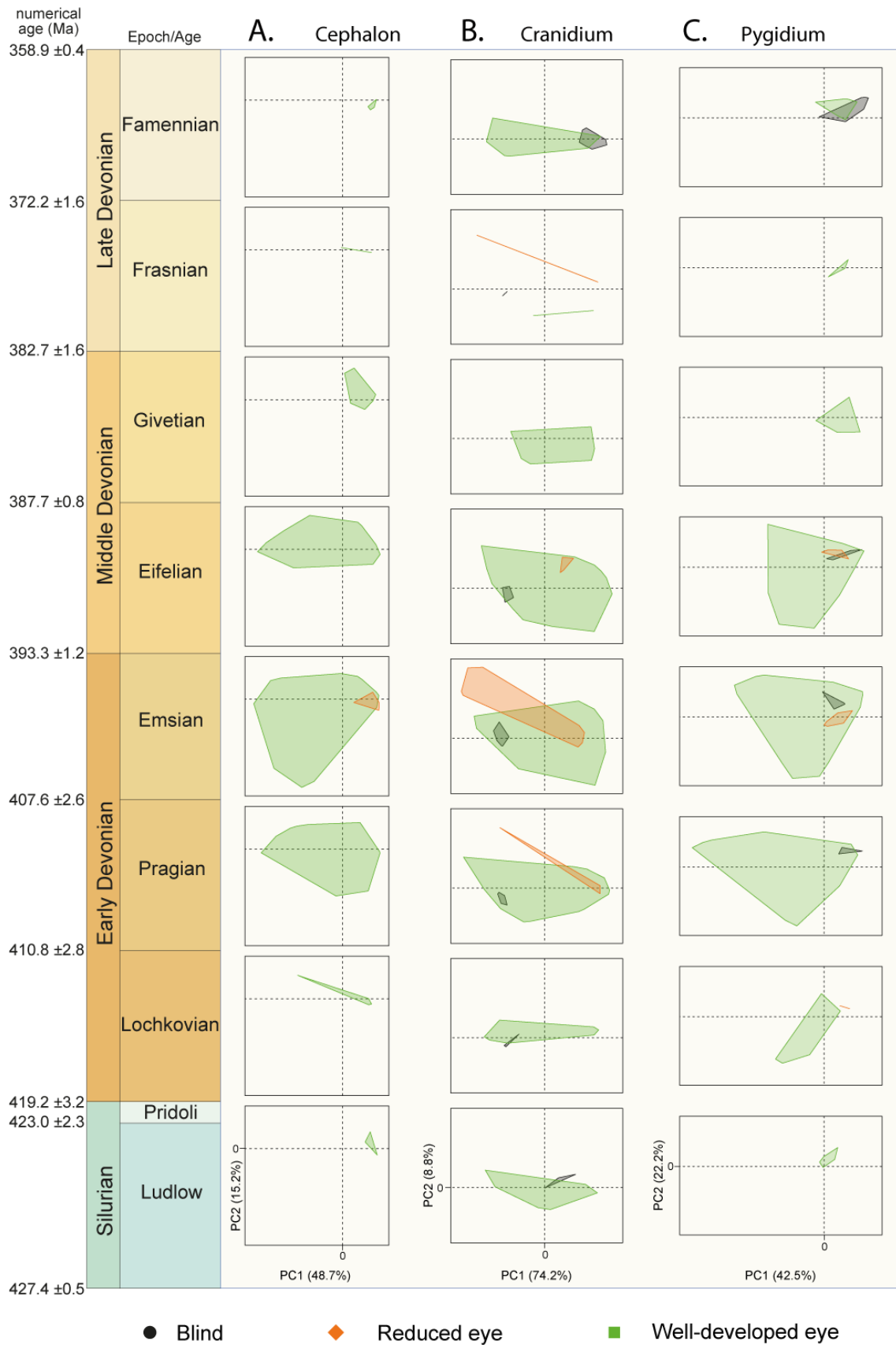


Figure S6. Location of the morphotypes of: A, cephalata; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for vision abilities. Ages from [Cohen et al. \(2013, updated with the version of 3/2020\)](#).

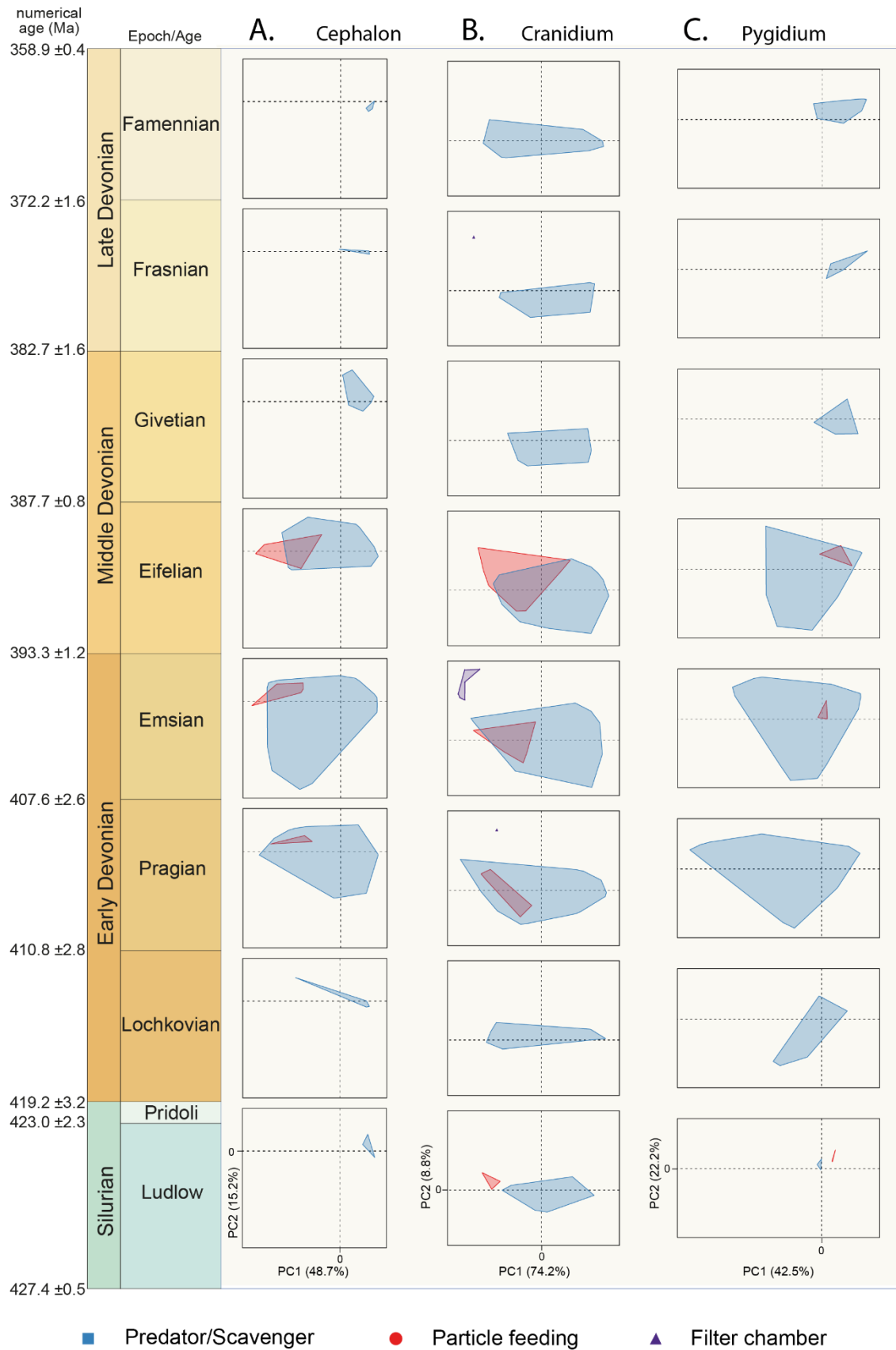


Figure S7. Location of the morphotypes of: A, cephalon; B, cranidium; and C, pygidium from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for feeding habits. Ages from *Cohen et al. (2013, updated with the version of 3/2020)*.

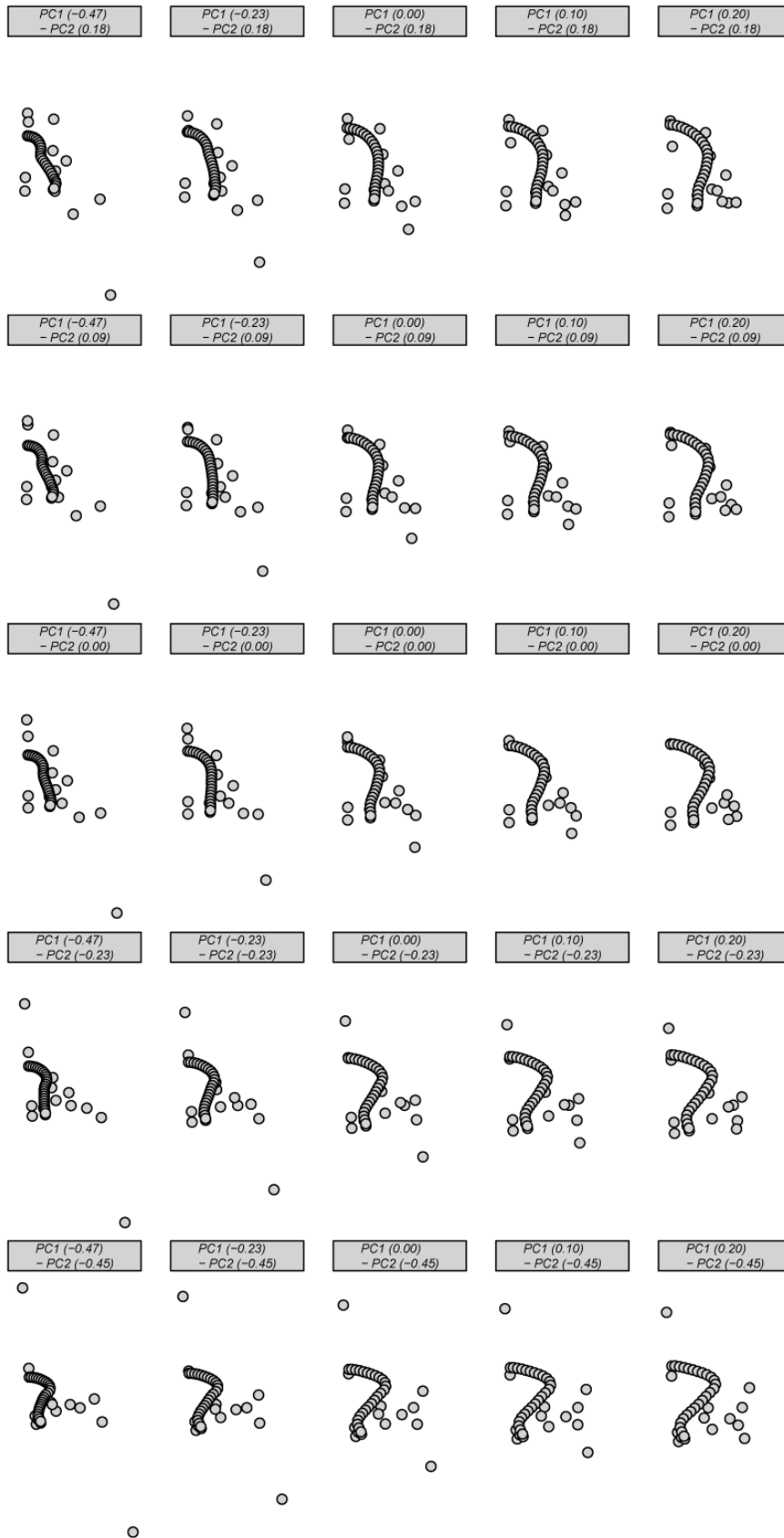


Figure S8. Reconstruction of virtual shapes for PC1 and PC2 of the cephalon.

2.3. Aucun découplage entre la diversité taxonomique et et la disparité morphologique des trilobites d’Afrique du Nord ?

Article 5 : No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa?

Pour être soumis à Historical Biology

No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa?

Valentin Bault^{a,*}, Catherine Crônier^a, and Claude Monnet^a

^a *Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France*

* Corresponding author at: Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France.

Email address: valentin.bault@univ-lille.fr (V. Bault), catherine.cronier@univ-lille.fr (C. Crônier), claude.monnet@univ-lille.fr (C. Monnet)

ORCID

Valentin Bault <https://orcid.org/0000-0002-9225-5195>

Catherine Crônier <http://orcid.org/0000-0002-7606-0822>

Claude Monnet <http://orcid.org/0000-0002-0899-8392>

Abstract

Morphological disparity and taxonomic richness are two important often decoupled in time, particularly in the early history of clades. Using morphometric methods and diversity indices, both morphological disparity and taxonomic diversity of Devonian trilobites from North Africa were analysed on three structures, i.e., cephalon, cranidium (without free cheeks) and pygidium. Morphospace occupancy and density as well as trilobite size were estimated and compared to generic richness through time. Whereas the cranidium showed only slight morphological diversification in the Early Devonian, the morphological disparity of the pygidium and the cephalon strongly increased. A disparity peak of pygidia was reached from the Pragian onwards while the cephalon continue to innovate. Along with the development of morphological novelties in the Early Devonian, the diversity increased, particularly in the Lochkovian. However, the Middle Devonian events affected the trilobite communities with simultaneous drastic loss of morphologies and richness. This coupling in diversity and disparity dynamics could be explained by either the intensity of extinctions or a high rate of internal constraints. Devonian trilobites represent a ‘Top-Heavy Clade’ implicating old clades with a more constrained morphology. The weak Famennian recovery did not allow trilobites to reach the Early Devonian diversity level, trilobites constituting a ‘Dead Clade Walking’ during their late evolutionary history.

Keywords:

Arthropods; Palaeozoic; morphology; size; extinction; diversity indices

1. Introduction

Studying successful clades ([Alfaro et al. 2009](#), [Benton 2015](#)) such as the trilobites during the Palaeozoic times remains fundamental in Macroevolution. Such evolutionary success requires the consideration of taxonomic diversity, assessing changes in the number of species through time, but also morphological disparity, assessing variation in morphology.

The trilobites were probably among the most abundant marine benthic macroinvertebrates during the Palaeozoic. Due to their high taxonomic diversity and their high morphological disparity, these arthropods constitute an important clade for documenting and testing macroevolutionary theories ([Eldredge and Gould 1972](#); [Foote 1991b, 1993](#)). They appeared and diversified during the Cambrian explosion (ca. 521 Ma), and showed an important evolutionary success to become one of the major groups of the Early Palaeozoic. However, the Hirnantian mass extinction, recognized as the first, severely affected them, leading to a strong biodiversity

decrease (Adrain et al. 1998). While the diversity remained relatively stable in the Silurian, the taxonomic richness changed importantly in the Devonian with the Pragian diversification followed by the Middle and the Late Devonian decline of diversity (Chlupáč 1994; Lerosey-Aubril and Feist 2012). These diversity changes took place in an unstable environmental context including quick sea-level fluctuations, anoxic/hypoxic events and climate upheavals (Walliser 1996; House 2002; Joachimski et al. 2009; Qie et al. 2019). These environmental events mainly affected the marine faunas and so the trilobites (Feist 1991; Lerosey-Aubril and Feist 2012), and triggered major biotic crises such as the Kellwasser events and the Hangenberg event, and subsequently major ecosystem restructuring (Raup and Sepkoski 1982; Buggish 1991; Sepkoski 1996; Bond and Grasby 2017). In the Late Palaeozoic, trilobites showed a low diversity, except for the last diversification in the Tournaisian, and they disappeared at the end of the Permian (Lerosey-Aubril and Feist 2012). Thus, the Devonian constituted a key period in the evolutionary history of trilobites with important increases and decreases of diversity.

At the macroevolutionary scale, the taxonomic component has been used traditionally as the major metric for a long time (Sepkoski 1978). However, numerous studies have shown the relevance of studying morphological disparity (Wills et al. 1994; Roy and Foote 1997; Foote 1997; Hopkins and Gerber 2017; Guillerme et al. 2020a) as an additional metric of biodiversity (e.g., Foote 1991a, 1993; Roy and Foote 1997; Neige 2003; Adams et al. 2004, 2013; Hopkins 2013; Minelli 2016; Jablonski 2019). Morphological changes could even be a better proxy to understand extinction events (Wan et al. 2021). While selective extinctions led to morphological losses, non-selective extinctions do not necessarily have the same effect (Foote 1991a; Puttick et al. 2020). Studies on trilobite morphology were one of the driving forces behind the development of disparity analyses, notably with the pioneering work of Foote (Foote 1989, 1990, 1991a). Further developments focused on modularity (Gerber and Hopkins 2011; Webster and Zelditch 2011; Oudot et al. 2019). Trilobites showed a constant rate of morphological evolution in the Cambrian (Paterson et al. 2019). With a rapid increase in morphological disparity early in their evolutionary history, trilobites reached maximum disparity in the Middle Ordovician (Foote 1991b, 1993; Webster 2007). Then, the morphological disparity decreased, rather slowly until the Late Devonian and then sharply until their disappearance at the Permian-Triassic boundary. Despite a slight increase of their morphological disparity during the Permian (Foote 1993), no significant increase has been observed in trilobites as a whole. However, at a smaller scale, trilobites could show reversible trends of morphological variation due to different factors (Webster 2007). Hopkins (2014) showed that environmental conditions affected morphologies, and that effects of some environmental

parameters changed through time. Developmental constraints also affected trilobite morphologies (Hughes et al. 2006; Gerber and Hopkins 2011; Crônier 2013; Oudot et al. 2019).

More particularly in the Devonian, trilobites were abundant, diverse and well preserved in North Africa. Due to their richness, they constitute an invaluable fossil record (Alberti 1969, 1981; Lebrun 2018). During the Devonian, North Africa was located in the northern margin of the Gondwana supercontinent, and most of the area was covered by epicontinental seas related to the Paleotethys Ocean (Guiraud et al. 2005). A major Early Devonian diversification was observed in this area before a decline in the Middle Givetian (Bault et al. 2021) related to environmental events (Kaufmann 1998). During the same period, numerous morphological innovations and morphological changes were also observed in trilobites in North Africa (Bault et al. submitted). Therefore, the present study provides a first comparison between the taxonomic diversity and the morphological evolution of trilobites during the Devonian and its unstable environmental context and global events (Joachimski et al. 2009; Becker et al. 2016). The relationship between these two metrics was investigated more accurately by using an updated dataset at the regional , in the well-documented North African fossil record, and using the stage as the temporal resolution . Comparing these two metrics leads to the exploration of large- biodiversity fluctuations, both in terms of patterns and processes, through time (Roy and Foote 1997) and space (Neige 2003).

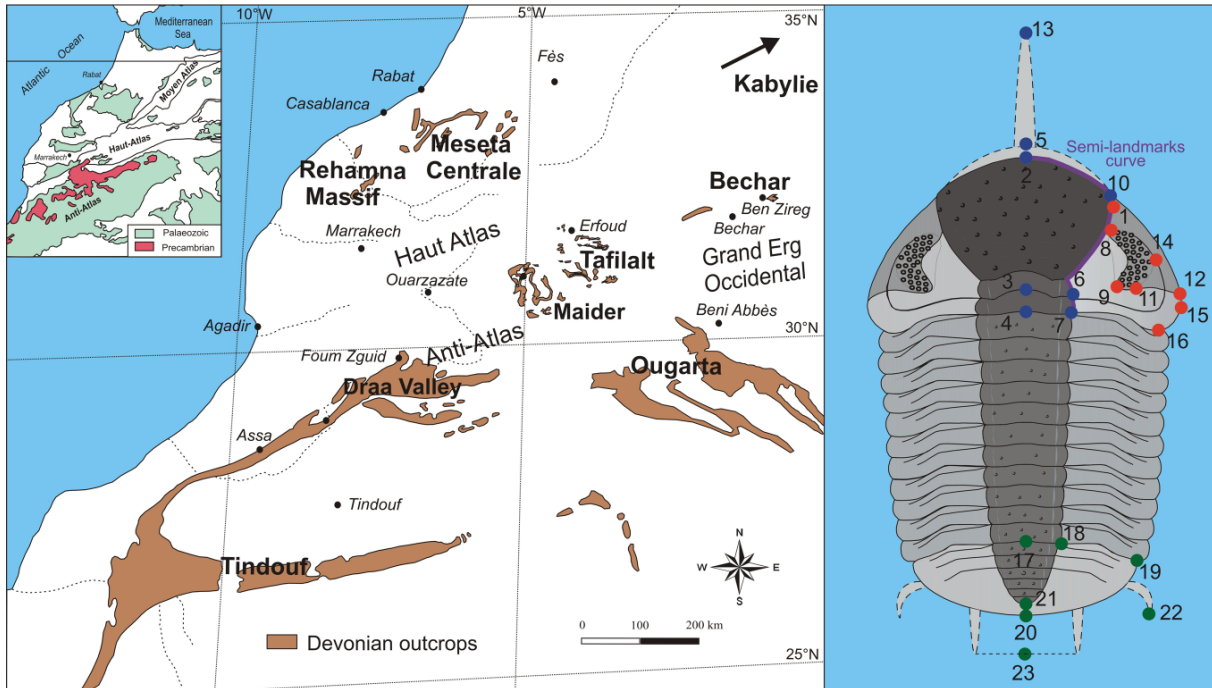
2 Material and methods

2.1. Data

Based on North African specimens (Fig. 1A) of trilobites illustrated in the literature (Appendix A), we compared the morphological dataset used in Bault et al. submitted and the associated taxonomic dataset. Analyses were performed to analyse two key structures, i.e., the cephalon and the pygidium (Whittington et al. 1997). Because in the fossil record, cephalons are more rarely preserved than cranidia (due to exuviation), cranidia on which numerous studies were done (Gerber and Hopkins 2011; Webster and Zelditch 2011; Hopkins 2013; Oudot et al. 2019) were added. Hopkins (2017) showed that morphological changes among cranidia depicted most of whole changes. From the literature, we selected the specimens with complete cephalon and/or complete cranidium and/or complete structure with a sufficient resolution to be analysed. We only used dorsal views and the right side (or the left side by using mirror image if the preservation was better) for each structure. Consequently, we analysed respectively 308 cephalons, 943 cranidia and 604 pygidia for both diversity (i.e., taxonomic diversity) and disparity

(i.e., morphological disparity) analyses. Only one cephalon and 35 cranidia used in our study correspond to early juveniles, i.e., meraspid stages, the rest of the dataset corresponds to late juveniles or adults, i.e., holaspid stages. Morphological changes studied correspond to adult morphological variations observed between holaspids and not to ontogenetic series.

Figure 1. (A) Geographical location of Devonian outcrops of North Africa (from [Hollard, 1968](#)) and



(B) complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight landmarks for cephalon (in red), plus eight for cranidium (in blue), and seven for pygidium (in green); and some linear measurements. Modified from [Crônier \(2013\)](#).

2.2. Geometric morphometrics and disparity indices

The three studied structures (i.e., cephalon, cranidium, pygidium) were investigated using geometric morphometrics with the acquisition of landmarks and semi-landmark coordinates (for a general overview of geometric morphometrics, see [Adams et al. 2004](#)). Twenty three landmarks and one semi-landmark curve were used to digitize each 2D shape from published illustrations. Fifteen landmarks were digitized on the cephalon, 7 on the cranidium and 7 on the pygidium (Fig. 1B; for a description of landmarks, see [Bault et al. submitted](#)). Six landmarks between the cephalon and the cranidium and the semi-landmark curve are common (Fig. 1B). The semi-landmark curve was automatically converted into a series of 16 points. The digitalisation was performed using the free software TPSdig 2.32 ([Rohlf 2005, 2015](#)); no landmarks were estimated. Landmarks are positioned on the key positions modelling trilobite shapes, known to be changed through time and between clades.

To standardize of the landmarks to remove the effect of size, location and orientation, they were processed using the Generalized Procrustes Analysis (Gower 1975; Rohlf and Slice 1990; Bookstein 1991; O’Higgins 2000; Zelditch et al. 2012). The superimposed landmarks are projected to a linear tangent space at the full Procrustes mean (Rohlf 1999).

In order to quantify accurately the morphological disparity changes through time based on the morphospaces, we used two disparity indices (Foote 1991a; Ciampaglio et al. 2001; Wills 2001; Guillerme et al. 2020b). Indeed, the disparity indices are essential to assess the different aspects of disparity changes (Puttick et al. 2020). Disparity measurement could be summarized in three different categories: the size, the density and the position of the morphological occupancy (Wills 2001; Guillerme et al. 2020b). Indices related to the size of the morphospace occupancy are the sum of range (SoR), the sum of variance (SoV), and the mean Euclidean distance from centroid (MECoid). The SoR is an index of magnitude, corresponding to the total range of morphospace occupancy. This index is particularly sensitive to the sampling effort (Foote 1991a) and could be influenced by rare outlier morphologies (Deline 2009). The SoV is an index based on the variance of the specimen scores on each morphospace axis (Foote 1991b, 1993), measuring the average morphological dissimilarity among specimens. This index depends on the taxonomy (Foote 1991a). Nevertheless, to avoid such bias we studied all the specimens available with sufficient quality and not one specimen per taxa. The MECoid corresponds to the Mean Euclidean distances between all pairs of specimens of each geological stage. The Nearest-Neighbour Distance (NND) is used as an index of density, corresponding to the shortest Euclidean distance between two points of a distribution of points.

The sample size being not homogeneous between the different time bins, we computed morphological rarefaction in addition to the raw value per bin for each time bin studied. For this, for 1000 repetitions, we extracted smaller subsamples of the same size from a larger group without replacement and recalculated the morphological indices each time. Confidence intervals correspond to the 25 and 75 percentiles.

Environmental events are known to have an effect on the size of organisms, such as the size reduction known as the ‘Lilliput Effect’ (Harries and Knorr 2009). In a context of global environmental changes, we analysed whether size changes occurred in the Devonian. Specimen size was estimated as the natural logarithm of the centroid size (CS), i.e., the square root of the sum of squared distances of all the landmarks from the centroid. Logarithmic values allow size to be analysed into convenient values as previously done by Dommergues et al. (2002) on ammonoids. Trilobite size is plotted using box plots.

2.3. Diversity indices and comparison with disparity values

We estimated the taxonomic richness of our dataset to compare the taxonomic diversity and the morphological disparity through time. Diversity was measured here as genus richness at the stage. Taxonomic richness was estimated with the Sample-in-bin diversity (SIB; [Foote, 2000](#); [Alroy, 2010](#)) corresponding to the raw count of taxa actually documented (see [Bault et al. 2021](#)). To establish the comparison between the two metrics from the same North African area, we used the diversity curves obtained by [Bault et al. \(2021\)](#).

The strength of the correlation between diversity and disparity was tested between the disparity indices and the diversity indices. Correlations were made from the Ludlow to the Famennian except for the Frasnian, which is characterized by a lack of data. In order to have sufficient stages for our analyses, these statistics were based on raw diversity and not on rarefied diversity. Different correlations were made for the cephalon, cranium and pygidium and in the same way, correlations were made for each disparity indices. The correlation index used is Kendall's tau ([Kendall, 1938](#)) and p values are adjusted in case of multiple correlation to avoid false positives.

Finally, a comparison between morphological disparity and taxonomic richness increase during the early Devonian diversification has been done. SIB, SoR and SoV have been standardized and are compared each over. [Jablonski \(2017\)](#) suggested that a higher increase of morphology than diversity suggests a less constrained developmental processes or exceptional ecological opportunities. This type 1 diversification is typical of 'early burst radiations'. Conversely, when the taxonomic diversification outstrips the morphological one, this type 3 diversification is rather a case of 'nonadaptive radiation'. An intermediate diversification exists with concordant morphology and diversity increase, this is the type 2 diversification.

All analyses were computed using the R scientific environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>) and the 'geomorph' (v. 3.2.1; [Adams and Otárola-Castillo 2013](#)) and 'epaleo' (v. 0.8.41; [Monnet, unpub.](#)) packages, as well as the PAST software (version 3.24; [Hammer et al. 2001](#)).

3. Results

3.1. Taxonomic diversity

The taxonomic richness showed the same trend between the three studied structures. Inherited from the reduced diversity of the Silurian, the diversity in the Lochkovian remained low, although it increased slightly especially for pygidia (Fig. 2). A sharp diversification

occurred in the Pragian with an important increase of taxa followed by a slowdown in diversity variably marked according to the studied structures (less marked in pygidia, more marked in cephalata). This slowdown did not prevent maximum diversity observed at the Emsian, illustrated by the impressive increase of the SIB index recorded through this stage (Fig. 2). Whatever the studied structure, the diversity began to decrease in the Eifelian before a severe decline in the Givetian. Finally, the trilobites did not recover their previous level of diversity despite a slight diversification in the Famennian.

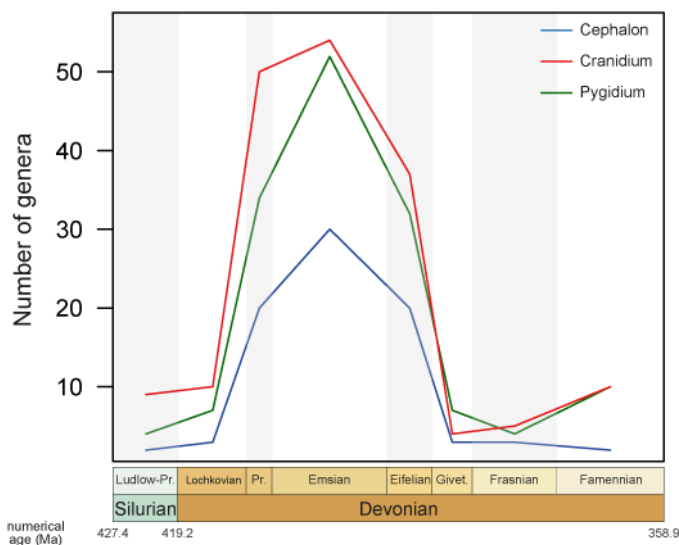


Figure 2. Diversity dynamics of Silurian and Devonian trilobites from North Africa. Number of genera per stage represented in each structure are represented in blue for cephalon; red for cranidium and green for pygidium. Modified from Crônier (2013). Ages from Cohen et al. (2013, v. 3/2020).

3.2. Size of the morphospace occupancy

The morphological disparity indices fluctuated differently according to the three studied structures (Fig. 3). Both raw data and rarefacted values show the same trends. There was a low level of morphological extent in the Silurian characterized by very low values of SoR, SoV and MECoid). An impressive increase of SoR index is recorded during the Lochkovian-Pragian (more impressive for cephalata than cranidia or pygidia), which reflects the filling of the morphospace. In the same time, SoV and MECoid increased for the cephalon and the

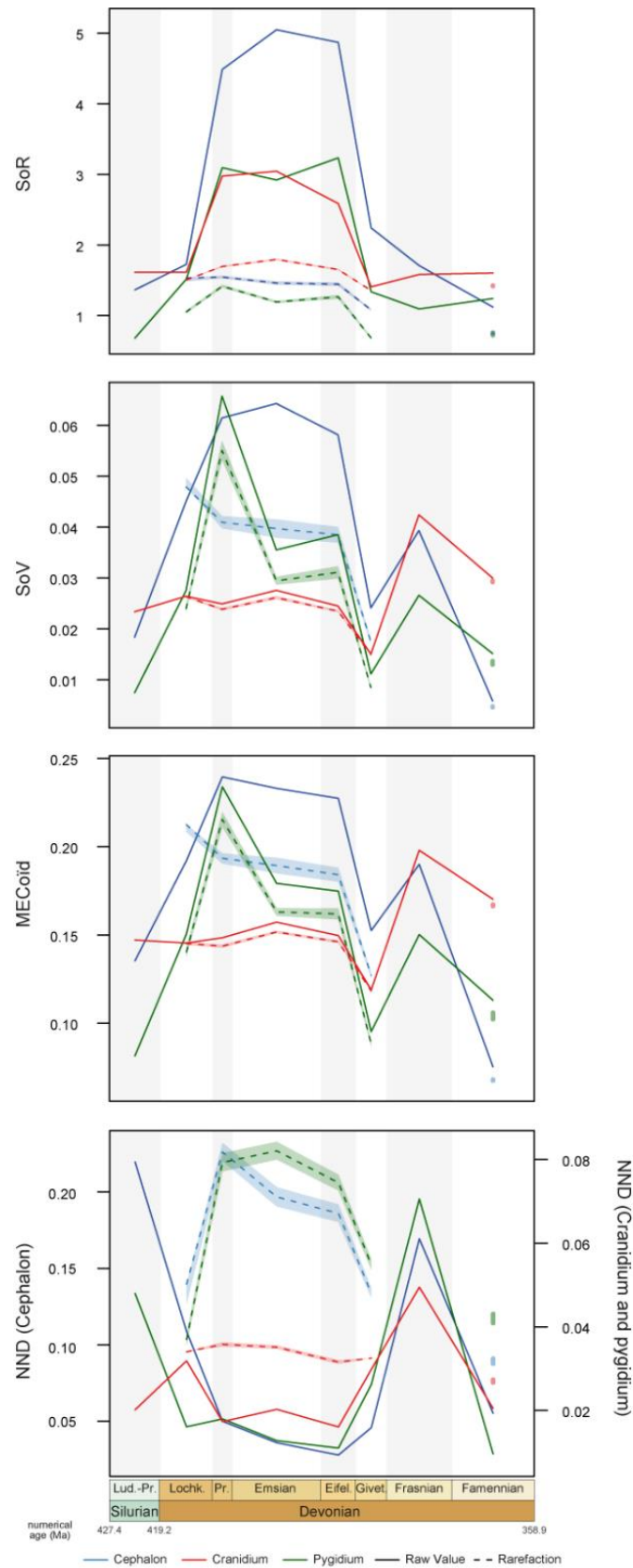


Figure 3. Morphological disparity indices according each structure of Silurian and Devonian trilobites from North Africa. Indices used are Sum of Ranges (SoR); Sum of Variance (SoV); Mean Euclidean distance from Centroid (MECoid) and the nearest Neighbour Distance (NND) and displayed for each stage.

pygidium but not for the cranidium. While the total range of morphospace occupancy remained high during the Emsian for the three studied structures (high values of SoR, Fig. 3), only cephalae were characterized by high values of SoV and MECoïd (Fig. 3). A morphological disparity peak occurred either in the Pragian or the Emsian depending on the metrics and the structure studied. Then, there was a slight decrease of morphospace occupancy in the Eifelian except for pygidia. A substantial decrease of SoR index is subsequently recorded during the Eifelian-Givetian (more impressive for cephalae than cranidia or pygidia). A low level of morphological disparity characterized the Givetian (all indices, SoR, SoV and MECoïd, show very low values; Fig. 3): morphospace occupancy collapsed in the Givetian for all structures. Then, a moderate but significant increase of the morphological disparity is observed during the Frasnian (increase of SoV and MECoïd index for the three studied structures). Only a moderate but significant decrease of the SoR index is recorded in cephalae and cranidia, while an increase is recorded in pygidia. Nevertheless, in the absence of a sufficient number of specimens, this trend remains highly uncertain and should be treated with caution. In the Famennian, while the total range of morphospace occupancy continued to decrease for cephalae compared to the Givetian (lower values of SoR, SoV and MECoïd, Fig. 3), cranidia and pygidia show moderate increasing morphological disparity indices. Both SoV and MECoïd indices show roughly similar trends (Fig. 3).

3.3. Density of the morphospace occupancy

The NND used as indicator of the density of the morphological occupancy is strongly influenced by the sampling effort (Fig. 3). For this index, raw values seem more reliable than rarefaction ones because the diversity was different between stages and thus the density is strongly modified in the case of a rarefaction method based on a same virtual abundance between stages. This is probably why it is the only index showing different trends between raw data and rarefaction data. The raw NND index sharply decreased in the Lochkovian for both cephalae and pygidia, while it increased for cranidia. As was the case for morphological occupancy indices, this density index shows an opposite trend for cranidia, for which it increased. Rarefacted NND also increased for the cranidium, but for the cephalon and the pygidium too. In the Pragian, the NND index shows very low raw values for the three studied structures suggesting a relatively low morphological disparity, whereas the rarefaction data show exactly the opposite, suggesting an evolution from depopulated Lochkovian assemblages to rich Pragian ones. Rarefaction and raw values are maintained at a plateau during the Emsian and Eifelian, two periods where many specimens were encountered in North Africa. The NND

index subsequently increased during the Givetian and the Frasnian, followed by a decrease in the Famennian, although rarefaction values indicate the opposite. As with the other indices, the lack of specimens in the Frasnian prevents us from drawing robust conclusions.

3.4. Correlation between diversity and disparity indices

Correlations (see Table 1) between the various disparity and diversity (i.e., number of genera) indices were computed. For cephalon, diversity trends are correlated to disparity trends, using SoR and SoV (p -value = 0.005, Kendall’s tau $t = 0.93$), MECoid and NND ($p < 0.05$). For cranidia, disparity and disparity trends are uncorrelated using SoV, MECoid and NND ($p > 0.05$), except for SoR (p -value = 0.021). For pygidia, disparity and disparity trends are uncorrelated, using SoR and NND ($p > 0.05$), but the SoV and MECoid are correlated to diversity trends ($p < 0.05$). Size of the trilobites was not correlated to diversity whatever the structure studied.

	SoR		SoV		MECoid		NND		CS	
	P	Tau	P	Tau	P	Tau	P	Tau	P	Tau
Cephalon	0.005	0.93	0.005	0.93	0.013	0.82	0.041	-0.68	0.351	0.31
Cranidium	0.021	0.75	0.120	0.51	0.282	0.35	0.167	-0.45	0.645	0.15
Pygidium	0.129	0.49	0.033	0.68	0.015	0.78	0.224	-0.39	0.129	0.49

Table 1. Correlation results between diversity and each morphological disparity index. *P* values adjusted and Kendall’s tau for each structure are displayed.

3.4. Diversification modes

The morphological disparity for the cephalon, the cranidium and the pygidium increased rather correlatively during the Early Devonian diversification (Fig. 4). This places the Devonian trilobites of North Africa in the type 2 diversification of Jablonski (2017). Nonetheless, the SoV of the cephalon and the cranidium showed higher variation than the taxonomic richness, suggesting a potential type 1 diversification. Conversely, the SoV of the pygidium less increased than the diversity index, indicating a link with the type 3 diversification.

3.6. Size range

In the Silurian, the trilobites exhibited large cephalon (and also large cranidia) but small pygidia. Cephalon and cranidia are characterized by high values for median size and an

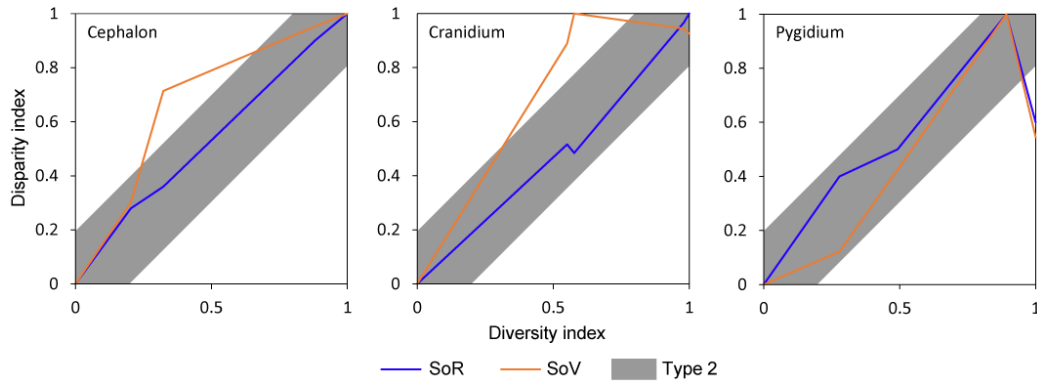


Figure 4. Diversity-disparity space (Jablonski, 2017) of the relation between taxonomic and morphological diversification of Devonian trilobites from North Africa. Type 1: Dominance of morphological diversification; Type 2: Morphology concordant with taxonomic diversification; Type 3: Dominance of taxonomic diversification.

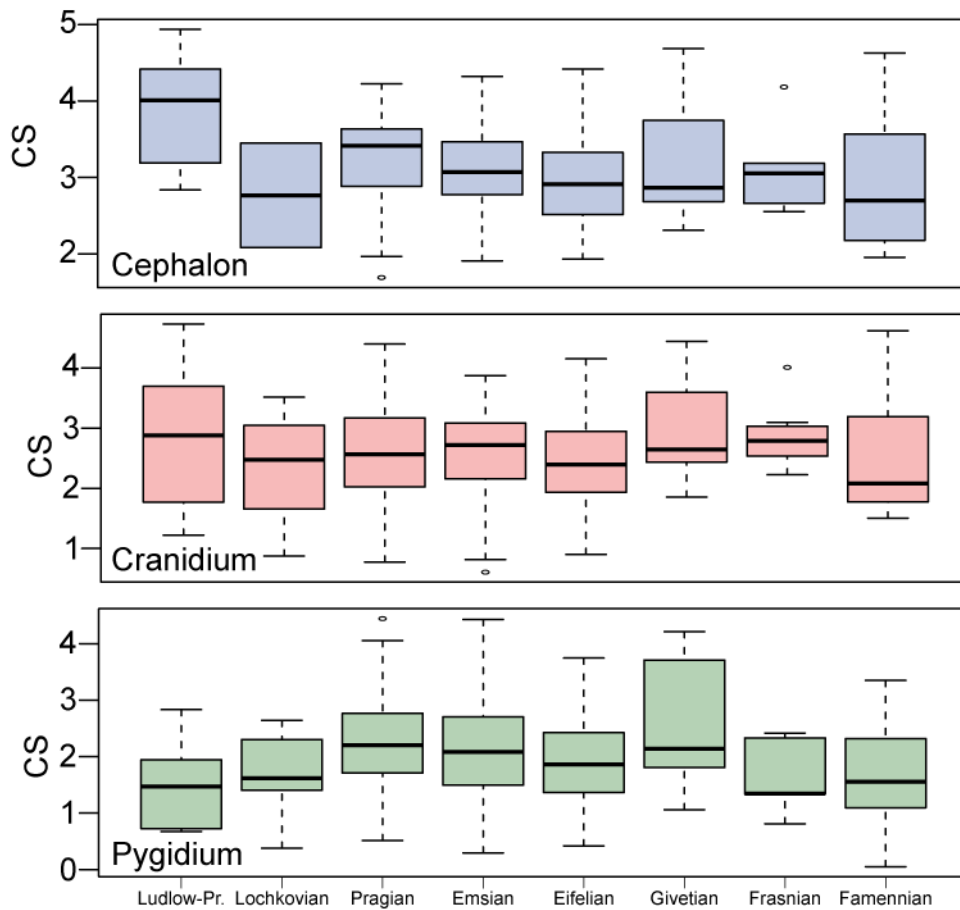


Figure 5. Centroid size through time of Silurian and Devonian trilobites from North Africa for each structure (i.e., cephalon; cranidium and pygidium).

expanded size range. Subsequently, for cephalon as for cranidia, the median size (according to CS) decreased strongly in the Lochkovian, while for pygidia, the median size increased moderately (Fig. 5): there was a loss of trilobites with larger cephalon. In the Pragian, an increase in the median size began for cephalon (and for cranidia) and continued for pygidia: trilobites

exhibited large morphologies, and pygidia were larger than those found in the Silurian. No particular size changes are noticed in the Emsian, and only a slight size reduction for both cephalo (and cranidia) and pygidia is recorded in the Eifelian. Major size changes are recorded in the Givetian with a more important size range towards large trilobites with large cranidia and pygidia although the median size remains similar to the size recorded in the Emsian. In the Frasnian, only pygidia show a median size reduction. Nevertheless, compared to the Givetian, cephalo and cranidia show an impressive reduction in the size range with the disappearance of the largest morphologies. Subsequently, in the Famennian, cephalo (and cranidia) recorded an impressive reduction of the median size (not observed in pygidia) and show a significant increase of their size range of the same order of magnitude as that observed in the Silurian or the Lochkovian (Fig. 5).

4. Discussion

4.1 Diversification: diversity vs. disparity

Both morphological disparity and taxonomic richness were very low at the end of the Silurian. Then, trilobites underwent two periods of diversification in the Devonian, in North Africa as well as at the global (Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021): in the Early Devonian and in the Famennian. However, these two periods of diversification diverge by their intensity and duration.

In the Early Devonian, the morphological disparity slightly increased in the Lochkovian, but the most important diversity and disparity rise occurred in the Pragian. This stage corresponded to the onset of the Early Devonian diversification (Chlupáč 1994), which arose with the Basal Pragian event, a regression that led to the development of shallow carbonate environments (Chlupáč and Kukul 1986). The morphospace density also progressively increased in the Lochkovian and the Pragian, particularly for the cephalo, suggesting the proliferation of taxa with similar shapes. This corresponded especially to the proliferation of some families such as proetids, tropidocoryphids, phacopids and scutelluids (Bault et al. 2021). Simultaneous increase in diversity and morphological disparity could indicate adaptive radiation (Foote 1993, 1997). A morphological disparity increase is generally linked to an ecological disparity increase (Cole and Hopkins 2021), although Bapst et al. (2012) emphasized the necessity to perform more detailed analyses to confirm this theory. With the establishment of new areas in North Africa (Morzadec 2001; Bault et al. 2021), clades rapidly colonised new territories and expanded both

in terms of diversity and disparity. Such colonisation has been recognized as the empty ecospace hypothesis (Erwin 1993; Ciampaglio 2002; Hughes et al. 2013; Novack-Gottshall 2016). Exceptional ecological opportunities could even lead to a higher rate of morphological evolution during a diversification (i.e., Type 1 diversification, Jablonski 2017). However, Devonian trilobites were rather in a case of concordant morphological and taxonomical diversification (i.e., Type 2 diversification, Jablonski 2017), an intermediate diversification between ‘early burst diversification’ and ‘nonadaptive radiation’ (Jablonski 2017). Nevertheless, it implied a radiation favoured by new environmental niches (Chlupáč 1994). In addition, the exoskeleton enlarged in the Pragian, particularly that of cephalon and pygidia, while the cranidia retained their Lochkovian size. This was the consequence of the appearance of spines (Bault et al. submitted).

With the maintenance of favourable environments, particularly in North Africa, the trilobites continued to diversify until they reached a diversity peak in the Emsian (Chlupáč 1994; Bault et al. 2021). During this period of intense taxonomic diversification, the morphological disparity still increased for both cephalon and cranidium. An increase of the size of the morphospace (i.e., SoR) shows that the increase of disparity corresponded to the appearance of new morphologies on the edges of the pre-existing morphospace (Ricklefs and Miles 1994; Roy and Foote 1997), in particular morphologies with both sagittal and genal spines (Bault et al. submitted). The proliferation of morphologies with spines among Early Devonian trilobites was interpreted as a potential response to increasing nektonic predation (Brett 2003) in the frame of the Devonian Nekton Revolution (Klug et al. 2010). Moreover, the proliferation of scutelluids contributed to the extension of the morphospace occupancy with the development of long sagittal pygidia with a small rachis (Bault et al. 2021).

On the other hand, decrease of ecological opportunities slow-down the rate of morphologic evolution (Mahler et al. 2010; Hopkins 2013). Trilobites having invaded most of the ecological niches appeared in the Pragian (Chlupáč 1994), it may explain the lower increase in disparity in the Emsian (or even the decrease depending on the structure and the metric observed). Indeed, the pygidium reached its maximum disparity from the Pragian onwards, while the cephalon continued to innovate until the Emsian. In the case of an adaptive radiation, trilobites still diversified morphologically but the novelties were concentrated on the cephalon. Hence, the morphological disparity of the pygidium and the cephalon became decoupled. This explains why both cephalon and cranidium were closer to the Type 1 diversification of Jablonski (2017), whereas for the pygidium, the morphological diversification was lower than the taxonomic one. A greatest cephalon diversification was possible because the cephalon was devoted to a wider

range of tasks, including feeding habits (Fortey and Owens 1999) and visual ability (Clarkson 1975; Schoenemann 2021).

The second period of diversification that occurred in the Famennian (Lerosey-Aubril and Feist 2012; Bault et al. 2021) was less intense than the Early Devonian diversification. The Famennian peak of taxonomic richness occurred after a period of low diversity due to the Kellwasser events (Feist 1991; Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021). In contrast to the Early Devonian diversification, where five orders contributed to diversity peaks, only two orders (i.e., Phacopida and Proetida) were responsible for the Famennian diversity peak. The Famennian recovery was not accompanied by a development of new morphologies except a slight increase of the cranidium and pygidium disparities. The decrease in the morphospace density suggests a clustering trend among the Famennian trilobites (Foote 1990; Wills 2001). The absence of a disparity burst after the Kellwasser mass extinction indicate that biological constraints such as competing clades did not disappear (Oyston et al. 2015). A recovery with few innovations was also reported in other clades like graptolites (Bapst et al. 2012).

4.2. Extinctions and recoveries: diversity vs. disparity

The diversity strongly dropped during the Middle Devonian of North Africa. At the global , the Middle Devonian ecosystem faced several extinction events, i.e., the Eifelian Choteč and the Kačák events and the Givetian Taghanic event (Walliser 1996; House 2002). Sea-level rise and anoxic/hypoxic conditions characterized these events (Kaufmann 1998; House 2002). At the North African , these successive events led to the loss of many genera and families within trilobites (Bault et al. 2021). This decrease began in the Eifelian to reach a minimum of diversity in the Givetian. The morphological disparity was not affected immediately and most of the morphospace occupancy persisted in the Eifelian. Nevertheless, the acceleration of the extinctions in the Givetian strongly influenced trilobite morphological disparity. Therefore, although the Choteč event greatly affected the Moroccan area (Becker and Aboussalam 2013), the following Kačák and Taghanic events had a stronger effect on trilobite morphologies. In particular, the Taghanic event corresponded to a global faunal overturn due to rapid eustatic changes and overheating pulses and affected Moroccan trilobites (Aboussalam and Becker 2011). This delay in the morphological loss was not specific to trilobites. Among macrobenthos, diplobathrid crinoids showed the same pattern with only a slight morphological loss in the Eifelian despite an important diversity decrease and the main morphospace collapse that

occurred only later, in the Late Devonian (Cole and Hopkins 2021). Through the Late Ordovician extinction, graptolites also underwent a decrease of diversity before the morphological disparity drop (Bapst et al. 2012). On the other hand, in ostracods, the morphological disparity declined before the taxonomic richness during the end-Permian mass extinction (Wan et al. 2021). Henceforth, the Middle Devonian events led to several shape losses among trilobites resulting in a collapse of the morphological range and a strong decrease of the variance. These changes indicate a non-random extinction (Ciampaglio et al. 2001) contrary to the Early Palaeozoic decline during which the extinctions were not morphologically selective and so the disparity and diversity were decoupled (Foote 1991a, 1993; Hopkins 2013). The shape losses among trilobites correspond especially to the disappearance of trilobites with genal spines as the aulacopleurid *Cyphaspides* Novák, 1890 or the asteropygin *Mrakibina* Morzadec, 2001 (Morzadec 2001; Chatterton et al. 2019).

The Frasnian-Famennian trends were more difficult to analyse because of the lack of data in the Frasnian. North African trilobites seem to lose their morphological disparity through the Late Devonian extinction, i.e., the Kellwasser events, which was one of five major extinction events in the life history on Earth (Buggisch 1991; McGhee 1996; Racki 2020). The cephalic morphologies were the most affected, notably with the disappearance of the remaining spiny shapes such as the genera *Gondwanaspis* Feist, 2002 or the trilobites with large cephalic shields such as harpetids (Feist 2002). The density of morphologies seemed not strongly affected by this decrease, suggesting only marginal or lateral extinctions (Foote 1991a; Korn et al. 2013). Consequently, not all the trilobite taxa were affected in the same way. In North Africa as at the global, the most impacted taxa were member of the orders Lichida, Odontopleurida, Harpetida and Corynexochida, which disappeared before the Famennian (Feist 1991; Lerosey-Aubril and Feist 2012; Bault et al. 2021).

In addition to the effects of extinctions, ecological constraints can limit the morphological disparity (Oyston et al. 2015). Thus, sea-level rise and a long-term eustatic rise affected the Middle and Late Devonian faunas (Johnson et al. 1985; Kaufman 1998; House 2002) and led to a decrease of the trilobite speciation rate by increasing range expansion (Abe and Lieberman 2009). The morphological disparity was also partly linked to environmental heterogeneities or changes (Hopkins 2014; Bault et al. submitted); a harmonization of environment led to a decrease in the morphological range. However, ecological stresses induced by unfavourable environmental changes could lead to increasing intraspecific variability (Crônier et al. 2015). Such ecological stresses could be induced by the development of potential predators in the second half of the Devonian leading to selective extinction. Non-random extinction is consistent

with standard environmental changes, whereas catastrophic events such as the end-Permian extinction were non-selective (Villier and Korn 2004). Moreover, a potential saturated taxonomic richness could favour such a decline, while the diversity reached its maximum during the Emsian (Bault et al. 2021). A self-regulation in a period of high diversity has been previously reported among trilobites (López-Villalta 2016).

Although most innovations occurred during the diversification phase of the Devonian (see previous section), some of them occurred during periods of low diversity across environmental events. The most emblematic case was the strong development of reduced-eyes and blind trilobites in the Late Devonian (Crônier et al., 2004; McNamara and Feist, 2006, 2016; Schoenemann 2018; Feist 2019; Bault et al. 2021). These morphological novelties were the consequences of ecological changes as deepening and turbiditic habitats for endobenthic behaviours (Feist and Clarkson 1989; Feist et al. 2009). In North Africa, this trend was represented by the development among others of the blind genera *Dianops* Richter and Richter, 1923, *Trifoliops* Crônier, 2003, *Trimercephalus* McCoy, 1849 and *Palpebralia* Richter and Richter, 1927 (Feist 2002; Crônier et al. 2013; Feist et al. 2016). However, despite the availability of ecospace after mass extinctions (Erwin 2015), no extensive morphological innovations occurred, and in North Africa, the Famennian morphological disparity of trilobites remained similar to the Frasnian values. At the global, the morphological innovations occurred later after the Kellwasser crisis, unlike the subsequent Hangenberg event for which the morphological innovations occurred immediately after (Feist 1991).

Following a biotic event, some clades showed a trend to decrease in size, known as ‘Lilliput effect’ (Harries and Knorr 2009). This trend was recorded for different crises and different clades (Twitchett 2007; Song et al. 2011; Brom et al. 2015; Berv and Field 2018; Wiest et al. 2018 among other) among which are some arthropods (Forel et al. 2015; Chu et al. 2015; Martínez-Díaz et al. 2016). However, a ‘Lilliput effect’ has not yet been reported under this name among trilobites although a decrease in size affected trilobites as a whole, for example in Norway in the Late Ordovician (Sigurdson and Hammer 2016). In the Devonian, such decrease in size was reported in other clades during the early Givetian (Bosetti et al. 2011; Corniskey et al. 2016; Zhuravlev and Sokiran 2020) or in the external platforms after the Taghanic transgression of the mid-Givetian within trilobites (Crônier 2013). Before the Taghanic transgression, trilobites were characterized by their large size and the genera *Hypsipariops* Struve, 1982 and *Drotops* Struve, 1990 (Struve 1995) were among the largest Devonian trilobites. In a context of sea-level rise, presence of large trilobites could have resulted the invasion of deep environments like North African Ordovician trilobites (Saleh et al. 2021).

However, in this case, these phacopids represent assemblages adapted to unstable, high energy environments of shallow internal platforms. They are morphologically characterized by their large, wide and high reniform eyes with numerous lenses, their developed tuberculation and their multisegmented pygidium (Crônier 1999; Crônier and Courville 2003; Crônier 2013). In the Eifelian and in the Famennian, the average size decreases, but only slightly, and large trilobites remained present. Hence, it appears that no ‘Lilliput effect’ affected North African trilobites throughout the Middle and the Late Devonian events. The late Frasnian Kellwasser events were not characterized by decrease of trilobite size no more than Russian microconchids (Zatoń and Krawczyński 2011) or crinoids, which even experienced body-size increase (Brom et al. 2018). However, our study focused on trilobites as a whole and at the stage level which might not be precise enough to identify such a pattern.

4.3 Coupled diversity and disparity trends?

At the global scale, during the Palaeozoic, the Early Devonian represents the second most important period of diversification, after the initial Cambrian radiation (Adrain 2008). This bimodal evolutionary radiation was not unique, being found in other taxa (i.e., dinosaurs, crinoids) and periods (i.e., Mesozoic and Cenozoic) (Romano et al. 2018; Romano 2021). The Devonian diversification was different to the Early Palaeozoic diversification for which diversity and disparity were decoupled (Foote 1993). The Cambrian-Ordovician was the early period of the trilobite evolutionary history, and the increase of their diversity corresponded to the appearance and the development of new orders (Fortey 2001; Paterson et al. 2019). The Devonian diversification, on the other hand, involved high taxonomic ranks (family and above) that already existed before (Chlupáč 1994). This difference could explain why morphological innovations stopped increasing at the same time as diversity during the Devonian Period. In addition, trilobites exhibited greater morphological variation early in their evolutionary life (Webster 2007), and thus, during the Cambrian, their morphologies were less constrained during their ontogenetic development than later during the Devonian (McNamara 1986; Hughes 1991, 2007). The moulting behaviour showed the same decreasing pattern with the disappearance of ventral sutures and the increasing importance of the cephalon moulting to the detriment of the other moulting characteristics (Drage 2019). Thus, the concordant increase in diversity and disparity observed during the Devonian diverge from the ‘early burst’ diversification characterised by high rates of disparity increases observed during the Cambrian-Ordovician (i.e., Type 1 diversification of Jablonski (2017)). Because a higher level of

constraint limits innovations (Oyston et al. 2015), the morphological disparity did not increase after the Emsian diversity peak. This pattern was already reported among trilobites during the Ordovician diversification when Phacopida showed simultaneous morphological and taxonomical changes (Foote 1993). Cole and Hopkins (2021) also noticed coupled diversity and morphological disparity dynamics among diplobathrid crinoids during the Palaeozoic.

The Early Palaeozoic and the Devonian also differ according to their timing of the end-diversification. In the Early Palaeozoic, after the taxonomic richness peak, trilobite diversity decreased progressively before a stronger decline in the Hirnantian (Adrain et al. 1998; Sheehan 2001; Fan et al. 2020). Conversely, in the Devonian, trilobite diversity decreased sharply (Lerosey-Aubril and Feist 2012). This dynamic was not specific to trilobites because the crinoid and conodont diversifications were also interrupted by the Devonian extinction events (Ginot and Goudemand 2020; Cole and Hopkins 2021). Consequently, the increase in disparity in the Devonian could be stopped during its rise and the coupling between changes in diversity and disparity would be a false pattern.

4.4. Dynamics and macroevolutionary patterns

Maximum morphospace occupancy occurred in the Early Devonian and then, decreased consistently from the Eifelian onwards until the Famennian. The morphological disparity changes were consistent with the diversity fluctuations (Feist 1991; Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021). Gould et al. (1977) defined an index to identify if the clades were more diverse before, after or midway through their evolutionary history. Although the Early Palaeozoic clades, including trilobites, showed greater diversity in their early evolutionary history and are characterized as ‘bottom-heavy’ clades (Gould et al. 1987), North African trilobites showed an increase in both diversity and morphological disparity in the Devonian, from the Pragian. Such diversification was unusual because it involved families and subfamilies which appeared in the Ordovician more than 35 Myr before, such as phacopids, proetids or acastids (Adrain 2013). Hence, most Silurian and later clades had higher taxonomic richness midway through their history, and are characterized as symmetrical clades, or later through their history and are characterized as top-heavy clades (Gould et al. 1987).

In Macroevolution, evolutionary rates are often higher in the early history of clades (Hughes et al. 2013) because of a slowdown due to an important morphological space saturation (Foote 1994; Villier and Eble 2004), diminishing ecological opportunities through time (Erwin 1993; Foote 1997) and internal constraints (Wagner 2000; Oyston et al. 2015). However, the

evolutionary rates varied through time, and other patterns such as ecomorphological shifts occurred (Hopkins and Smith 2015). The widening of favourable environments since the Pragian (as discussed above) promoted a morphological and taxonomical diversification with new ecological niches. Phenotypic plasticity could foster diversity increase with new environmental opportunities, although its role on disparity remaining uncertain (Minelli 2016). However, phenotypic plasticity seemed less important among Devonian trilobites (McNamara 1986; Hughes 1991, 2007; Webster 2007), although with respect to Devonian trilobites it remains largely unexplored and needs more investigation. Subsequently, a strong decline of diversity and morphological disparity occurred in the second part of the Devonian. Most of the trilobite families disappeared before the Carboniferous with the exception of proetids (Lerosey-Aubril and Feist 2012), confirming that Devonian trilobite families did not constitute a Bottom-heavy clade but rather a Symmetrical or a Top-heavy clade.

After the peak of both diversity and disparity in the Emsian, trilobites strongly declined and never reached their previous taxonomic and morphological richness. The Middle Devonian extinctions occurred at both regional and global at low taxonomic ranks among trilobites (Lerosey-Aubril and Feist 2012; Bault et al. 2021). However, the demise of several families and orders occurred later, in the Frasnian (Feist 1991). Some extinctions led to evolutionary bottlenecks with a reduction of the morphological and taxonomic diversification afterwards, like the Late Devonian extinction (Sallan and Coates 2010; Cole and Hopkins 2021). Conversely, the disappearance of taxa can trigger new diversification events leading to increase the ecological opportunities (Erwin 1993, 2001). With regard to the trilobites in particular, the Devonian extinctions hampered the subsequent great diversifications (Lerosey-Aubril and Feist 2012) and the new opportunities were not sufficient to reverse this trend, as for Early Triassic anomodonts (Ruta et al. 2013). This delay places many trilobite taxa among the Dead Clade Walking (DCW) of Jablonski (2002). Only the order Proetida, which showed another important diversification later, in the Tournaisian (Lerosey-Aubril and Feist 2012), did not exhibit a DCW pattern. Because Phacopida survived more than one stage after the Middle Devonian extinction, they were not a DCW strictly speaking (Jablonski 2002) but they showed a similar pattern. Nevertheless, Barnes et al. (2021) extended the concept to longer duration, impacts of mass extinction having longer influence than expected. This is partly due to the long-term impact of selective extinctions on the trait distributions of later species (Puttick et al. 2020). Although trilobites slightly recovered after the Kellwasser events (Feist 2019), they remained poorly diversified in the Famennian in North Africa (Fig. 2, Bault et al. 2021) as well as at the global (Feist 1991; Chlupáč 1994). On the contrary, many clades recovered strongly in the Famennian,

among which are many nektic organisms (Klug et al. 2010) and some benthic organisms such as echinoderms (Waters and Webster 2009). Other taxa (i.e., brachiopods for instance (Baliński 2002; Curry and Brunton 2007)) were less affected and remained quite diverse despite extinction as they recovered quickly. The Late Devonian events led to bottleneck periods for the trilobites but also for other organisms such as diplobathrid crinoids, which vanished in the Carboniferous after having come close to extinction in the Devonian (Cole and Hopkins 2021). This trend suggests that trilobites were a major clade during the first half of the Palaeozoic but not at the end-Palaeozoic although they survived until the Permian with few periods of diversification (Lerosey-Aubril and Feist 2012). Apart from proetids, trilobites are a Dead Clade Walking (Jablonski 2002; Barnes et al. 2021).

5. Conclusion

Trilobites proliferated in North Africa during the Devonian. As on a global scale, there was an important Early Devonian diversification which led to both an increase of taxonomic richness and morphological disparity. Several innovations occurred, including coupled increases, favoured by welcoming environmental conditions and changing ecological conditions. Because the Early Devonian diversification involved families existing for several million years, the Devonian trilobite families were a Bottom-Heavy clades, characterized by a late diversification. Coupled increases in diversity and morphological disparity are not common in the fossil record and can be explained by the higher morphological constraint in the late evolutionary history of the clade. Another explanation is that the disparity peak could be interrupted by the Middle Devonian extinction. Indeed, the Middle and Late Devonian events affected North African trilobites and the diversity decreased since the Eifelian. At the same time, there were important shape losses, but the majority of losses occurred later, in the Givetian. Lateral extinctions in the morphospace occurred, indicating non-random extinctions in the context of environmental changes, including sea-level variations. Devonian trilobites maintained a relative uniform size throughout the Devonian and no real ‘Lilliput effect’ occurred after extinctions. After the Kellwasser events, another diversification occurred in the Famennian, of a less intensity. Because the trilobites survived for a long time at low level of diversity, in the Middle and the Late Devonian, we can consider them as a Dead Clade Walking.

Acknowledgements

This work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic time’, to

the project ECOS Sud-MINCYT A17A01 (Argentina), and to the French CNRS UMR 8198 Evo-Eco-Paleo. The authors thank the Région Hauts-de-France, the Ministère de l'Enseignement Supérieur et de la Recherche (CPER Climibio) and the Université de Lille for their financial support.

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2.4. Influence de la paléogéographie et de la tectonique sur la répartition des trilobites du Maroc et du Nord-ouest de l'Algérie

Article 6 : The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria

Accepté avec revisions par Geological Magazine

The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria

Valentin Bault^{a*}, Catherine Crônier^a, and Arnaud Bignon^b

^a *Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France*

^b *Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional de Córdoba, Córdoba (X5016GCA), Argentina*

Corresponding author. *Email address:* valentin.bault@univ-lille.fr

ORCID

Valentin Bault <https://orcid.org/0000-0002-9225-5195>

Catherine Crônier <http://orcid.org/0000-0002-7606-0822>

Arnaud Bignon <http://orcid.org/0000-0002-5331-00761>

ABSTRACT

The effects of sea-level changes and anoxia on Devonian trilobites have been studied for a long time but the importance of palaeogeographic and tectonic events in this key-period is still not well understood. In the Devonian, trilobites invaded many different marine environments and areas in North Africa where important palaeogeographic changes occurred. Distribution patterns of trilobites through time and space have been analysed using a hierarchical cluster analysis and diversity indices. Our examination of the literature suggests that trilobites were scarce during the Lochkovian before an important diversification, which occurred during the Pragian. Trilobites flourished in many North African regions without there being important taxonomic differences between basins, because of free migration in relatively flat palaeotopography and homogeneous environments. During the Middle Devonian, early Variscan tectonic movements transformed the Eastern Anti-Atlas area into a basin with a platform topography. Geographical barriers such as deep basins prevented trilobite migrations. At the beginning of the Eifelian, the reduction of migration between the different regions of this area coincided with a decrease in diversity. Consequently, tectonic events played an important role in the decline of trilobites during the Middle Devonian, especially when these were combined with sea-level changes and anoxic/hypoxic events. A recovery occurred in the Famennian involving only new genera. As at the global , cyrtosymbolines developed in shallow seas whereas phacopids evolved in deeper environments. The basin and platform system still

hampered migrations although sea-level variations led to episodic exchanges. The late Famennian regression reduced trilobite diversity and abundance dramatically in the study area.

Keywords:

Arthropods, Anti-Atlas, associations, diversity, faunal succession, tectonic, palaeobiogeography

1. Introduction

During the Devonian, trilobite communities were strongly influenced by spatial and temporal ecological changes at the global as well as regionally (Crônier & Van Viersen, 2007; Abe & Lieberman, 2012; Crônier & François, 2014; Bignon & Crônier, 2015). The development of hospitable shallow platforms during the Early Devonian led to a trilobite diversification (Chlupáč, 1994) but the sea-level changes and anoxic/hypoxic events during the Middle Devonian caused a sharp decrease of their diversity (Feist, 1991; Lerosey-Aubril & Feist, 2012). These kinds of spatial and temporal palaeoenvironmental changes were observed in the trilobite communities from North Africa (Bault et al., 2021). This area was located on the continental shelf of north-western Gondwana (McKellar & Chatterton, 2009) and was flooded during the Silurian transgression (Bultynck & Walliser, 2000) leading to a Devonian epicontinental sea (Kauffman, 1998). Thus, an abundant and diverse trilobite fauna proliferated during the Early Devonian before a long decline due to events that occurred during the Middle and Late Devonian.

To understand the trilobite response to palaeoenvironmental changes and their biodiversity dynamics at a regional , our study is focused on the Devonian North African communities from two well-known areas, i.e., the Moroccan Anti-Atlas and the Algerian Ougarta Range. These two areas are famous for their detailed stratigraphy, their numerous faunal studies and their recognised environmental changes (Wendt et al., 1984; Wendt, 1985, 1993, 2021a, 2021b; Wendt & Belka, 1991; Benhamou et al., 2004; Ouali Mehadji et al., 2011; Abbache et al., 2019; Frey et al., 2019). The trilobite fauna from this North African area was first studied by Le Maître (1952) followed by numerous publications by G. Alberti (e.g. 1964, 1966a, 1966b, 1967a, 1967b, 1969, 1970, 1981a, 1981b, 1982, 1983) and H. Alberti (e.g. 1972, 1973, 1974, 1975a, 1975b, 1976a, 1976b). This area is still studied nowadays as is reflected in more recent publications by Becker et al. (2018), Crônier et al. (2018a-b), Feist & Belka (2018), Feist & Weyer (2018), Zaplaski & Klug (2018), Van Viersen & Lerouge (2019) and Chatterton et al. (2020). There were many taxonomic changes in the study area throughout the Devonian

including periods of great taxonomic diversity among the trilobites, following trends identified on a global (Chlupáč, 1994; Bault et al., 2021). The Anti-Atlas Range and Ougarta Range also provided a high diversity of environments exhibiting temporal and geographical changes because of sea-level fluctuations. The Variscan tectonic events led to different palaeotopographies (Hollard, 1967, 1981; Wendt, 1985; Bultynck & Walliser, 2000).

The present work concentrates on trilobite occurrences to analyse the dynamic of trilobite faunas confronted with environmental changes in time and space and to thus understand how the diversity of trilobites may be influenced by the diversity and nature of environments. Trilobite associations were determined by performing multivariate analyses before their diversity and ecology were assessed.

2. Geological settings

The Moroccan study area, i.e., the Anti-Atlas Range, extends from the Dra region in the south-west toward the north-east, to the Tafilalt in Morocco and ends below the Bechar Basin in Algeria (Hollard, 1967). The Algerian study area, i.e., the Ougarta Range (Saoura Valley, North-western Algerian Sahara), extends towards the north-west, in the Anti-Atlas (Fig. 1A). During the Devonian, the study area included numerous marine basins, which were part of the Sahara platform, a passive continental margin of Gondwana (Wendt et al., 1984). From the south-west toward the north-east, these basins are the Fougou area, the Maïder Basin and Tafilalt Basin in the eastern Anti-Atlas in Morocco, the Ougarta Basin and to the North the Bechar Basin (i.e., Ben Zireg area) in Algeria (Fig. 1B).

The current correlation based on conodonts between the Tafilalt and the Maïders (Bultynck & Walliser, 2000) is associated here with their main environmental characteristics (Fig. 2). The succession of Ougarta was described by Boumendjel et al. (1997). Although the connection between the Devonian strata of the Ougarta Range and those of the Anti-Atlas region are covered by the Cretaceous 'Kem-Kem Group' (Benhamou et al., 2004), the similar basinal facies found in these areas suggests a connection during the Devonian (Hollard, 1967; Wendt et al., 1984). The northern and western parts of the Maïder region were continental during the main part of the Devonian and were only flooded during the Famennian when the sea level rose (Kaufmann, 1998). Figure 2 summarises the studied areas along with their dominant lithologies (Fig. 2).

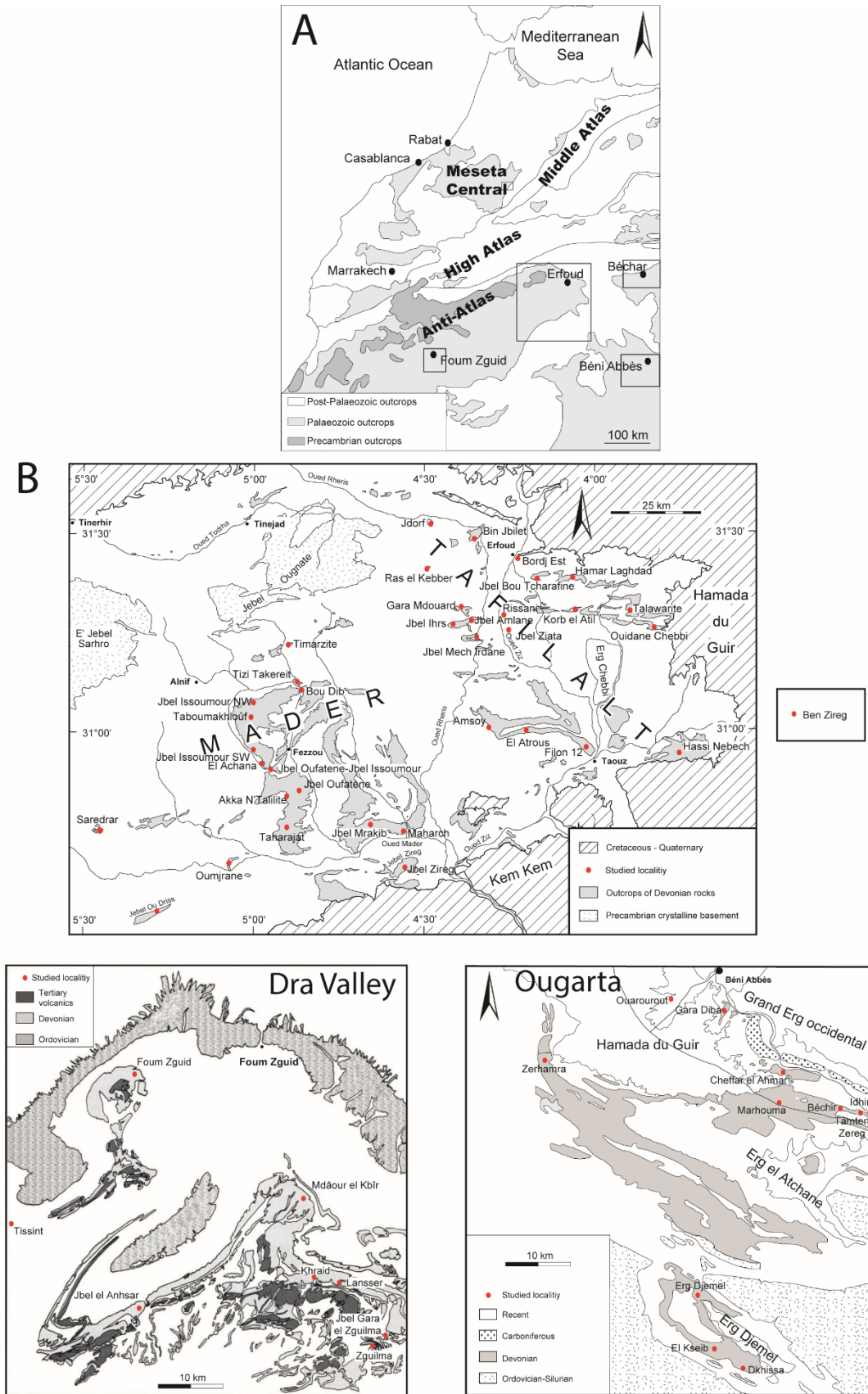


Fig. 1. (A) Simplified geological map of Morocco and Algeria (modified from Crônier et al. 2018b) and location of the five study areas in North Africa within the Anti-Atlas and Ougarta Ranges. (B) Geographical location of the 69 studied localities from the Maïder/Tafilalt area in Morocco and from the Ougarta area in Algeria.

2.1. Early Devonian

In the Lower Devonian, the eastern Moroccan Anti-Atlas was characterised by rather uniform facies (i.e., Maïder and Tafilalt; Fig. 2) varying mostly in thickness due to a homoclinal carbonate ramp topography (Lubeseder et al., 2010). However, palaeocurrents indicate the presence of a shallow pelagic platform in the Tafilalt with two distinct slope directions - one to the south-west and the other to the north-east (Wendt, 1995). The dominant sedimentology consists of shales interbedded with cephalopod limestones (Kaufmann, 1998). In Algeria, the Ougarta corresponded to a platform (Ouali Mehadji et al., 2011).

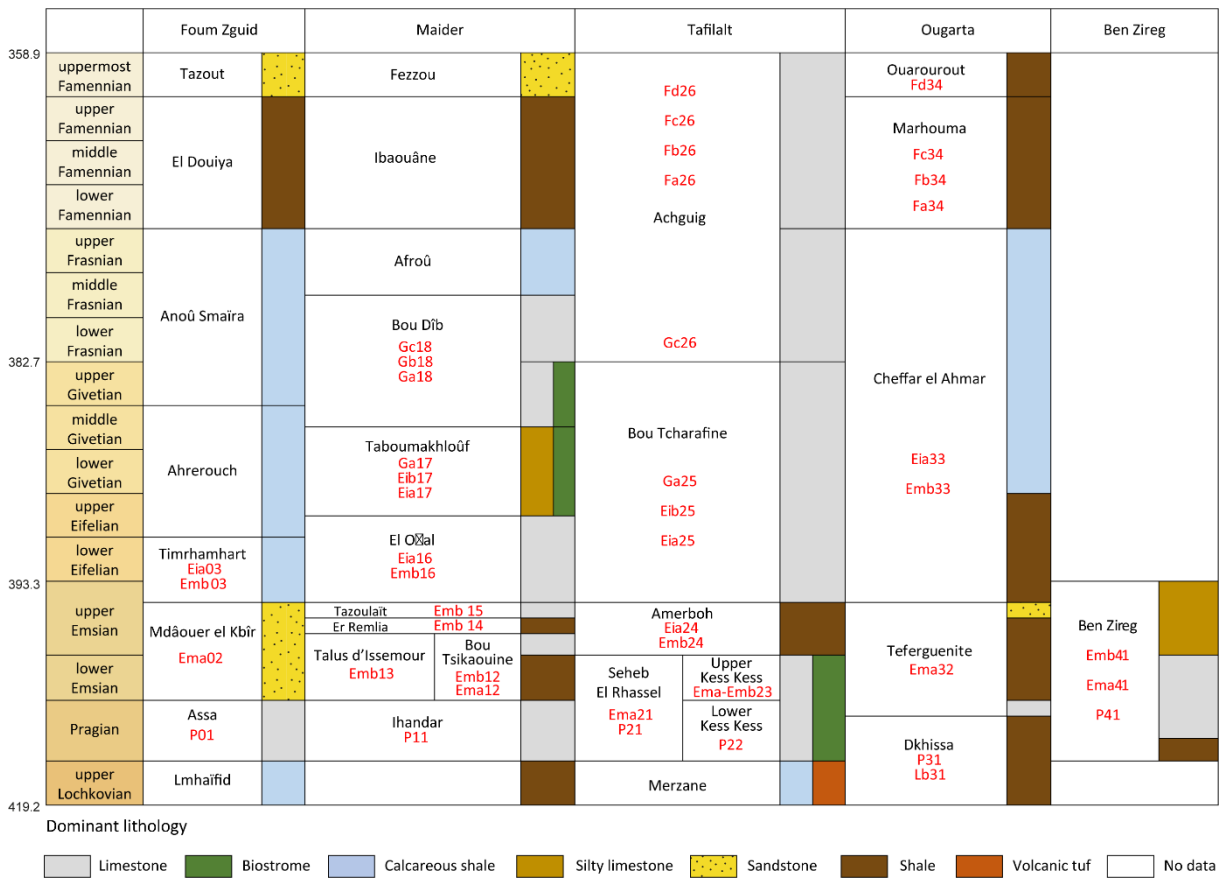


Fig. 2. Main lithology for each present in the five Moroccan Anti-Atlas and western Algeria basins for the Devonian. names in black, ID of samples in red. Ages from Cohen et al. (2013, updated).

The Lochkovian deposits of the eastern Anti-Atlas are mainly composed of shales and black graptolite limestones (Fig. 2). These deposits reflect relatively deep environments, which are not favourable for benthic faunas (Morzadec, 2001; Klug et al., 2013; Frey et al., 2014). In the Tafilalt, the particular Hamar Lagdad area is characterised by volcanic tuff deposits (Hollard, 1967; Klug et al., 2018). At the end of Lochkovian and the beginning of Pragian, a regressive phase enabled benthic faunas to develop (Hollard, 1967; Morzadec, 2001). Nevertheless,

Bultynck and Walliser (2000) reported a dominance of shales and hemipelagic limestones in the eastern part of the Anti-Atlas whereas the western part was composed of neritic deposits. At the same time, in the Hamar Laghdad area, a reef system settled on volcanic shoals (Hollard, 1981; Brachert et al., 1992). In the Ougarta Basin, the late Lochkovian-Pragian regressive phase led to a mud-dominated platform environment subjected to storm and fair-weather waves while to the north the Bechar Basin corresponded to a carbonate platform (Ouali Mehadji et al., 2011).

During the early Emsian (Fig. 2), limestones and argillaceous limestones still covered the Anti-Atlas without important environmental changes (Hollard, 1967) and are very fossiliferous (Kaufmann, 1998; Klug et al., 2008; De Baets et al., 2010). Conversely, in the Foug Zguid area shallow environmental conditions above storm-wave base led to sandstone deposits despite transgressive sequences (Jansen et al., 2004; Ouanaimi & Lazreq 2008). In Algeria, the Ougarta Basin deepened from the late Pragian due to a subsidence phase and was covered by shales and marls while the Bechar Basin became more siliciclastic (Ouali Mehadji et al., 2011).

The transition between the early and late Emsian was marked by a global transgression: in the Anti-Atlas the Daleje event (House, 1985) led to green shale deposits in a basinal environment (Kaufmann, 1998). Hollard (1967) noted a difference of faunas and facies between the Maïder and the Tafilalt with the Tafilalt becoming more argillaceous with a less diverse benthic fauna than the Maïder (Fig. 2). The northern Tafilalt was a pelagic platform with thinner deposits (Kaufmann, 1998). In Algeria, the Ougarta Basin remained deep and dominated by shales and marls (Ouali Mehadji et al., 2011) whereas the Bechar Basin was covered by shales and siltstones (Massa, 1965). At the end of the Emsian, limestone deposits formed in the Anti-Atlas (Fig. 2) because of a fall in the sea level. Conversely, the Foug Zguid area was characterised by shales and nodular limestones corresponding to more open water and hemipelagic conditions (Jansen et al., 2004). Based on trilobites, Chatterton et al. (2006) confirmed the establishment of a relatively deep environment, which was below the storm wave base but within the photic zone while the north of the Dra Valley was deepening. This area was influenced by the tectonic subsidence triggered by the Variscan extent phase (Ouanaimi & Lazreq, 2008). In Ougarta, the regression led to a shoreface or a foreshore environment with sandstone deposits (Ouali Mehadji et al., 2011).

2.2. Middle Devonian

During the Middle Devonian, the collision of Gondwana and Laurussia resulted in the Variscan orogeny. In the Anti-Atlas, this episode is marked by the development of a neritic shelf followed by a platform and basin system, accompanied by palaeoenvironmental changes

(Wendt et al., 1984; Kaufmann, 1998; Baidder et al., 2008; Wendt, 2021a). The first phase of this tectonic movement occurred at the Emsian/Eifelian boundary (Lubeseder et al., 2010). The Maïder Basin separated the Tafilalt Platform in the north-east from the Maïder Platform in the south-west (Fig. 3). While the Maïder Platform was emerging, the Tafilalt Platform remained a pelagic platform with the north-eastern Dra Valley and the Ougarta Basin deepening to a distal ramp (Limam et al., 2021).

The Foug Zguid area continued its transition toward a hemipelagic platform from the Emsian onwards (Jansen et al., 2004). During the Eifelian, marlstones and shales became increasingly important. To the north-east, the environment was less uniform. Kaufmann (1998) explained that three different facies occurred in the Maïder and the Tafilalt. A neritic facies characterised by argillaceous wackestones and numerous fossils was present in the northern and western parts of the Maïder near the emerged Maïder Platform. A neritic fauna including trilobites developed in the limestones of the western side of the Maïder Platform at Jbel Ou Driss (Bultynck, 1985; Feist & Orth, 2000). Condensed pelagic deposits, i.e., condensed nodular limestones and marls with abundant fossils, accumulated in the pelagic Tafilalt Platform. These two platforms corresponded to shallow water environments (Wendt et al., 1984). Finally, a basinal facies existed in the centre of the Maïder Basin and to the east of the Tafilalt Platform in the Tafilalt Basin. It mainly corresponded to marlstones and shales with scattered faunas. Wendt et al. (1984) specified that the Maïder Basin was deeper than the Tafilalt Basin. In Algeria, the Ougarta Basin became deeper during the Eifelian, from a foreshore environment at the end of the Emsian to a distal platform (Maillet et al., 2013; Crônier et al., 2018a). Henceforth, hemipelagic deposits were found as marlstones interbedded with thin-bedded limestones.

The global transgression events of the Middle Devonian were well pronounced in the Anti-Atlas (Kaufmann, 1998). The successive Choteč and Kačák events corresponded to hypoxies, which was probably due to a sea level rise during the Eifelian leading to black shale deposits (Kaufmann, 1998; Döring, 2002).

The differentiation between platforms and basins in the eastern Anti-Atlas continued to intensify in the Givetian. On the edge of the Maïder Platform, coral-stromatoporoid limestones developed and extended to the early Givetian (Kaufmann, 1998). A second tectonic phase of early Variscan movements occurred during the middle Givetian (Lubeseder et al., 2010). It implied the subsidence of the Maïder Basin, which induced the extension of the basinal facies (Kaufmann, 1998). The mid-Givetian Taghanic event was identified in Morocco and Algeria with shale deposits and condensed layers (Kaufmann, 1998). The distal platform of the Ougarta

region continued to subside during the Givetian with shale deposits interbedded with limestones (Maillet et al., 2013). To the north, the Bechar Basin showed similar facies to the Tafilalt Platform with the appearance of pseudonodular limestones in the Givetian (Massa, 1965).

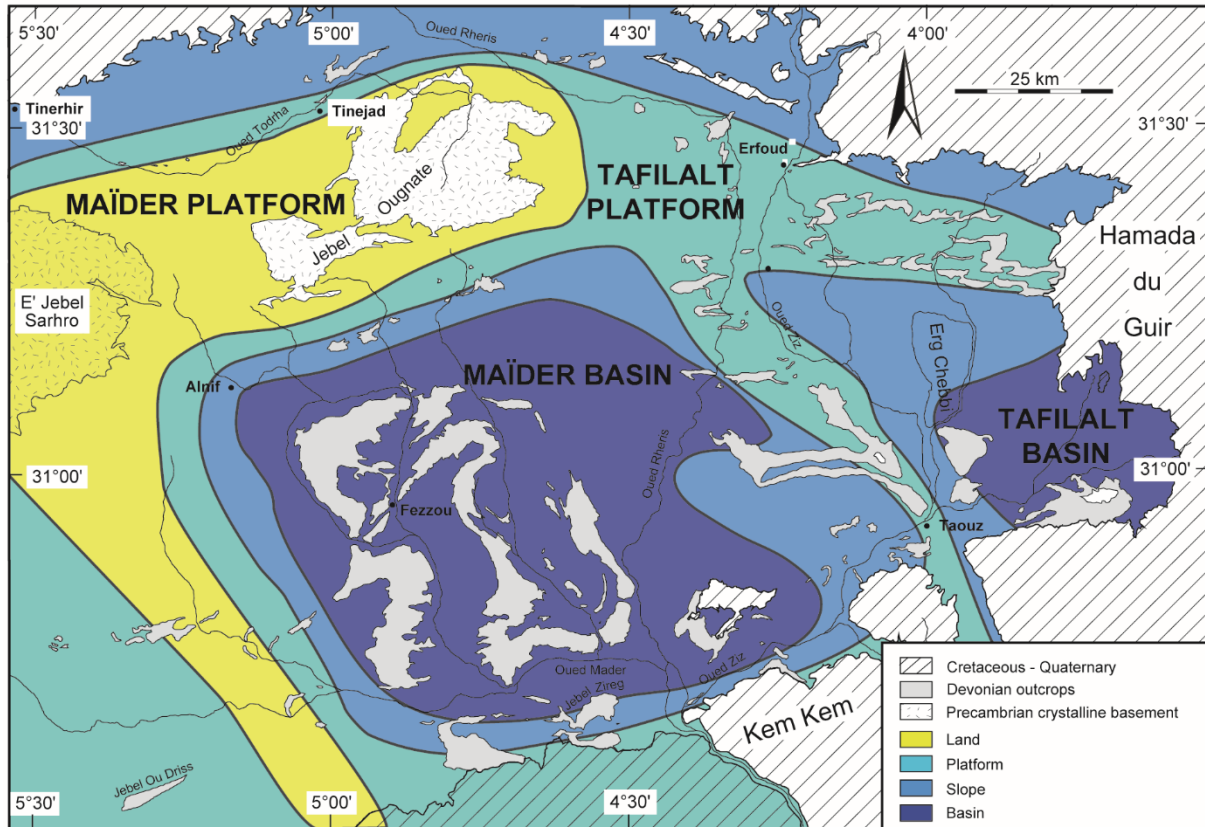


Fig. 3. Geographical map of the eastern Anti-Atlas in Morocco with the limits of the Maïder Platform and Basin and the Tafilalt Platform and Basin in the Middle and Late Devonian (Modified from Wendt and Belka, 1991 and Frey et al., 2019).

2.3. Late Devonian

During the Late Devonian, the Anti-Atlas Range and Ougarta Range were influenced by the same regional events (Benhamou et al., 2004). Variscan tectonics intensified in the eastern Anti-Atlas, which is reflected in differences of facies and thickness (Hollard, 1974; Wendt, 1985, 1988; Wendt & Belka, 1991; Belka et al., 1999; Frey et al., 2019) resulting in the differentiation of basins and platforms (Wendt et al., 1984, 2021a, 2021b; Michard et al., 2008). The active extensional dislocation of the former platform caused by early Variscan tectonic movements and differential subsidence (Wendt et al., 1984) led to the differentiation of two sub-basins; i.e., the Tafilalt Basin, a slowly subsiding shallow basin in the east and the Maïder Basin, a rapidly subsiding basin in the west (Fig. 3). These two sub-basins were connected *via* the narrow N-S Cephalopod Ridge, i.e., the Tafilalt Platform with shallower water (Wendt, 1985, 1995; Wendt et al., 2006; Toto et al., 2008; Lubeseder et al., 2010). At the beginning of the Frasnian, the

Tafilalt Platform emerged before being flooded again (Michard et al., 2008) and the Maïder Platform partly emerged (Wendt et al., 1985). On the north-western margin of the Algerian Sahara, a tectono-eustatic control is reflected in differences in lateral facies and thickness in sediments accumulated on a distal platform and in basins (Abbache et al., 2019). The Late Devonian marked the most important phase of epirogenic movements in the Saoura leading to an important subsidence (Benhamou et al., 2004). The Upper Devonian is characterised by alternate deposits of clay-sand and limestone, especially including "griottes" nodular limestones with benthic and pelagic faunas, which indicates an opening to marine environments (Crônier et al., 2018a; Abbache et al., 2019).

In North Africa, a transgression occurred during the Late Devonian. In Morocco, the highest sea-level occurred in the late Famennian (Wendt & Belka, 1991; Becker et al., 2004). In the Ougarta, the high stand occurred at the end of the Frasnian but the sea-level stayed high with high stand deposits until the late Famennian (Ouali Mehadji et al., 2012) when a regression led to shallower environments in Morocco and Algeria.

During the Frasnian, in the Anti-Atlas a clay sedimentation with sideritic and nodular levels (Frey et al., 2019) developed in the Tafilalt Basin and the Maïder Basin and even occasionally on the Tafilalt Platform, reflecting rising sea levels (Wendt, 1988; Lubeseder et al., 2010; Frey et al., 2019). At the same time, sandy limestones, thick-bedded crinoid or cephalopod limestones rich in nektonic and planktonic faunas associated with black bituminous shales were deposited on the Tafilalt Platform (Wendt, 1985; Michard et al., 2008; Frey et al., 2019). A condensed sedimentation took place in the south-western Maïder Basin and on the northern Tafilalt Platform (Wendt, 1988; Wendt & Belka, 1991; Hüneke, 2006), probably reflecting a differentiation in both water depth and oxygen availability (Frey et al., 2019). In the late Frasnian, shallow subtidal to supratidal deposits developed in the Tafilalt Platform that are characterised by strongly reduced thicknesses and the Maïder Platform emerged (Wendt et al., 1984; Wendt & Belka, 1991). In the south-eastern part of the Maïder Basin, the Kellwasser levels are represented by dark and massive cephalopod limestones (Wendt & Belka, 1991; Frey et al., 2019). The Ougarta Basin is the continuation of these Tafilalt and Maïder basins to the south-east in the Algerian Sahara (Wendt et al., 1984; Wendt, 1985; Abbache et al., 2019). In this area, the top of the Cheffar el Ahmar is a distal ramp sedimentation with green shales interbedded with nodular limestones followed by "griotte" limestones interbedded with red shales. The fauna consists of ammonoids, ostracods and chitinozoans (Abbache et al., 2019).

During the Famennian, a marly and nodular calcareous sedimentation developed in the Tafilalt Basin, in shallow environments. At the same time basinal facies dominated by shaly

and calcareous sedimentation with intercalations of siliciclastic turbidites were laid down in the Maïder Basin, in deeper environments (Wendt et al., 1984; Döring, 2002) with diverse cephalopods (Korn & Bockwinkel, 2017). In the Tafilalt Platform, deposits of quartz-rich brachiopod coquinas, crinoidal limestones, thick-bedded cephalopod limestones and nodular limestones formed during the early Famennian. Similar facies were found in the eastern Maïder Platform (Wendt, 1985). A deeper environment like a slope or basin with shale deposits characterised the Ougarta region. Pyritised ammonoids and brachiopods were found in nodular limestones interbedded with shales (Abbache et al., 2019). The deepening of the Ougarta trough was probably due to subsidence and not to transgression (Ouali Mehadji et al., 2012). The deepening continued during the middle and late Famennian in the Tafilalt Platform where marls and nodular limestones were deposited in slightly deeper environments and debris flows and slumps on the margins during the late Famennian (Wendt et al., 1984). Locally, limestones varied greatly in thickness and fossil content (cephalopods, crinoids, brachiopods). Sedimentology documented phases of moderate to good aeration in more or less shallow water conditions (Wendt et al., 1984; Wendt, 1988). The continuous deepening during the late Famennian led to the decrease of diversity of benthic faunas (Wendt et al., 1984) while the centre of the Maïder Platform was henceforth flooded and pelagic cephalopod limestone accumulated (Wendt, 1985). The Ougarta region remained deep during the middle and the late Famennian and became a basin with a restricted water circulation (Benhamou et al., 2004; Abbache et al., 2019). In this environment, red “griottes” limestones were deposited with shaly beds and turbidites (Ouali Mehadji et al., 2012; Abbache et al., 2019). Ammonoids, brachiopods and trilobites were found within the nodular limestones (Benhamou et al., 2004; Crônier et al., 2013; Mottequin et al., 2015; Allaire et al., 2020). Although this facies is not an indicator of palaeobathymetry (Benhamou et al., 2004), Abbache et al. (2019) concluded that these sediments were deposited in a basinal environment. The *Nereites* ichnofacies confirms this kind of deep environment (Bendella et al., 2014). Ouali Mehadji et al. (2012) identified a narrow basin during the middle Famennian leading to a more homogeneous elongated basin in the late Famennian.

At the end of the Famennian, a fine-grained clastic sedimentation, the Hangenberg Black Shale, was sedimented in most parts of north-western Africa (Kaiser et al., 2011; Klug et al., 2016). Sandy marls and cross-bedded sandstones covered the southern part of the Tafilalt Platform (Wendt et al., 1984). In Ougarta, sandstone beds occurred that were devoid of fossils and sometimes included channels (Abbache et al., 2019). Within sandstones assigned to the “Grès de Ouarourout”, Ouali Mehadji et al. (2012) identified the maximal regression surface.

At the beginning of the Tournaisian, the Tafilalt and southern Maïder Platforms corresponded to a deltaic environment (Wendt et al., 1984). The Ougarta region corresponded to a siliciclastic platform (Abbache et al., 2019) with temporary emersions leading to deltaic environments or lagoons (Ouali Mehadji et al., 2012).

In the southern Ougarta region, in the Erg Djermel area, no trilobites were found within the Upper Devonian deposits, i.e., in black shale deposits corresponding to deep environments from the Frasnian to the late Famennian (Abbache et al., 2019). In the north of Ougarta, in the Ben-Zireg area, trilobites have not yet been recorded within “griottes” calcareous deposits associated with rare shaly layers corresponding to a middle to distal platform (Abbache et al., 2019). In Morocco, the Fougoum Zguid area and the Dra Valley deepened from the Eifelian to the late Famennian due to global transgression (Becker et al., 2004). These deep environments are not favourable to the development of trilobite communities and thus fossils are rare apart from ammonoids and crinoids (Hollard, 1963; Becker et al., 2004).

3. Material and methods

3.1. Material

In order to analyse the trilobite records and their shifts, we completed an existing dataset (Bault et al., 2021) based on the occurrence of trilobites from Morocco and Algeria (Fig. 1). 77 studies from the literature were considered because of their updated taxonomy and/or good temporal resolution (Appendix A). The dataset contains 2892 specimens (Appendix B) from the Lochkovian to the Famennian distributed within 69 localities from five basins (Fig. 1). Sections separated by a few hundred metres were combined within the same locality. To avoid possible duplicates the specimen count was restricted to only the highest number of complete exoskeletons plus the disarticulated cephalon or pygidia per occurrence. Other parts of trilobites such as free cheeks or hypostomes were not included. For each relevant occurrence, the dataset contains the following information: taxonomic information, abundance, location, stratigraphic position (substages) and lithological information (formations). Throughout our data compilation work, only genera were considered to maximise potential correlations between the distinct assemblages, as many species are only described locally. Species level is often inadequate for biodiversity purposes (Cecca, 2002). As the Late Devonian *Phacops* Emmrich 1839 differs from the Early and the Middle Devonian representatives of the genus, they were counted as a distinct genus called *Phacops* sensu lato (Crônier et al., 2011). We used a preliminary revision of asteropygines in open nomenclature while waiting for the revision of the whole subfamily. As a result, previous *Metacanthina* species *M. issoumourensis* Morzadec,

2001, and *M. maderensis* Morzadec, 2001 are joined with *Minicryphaeus giganteus* Bignon et al., 2014 in the Genus 1, whereas *Asteropyge wallacei* Termier and Termier, 1950 is included in the Genus 2. Overall, the dataset comprises 135 genera (Appendix B) used for biodiversity indices (see section 4.3). However, we excluded genera found in only one sample because they did not provide any linkage with other samples for the clustering, which led to a selection of 67 genera spread over 123 samples (or assemblages) used for a cluster analysis.

3.2. Clustering

An analysis of associations was carried out using 123 samples at a given substage and to help us understand the temporal and spatial relationships between trilobite faunas and their environments. The term association is used here for recurrent assemblages of trilobites with a similar taxonomic composition (Brenchley & Harper, 1998; Crônier & Van Viersen, 2007; Crônier & François, 2014; Bignon & Crônier, 2015). To reduce sampling bias the relative abundances of 67 genera were quantified in seven classes, i.e., the percentage of the abundance of each genus in a sample (Harnik, 2009). Indeed, the number of specimens is influenced by the sampling effort (Thompson, 2004), which cannot be estimated as our data were obtained from various bibliographic references.

Data were analysed using a hierarchical cluster analysis (HCA). This agglomerating technique groups recurring samples according to their level of taxonomic similarity (Davis, 1986; Harper, 1999; Hammer & Harper, 2008). It produces dendrograms highlighting the relationships in two modes - an R-mode clustering, grouping the taxa according to their probability of co-occurrence and a Q-mode clustering, grouping the samples, i.e., of similar generic composition. HCA was carried out using the average linkage algorithm and the Pearson correlation similarity index (Hammer & Harper, 2008).

To identify environmental gradients, a Detrended Correspondence Analysis (DCA) was carried out. Correspondence Analysis (CA) is suitable for grouping samples from taxonomic abundance (Greenacre, 1984; Jongman & Jongman, 1995; Legendre & Legendre, 1998) but DCA is more reliable (Hammer & Harper, 2008; Holland et al., 2001; Bonelli & Patzkowsky 2008) for reducing the Pinocchio (Fig. SUPPL. A1) and arch effects (Fig. SUPPL. A2). This ordination method maximises the correspondences between taxa and samples. It also provides ordination scores for both taxa and samples according to the relative abundance of taxa by involving a compression of the total information along the first axis, which often reflects paleoenvironmental gradients (Hammer & Harper, 2008). Unfortunately, several taxa need modern revision to clarify their generic determination. Moreover, microfacies analyses would

be suitable for a better characterization of the environments. In their absence, an additional DCA would improve our determination of the relationships between some samples.

Finally, an analysis of similarities (ANOSIM) was carried out to statistically test the differences in the generic composition of groups of taxa. This non-parametric test is based on Bray-Curtis dissimilarity values as it only uses the rank order of dissimilarity values between groups and within groups (Clarke, 1993; Hammer & Harper, 2008). P-values were obtained through 5000 random permutations.

3.3. Diversity indices

To complete the multivariate analysis information and help understand the impact of migrations and environmental changes on the diversity, α and β diversities (Whittaker, 1960) were estimated. The total taxa diversity is determined by the mean taxa diversity at the habitat level (α) and the differentiation among habitats (β). The Shannon index H' of α diversity was used to take into account the number of taxa within a sample (taxa richness) and the individual distribution within these taxa (taxa equitability). It considers the relative abundance of each taxon and gives weight to rare species. This index varies from 0 for a sample with only one single taxon to high values for samples with many taxa. $H' = -\sum_{i=1}^S p_i \log_2 p_i$, with S the number of taxa and $p_i = \frac{n_i}{N}$, with n_i the number of individuals of the taxon i and N the number of individuals for all taxa. The Shannon index H' of α diversity was estimated through time according to substages ors and through environment according to associations. Diversity for associations is calculated as the mean taxonomic richness of samples of each association while the diversity for substages ors is calculated as the total taxonomic richness in these stratigraphic units.

Several measures related to compositional heterogeneity of β diversity were used to quantify differentiation (Baselga, 2010; Balsega & Orme, 2012). The first measure is an index of taxa replacement (i.e., turnover) emphasizing the role of rare taxa as the difference in taxa composition between localities measured as Simpson dissimilarity (i.e., turnover component of Sørensen dissimilarity). This measure enables the identification of the environmental impact or spatial and temporal constraints on the number of taxa that are replaced between localities (Qian et al., 2005). The second measure is an index of nestedness, which occurs when taxa-poor assemblages are a subset of more diverse assemblages (Wright & Reeves, 1992; Ulrich & Gotelli, 2007) measured as nestedness-resultant component of Sørensen dissimilarity (Baselga, 2010). This measure indicates non-random species loss as common species are less likely to

disappear (Gaston et al., 2000). The last measure is an index of the Overall β diversity measured as Sørensen dissimilarity (Sørensen, 1948) corresponding to the global taxonomic difference between samples. Components of β diversity were estimated through time between substages and through environment between associations.

HCA, ANOSIM, DCA and Shannon index H' were achieved by using the software PAST v3.24 (Hammer et al., 2001). β diversity was computed by using the 'Betapart' package (Baselga & Orme, 2012) in the R statistical environment (version 3.6.3; R Core Team 2020).

4. Results

4.1. Delineated associations and faunal gradients

The 67 trilobite genera distributed within the 123 assemblages are grouped into 16 associations or occurrences, in four main clusters by HCA (Fig. 4; details in fig. Suppl. B). Details of each trilobite association are given in table.

Cluster I groups five associations (i.e., *Morzadecops* Association Ia, *Ganetops* Association Ib, *Montanproetus* Association Ic, *Sculptoproetus* Association Id and *Piriproetus* Association Ie), covering the entire Early Devonian and the early Eifelian; Cluster II groups six associations (i.e., *Hollardops* Association IIa, *Morocops* Association IIb, *Gerastos* Association IIc, *Chotecops* Association IId, *Paralejurus* Association IIe and *Psychopyge* Association II f), from the Pragian to the Givetian; Cluster III groups only one association (*Lepidoproetus* Association IIIa) mainly found in the Maïder during the Pragian. Finally, Cluster IV groups all four associations (*Cyrtyosymbolina* association IVa, *Osmolskabole* Association IVb, *Trimerocephalus* Association IVc and *Phacops s.l.* Association IVd) restricted to the Late Devonian (Famennian) of the Tafilalt and Ougarta. The ANOSIM results show a significant difference between the 16 associations (R coefficient = 0.59, p value = 0.0002).

Associations	Samples	Geological time	Basins	Remarks
<i>Morzadecops</i> Association (Ia)	JO-Ema12/MEK-Ema03/ F12-Ema21/OC-Ema21	early Emsian	Dra Valley, Maïder and Tafilalt	<ul style="list-style-type: none"> • Only OC-Ema21 is diverse with six distinct genera recorded.
<i>Ganetops</i> Association (Ib)	Dkh-Lb31/EK-Lb31 /ED-Lb31/Zer-Lb31	late Lochkovian	<i>Ougarta</i>	<ul style="list-style-type: none"> • Zer-Lb31 added to the <i>Ganetops</i> Association based on the presence of both <i>Ganetops</i> and <i>Protacanthina</i> and DCA result • Dominated by two asteropygine genera (<i>Ganetops</i> and <i>Protacanthina</i>) • High overall β diversity.
<i>Montanproetus</i> Association (Ic)	BZ-Emb41/JA-Ema21/JBT-Ema21/JISW-Emb14	Emsian	Maïder, Tafilalt and Ben Zireg	<ul style="list-style-type: none"> • In limestone deposits
<i>Sculptoproetus</i> Association (Id)	JA-Eia21/EAt-Emb24/Ris-Emb24/Tim-P11/ EAt-Ema21/JISW-Ema12	Pragian to Eifelian	Tafilalt and Maïder	<ul style="list-style-type: none"> • Low overall β diversity • In shales or calcareous-shale alternations
<i>Piriproetus</i> Association (Ie)	GM-Eia24/GM-Emb24/GM-Eia25/JI-Eia25/JA-Eia25/JA-Emb24/HL-Eia25/JBT-Eia25/HL-Emb23/HL-Ema23	late Emsian to early Eifelian	Tafilalt	<ul style="list-style-type: none"> • In marly limestones deposits
<i>Hollardops</i> Association (IIa)	Tim-Emb15/BD-Eia16/BD-Emb15/FZ-Emb-02/EK-Emb33/Zer-Emb33/JeA-Emb02/BD-Emb14/Zgu-Eia02/Zer-Ema32/Mar-Emb33	late Emsian to early Eifelian	the entire Anti-Atlas	<ul style="list-style-type: none"> • In limestones interbedded with shales from a relatively deep platform. • Association dominated by <i>Hollardops</i> and <i>Timsaloproetus</i> but they occurred together only in sample Zgu-Eia02
<i>Morocops</i> Association (IIb)	HL-Emb24/BD-Eia16/FZ-Eia02/BD-Emb15 /Tal-Emb15/JISW-Emb15/TO-Emb15/ED-Eia33/JO-Eia16/ED-Emb33/JGEZ-Emb02/JGEZ-Eia02/Mah-P11/Khr-Emb02/TT-Emb/Tis-Emb02/JO-Emb15/JO-Emb16/Tal-Emb24	Pragian, late Emsian to early Eifelian	Tafilalt, Maïder, Ougarta and Dra Valley	<ul style="list-style-type: none"> • Five other samples were added according to their taxonomic composition and from DCA results: TT-Emb, Tis-Emb02, JO-Emb15, JO-Emb16 and Tal-Emb25 • <i>Morocops</i>, <i>Cyphaspis</i> and <i>Austerops</i> represent the most widespread genera • Most diverse association of the whole Devonian
<i>Gerastos</i> Association (IIc)	JZg-Eia17/JeM-Ga18/ Tab-Gb18/JeM-Eia16/JZg-Eia16/Sar-Eia16/JeM-Eia17/JeM-Eib17/JO-Eib17/Tab-Ga18/JOD-Ga17/JISW-Eia16/JISW-Emb16	lower Eifelian to middle Givetian	Maïder Basin	<ul style="list-style-type: none"> • Association dominated by <i>Gerastos</i>, which is invariably present in all samples • In limestones
<i>Chotecops</i> Association (IIId)	HN-Gc26/Oua-Eia33/JMI-Ga25/JMI-Eib25/JZa-Ga25/JBT-Eib25/Mar-Eia33	Middle Devonian	Tafilalt and Ougarta	<ul style="list-style-type: none"> • Association dominated by three genera: <i>Chotecops</i>, <i>Struveaspis</i> and <i>Helmutia</i> • In marly limestones of pelagic environments
<i>Paralejurus</i> Association (IIe)	BZ-P41/MeK-P01/JOJI-P11/F12-P21/HL-P22/JO-P11/Tab-P11/Tis-P01/EAt-P21/BZ-Ema41	Pragian , early Emsian	Maïder, Tafilalt, Ben Zireg and Dra Valley	<ul style="list-style-type: none"> • Sample BZ-Ema41 was removed from the <i>Psychopyge</i> association to be placed in the <i>Paralejurus</i> Association based on the presence of <i>Prodrevermannia</i> and DCA results • High overall β diversity
<i>Psychopyge</i> Association (IIIf)	JBT-Emb24/JO-Emb12/EIH-Emb02/BD-Emb13/Mar-Ema32	Emsian	Maïder, Tafilalt and Ougarta basins	<ul style="list-style-type: none"> • Low overall β diversity • In interbedded marl and limestones
<i>Lepidoproetus</i> Association (IIIa)	AnT-P11/JeM-P11/JZg-P11/OJ-P11/JINW-P11/EAc-P11/Ams-P21/Lan-Emb02	Pragian , late Emsian	Tafilalt , Dra Valley	<ul style="list-style-type: none"> • Although <i>Lepidoproetus</i> was the most abundant genus, there is no dominant genus. • Low overall β diversity
<i>Cyrtosymbolina</i> Association (IVa)	BE-Fa26/BJ-Fa26	early Famennian	Tafilalt Platform	<ul style="list-style-type: none"> • Low overall β diversity
<i>Osmolskaboie</i> Association (IVb)	BE-Fb26/ BE-Fc26/HL-Fb26/JBT-Fb26/OC-Fb26/ BE-Fd26	middle Famennian to latest Famennian	Tafilalt Platform	<ul style="list-style-type: none"> • Most diverse association of the Late Devonian • In limestone only
<i>Trimerocephalus</i> Association (IVc)	KeA-Fb26/ Mar-Fa34/CeA-Fb34/GD-Fb34/Mar-Fb34/Bec-Fc34	early to middle Famennian	Ougarta Basin , Tafilalt	<ul style="list-style-type: none"> • Low overall β diversity • Relatively deep environment
<i>Phacops s.l.</i> Association (IVd)	TZ-Fb34/Idh-Fc34/TZ-Fc34/Mar-Fc34	middle Famennian to late Famennian	Ougarta Basin	<ul style="list-style-type: none"> • Poorly diverse

Table 1. Trilobite associations and their environmental, faunal and temporal features. The remark column includes data on: diversity (Fig. 9) and occurrences (Appendix A and B). Reattributions of samples were made using DCA data (Fig. 5). Bold font indicates the main characteristic for the associations.

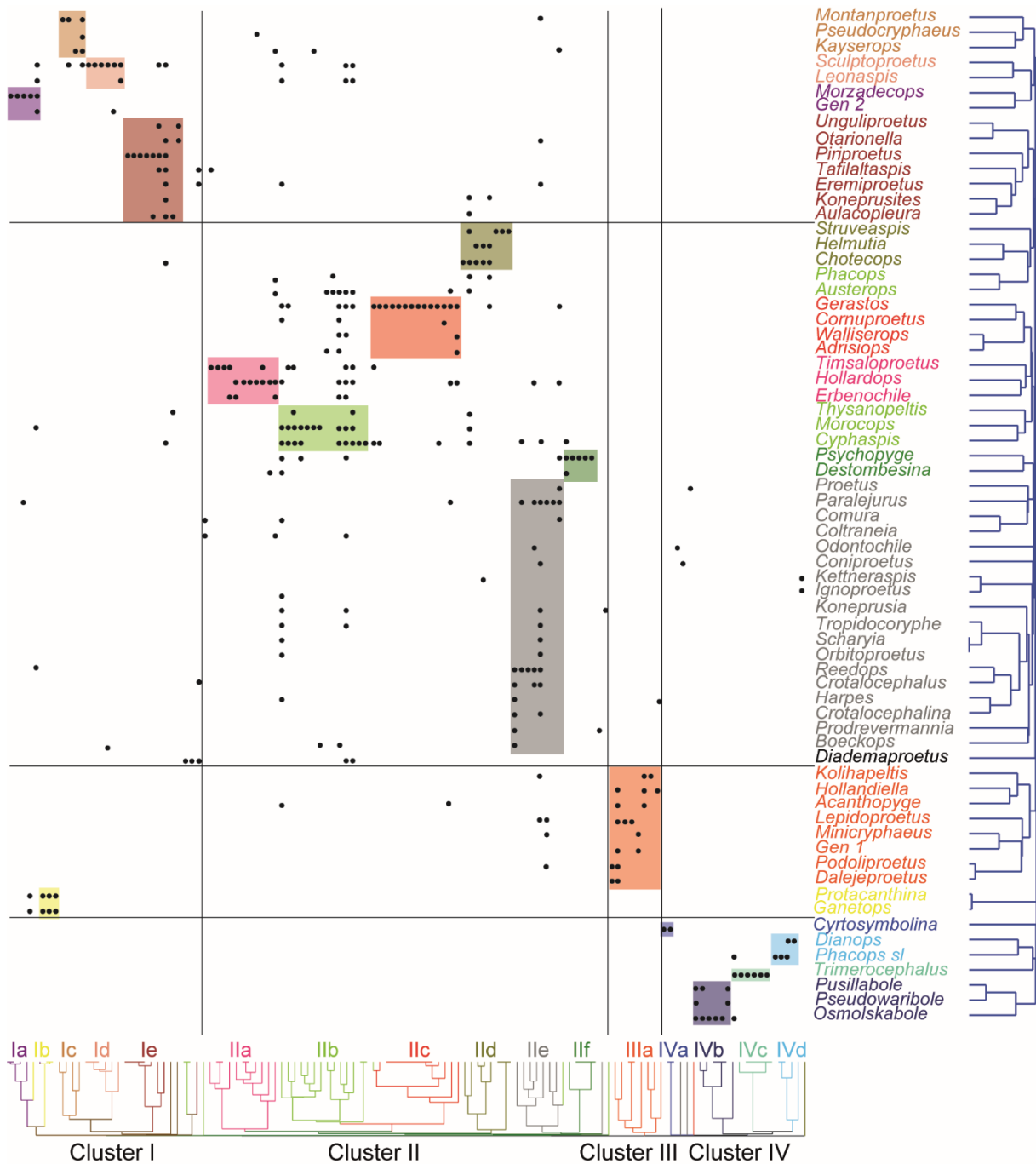


Fig. 4. Simplified dendrogram with R and Q modes from hierarchical cluster analysis (HCA) using the average linkage method as correlation setting and the Pearson correlation index as similarity index (Hammer & Harper, 2008). 67 taxa (genera) are clustered according to 123 analysed samples (localities) from the Devonian of North Africa. Four clusters (I to IV) and 16 associations are identified. Sample names and proportions of each occurrence are given in Fig. SUPPL. B).

DCA enabled us to offset HCA limits and better understand the spatio-temporal distribution of the assemblages according to their taxonomic record. The Famennian samples did not share trilobites with the Early and Middle Devonian (Fig. 4) so they were removed from DCA to

avoid a Pinocchio effect and were analysed in an additional DCA (Fig. 5). Similarly, the early Famennian samples BJ-Fa26 and Be-Fa26 were removed.

For the Early and Middle Devonian, DCA shows a time trend (Fig. 5A). The Early Devonian (Lochkovian, Pragian and early Emsian) associations show the highest values on both DC1 and DC2 axes, whereas the Middle Devonian associations show the lowest values on both DC1 and DC2 axes (Fig. 5A). The Early Devonian associations group mostly the Order Phacopida, whereas the Middle Devonian associations group mostly the Order Proetida (Fig. 5A).

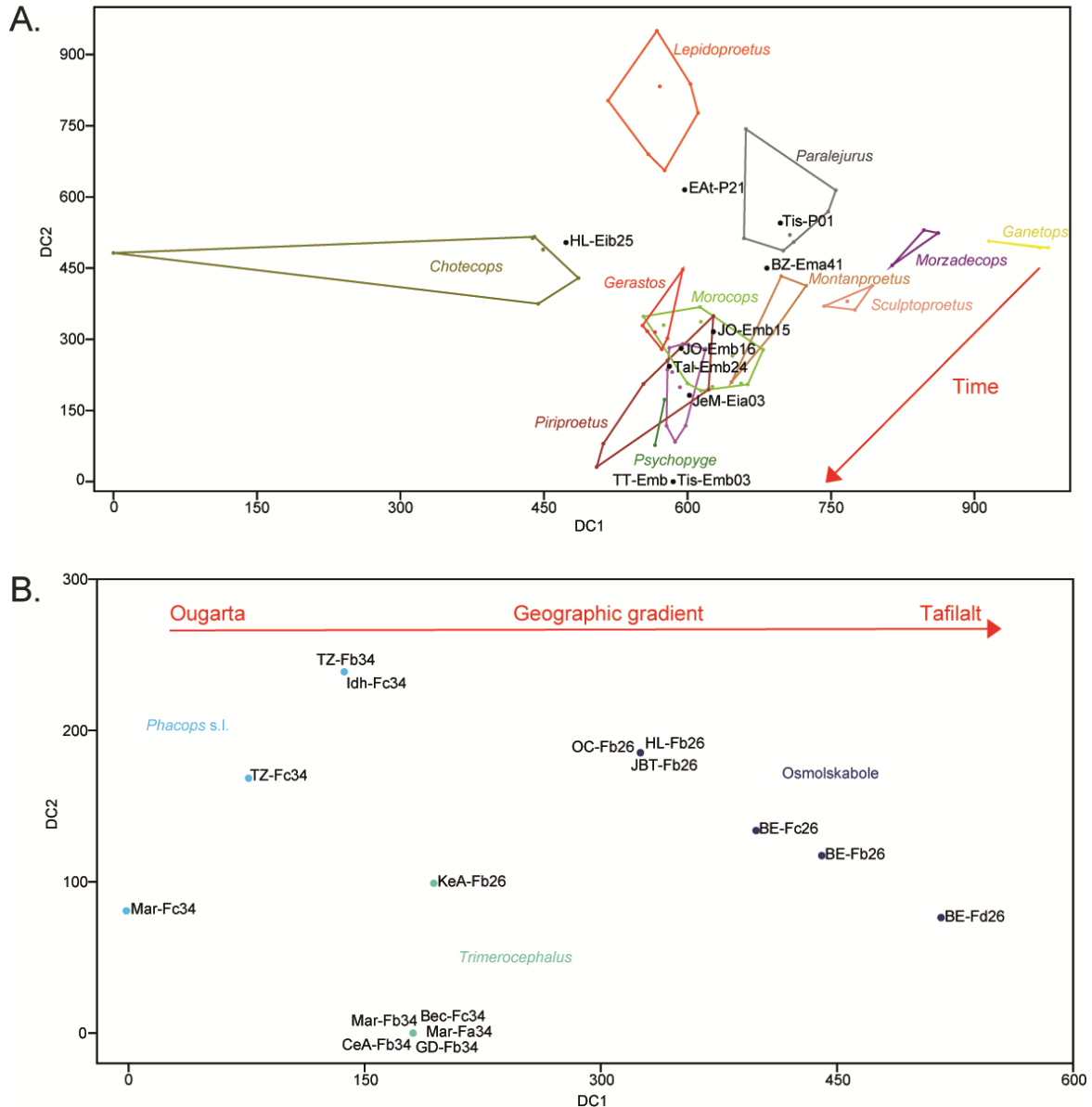


Fig. 5. Scatter plot of North African samples according to DCA for (A) the Early and Middle Devonian, and (B) the Famennian; DC1 and DC2 axes reflecting potential environment gradient. Eigenvalues for DC1 and DC2 axes are respectively 0.96 and 0.91 for the Early and Middle Devonian with 105 samples, 0.95 and 0.09 for the Famennian with 16 samples. Associations defined by clustering have been reported: 12 associations for the Early and Middle Devonian, and 4 associations for the Famennian.

However, a look at the results in detail shows five associations are not overlapped by others along one axis of DCA or another. *Chotecops*, *Morzadecops*, *Ganetops* and *Sculptoproetus* associations are clearly independent along the DC1 axis and *Paralejurus* and *Lepidoproetus* associations alone appear along the DC2 axis in the higher values (Fig. 5A). These associations belong to either the Lochkovian, or Pragian, or early Emsian or Givetian. In contrast, late Emsian and Eifelian associations were strongly overlaid on both axes.

For the Famennian, DCA shows a geographic gradient along DC1 axis, from Ougarta with the lowest values to the Tafilalt having the highest ones (Fig. 5B).

4.2. Temporal and spatial distribution of clusters

4.2.1. Early Devonian

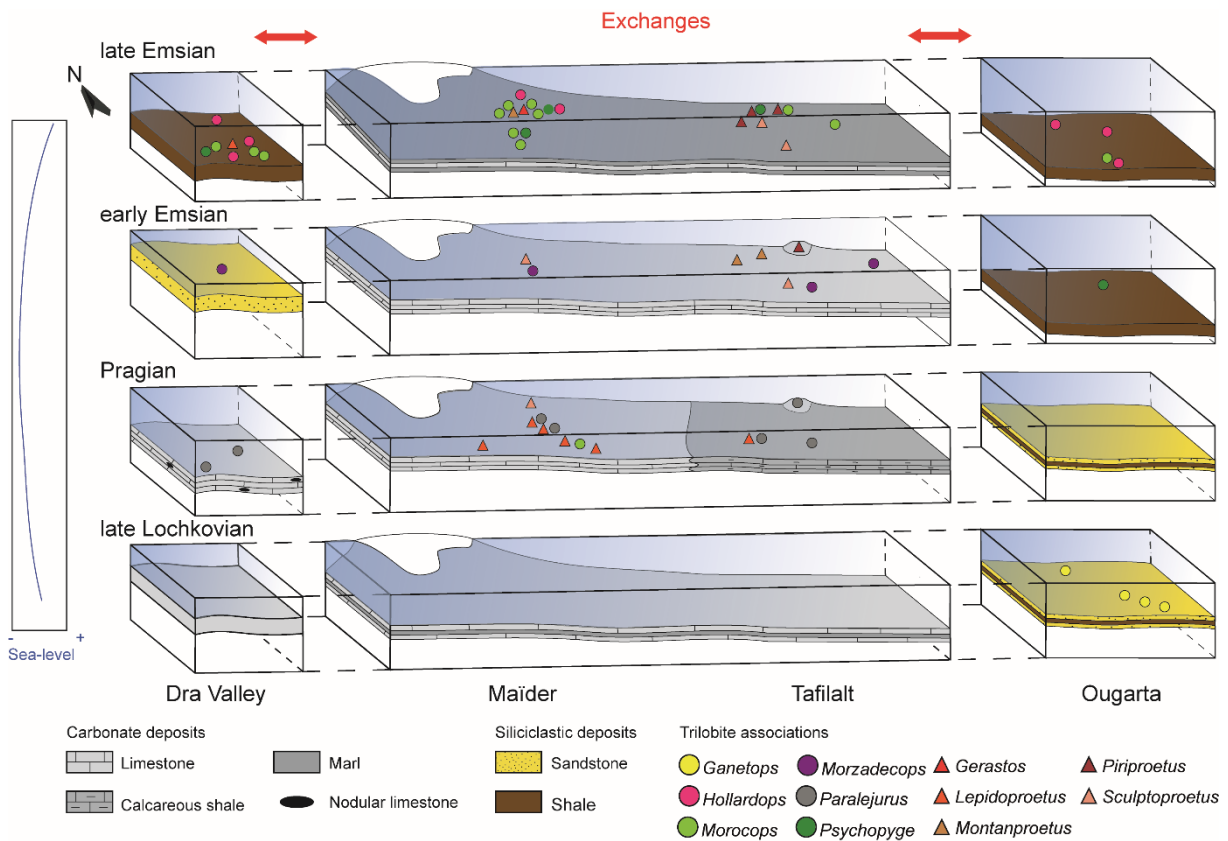


Fig. 6. Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Early Devonian. Associations defined by clustering have been reported.

4.2. Temporal and spatial distribution of clusters

4.2.1. Early Devonian

Details of temporal and spatial distributions are given in supplementary figures (Figs. SUPPL. C to H). During the Lochkovian, trilobites seemed restricted to the Ougarta Basin.

They were few and dominated by the *Ganetops* genus (within Ass. *Iib*), which was the sole genus in the southern part of the Ougarta region (Fig. 6). To the North, *Ganetops* was associated with the *Morzadecops* genus at Zerhamra - the only genus capable of persisting in the Pragian, which thus occurs in another association (i.e., *Morzadecops* Association *Ia*).

At the beginning of the Pragian, trilobites flourished in the Anti-Atlas area but are unknown from the Ougarta Basin. Four associations covered this period but two were more dominant, widespread over all the Anti-Atlas and intersected (Fig. 4), the *Lepidoproetus* (*IIIa*) and *Paralejurus* (*Iie*) associations. The *Paralejurus* Association occurred in the Ben Zireg area and developed in the Tafilalt and the Maïder areas too, whereas the *Lepidoproetus* Association occurred predominantly in the Maïder area although it occurred also in the south-western part of the Tafilalt area (Fig. 6). These two widespread associations were strongly affected during the Emsian: the *Paralejurus* Association (*Iie*) disappeared and the *Lepidoproetus* Association (*IIIa*) occurred only in the Dra Valley (at Lansser locality) for the last time in the late Emsian. The *Sculptoproetus* Association (*Id*) and *Morocops* Association (*Iib*) appeared in the Maïder area (respectively at Timarzite and Maharch localities) during the Pragian but were rarer. They developed considerably during the Emsian where they occurred in almost all basins (Fig. 6). The Emsian is represented by nine associations (Fig. 4). In addition to the three associations, which had already occurred in the Pragian, five new ones appeared in the early Emsian and an additional association in the late Emsian. The *Morzadecops* Association (*Ia*) proliferated everywhere in the early Emsian but disappeared immediately afterwards. The *Psychopyge* (*IIf*) and *Hollardops* (*Iia*) associations originated in the early Emsian of Ougarta and then colonised the Anti-Atlas area during the late Emsian (Fig. 6). The *Montanproetus* (*Ic*) Association lasted until the late Emsian and extended from the Anti-Atlas toward the west (Ben Zireg). The two latter associations were rare during the Emsian: The *Piriproetus* Association (*Iie*) is present only in two north-western Tafilalt localities (Gara Mdouard-Jbel Issoumour) and the *Gerastos* Association (*Iic*) only during the late Emsian of the Maïder area (Jbel Issoumour SW).

4.2.2. Middle Devonian

Five Early Devonian associations are still found in the Eifelian but the *Hollardops* and *Sculptoproetus* associations disappeared after the early Eifelian. These associations were already rare and restricted to one basin: the *Hollardops* Association was restricted to the western part of the study area (i.e., Maïder and Fom Zguid areas) and the *Sculptoproetus* Association stayed confined in the Tafilalt area (Jbel Amlane, Fig. 7). In contrast, the *Morocops* Association

continued to be widespread in different basins during the early Eifelian but also disappeared in the late Eifelian in many places despite a last occurrence (i.e., presence of

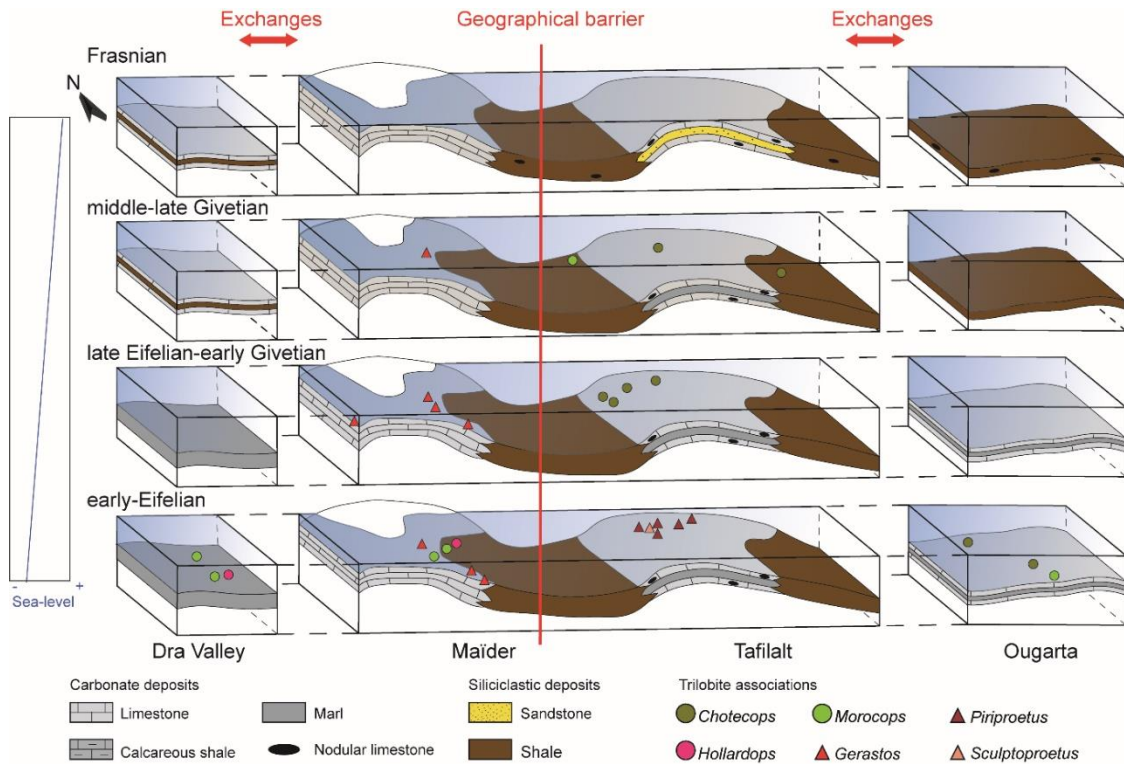


Fig. 7. Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Middle Devonian and Frasnian. Associations defined by clustering have been reported.

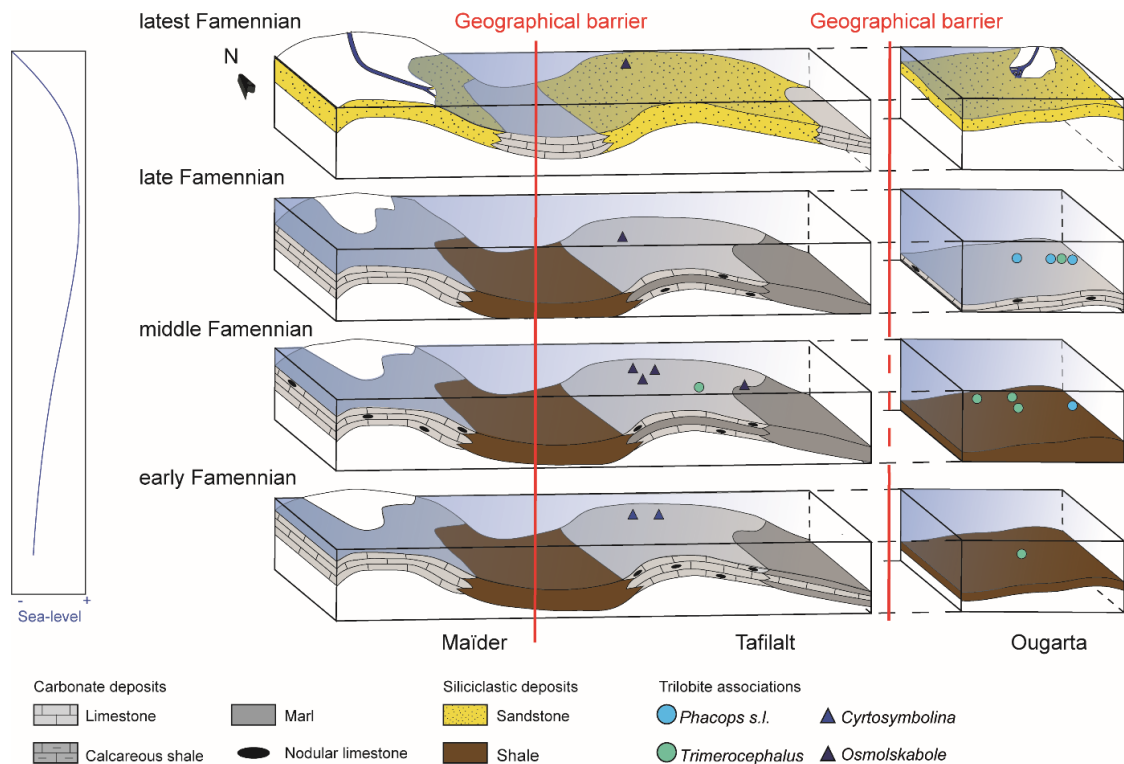


Fig. 8. Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Famennian. Associations defined by clustering have been reported.

Koneprusia) during the late Givetian in the north-western Tafilalt (Ras el Kebbar locality). Similarly, the *Piriproetus* Association (*Ie*), which appeared in the northern Tafilalt during the Emsian, proliferated during the early Eifelian but has not been recorded in strata laid down later. They developed everywhere in the northern Tafilalt area but never occurred elsewhere. Conversely, the *Gerastos* Association (*Iic*) occupied exclusively the Maïder area where it appeared during the late Emsian although some *Gerastos* were also found outnumbered in one Tafilalt locality and one Dra Valley locality. During the Givetian, the *Gerastos* Association (*Iih*) was still limited to the Maïder area but also developed in the western part of the platform at Jbel Ou Driss (Fig. 7). Finally, the *Chotecops* Association (*IId*) was first identified in the Ougarta area (Ouarourout) during the early Eifelian before invading the Tafilalt area during late Eifelian (Fig. 7). The *Chotecops* Association (*IIj*) was still found in the western and the southern Tafilalt area during the Givetian but was apparently no longer present in Algeria. All these associations disappeared at the end of the Givetian.

4.2.3. Late Devonian

Only one genus occurred in the study area during the Frasnian, at Marhouma in the Ougarta region. *Chlupacops* is not found in another stage or in another locality and has not been attributed to a particular association.

During the early Famennian, the Tafilalt area was only occupied in its northern part (at Bin Jbilit-Bordj Est locality) by the genus *Cyrtosymbolina* (from Ass. *IVa*, Fig. 8). At the same time, in the western Ougarta (Marhouma), the biodiversity was greater with three identified genera, which are equally abundant within the *Trimerocephalus* Association (*IVc*). When the *Cyrtosymbolina* association disappeared during the middle Famennian, the *Trimerocephalus* Association invaded the Ougarta region but also the western edge of the Tafilalt area. In the extreme south-east of this area (Tamtert Zereg locality), the new *Phacops s.l.* Association (*IVd*) appeared. This genus is also associated with *Trimerocephalus* in the Tafilalt area ('KeA-Fb34' sample) (Fig. 4). The *Phacops s.l.* Association replaced the *Trimerocephalus* Association in many late Famennian localities although *Trimerocephalus* remained only at Bechir locality (Ougarta). However, none of these two associations have been found in the uppermost Famennian. In the Tafilalt area, the *Osmolskabole* Association (*IVb*) replaced the *Cyrtosymbolina* Association (*IVa*) in many places from the middle Famennian and persisted until the latest Famennian where they occurred only in the extreme north-western part (at 'Bordj Est' locality, Fig. 8). *Osmolskabole* was found with *Trimerocephalus* and *Phacops s.l.*

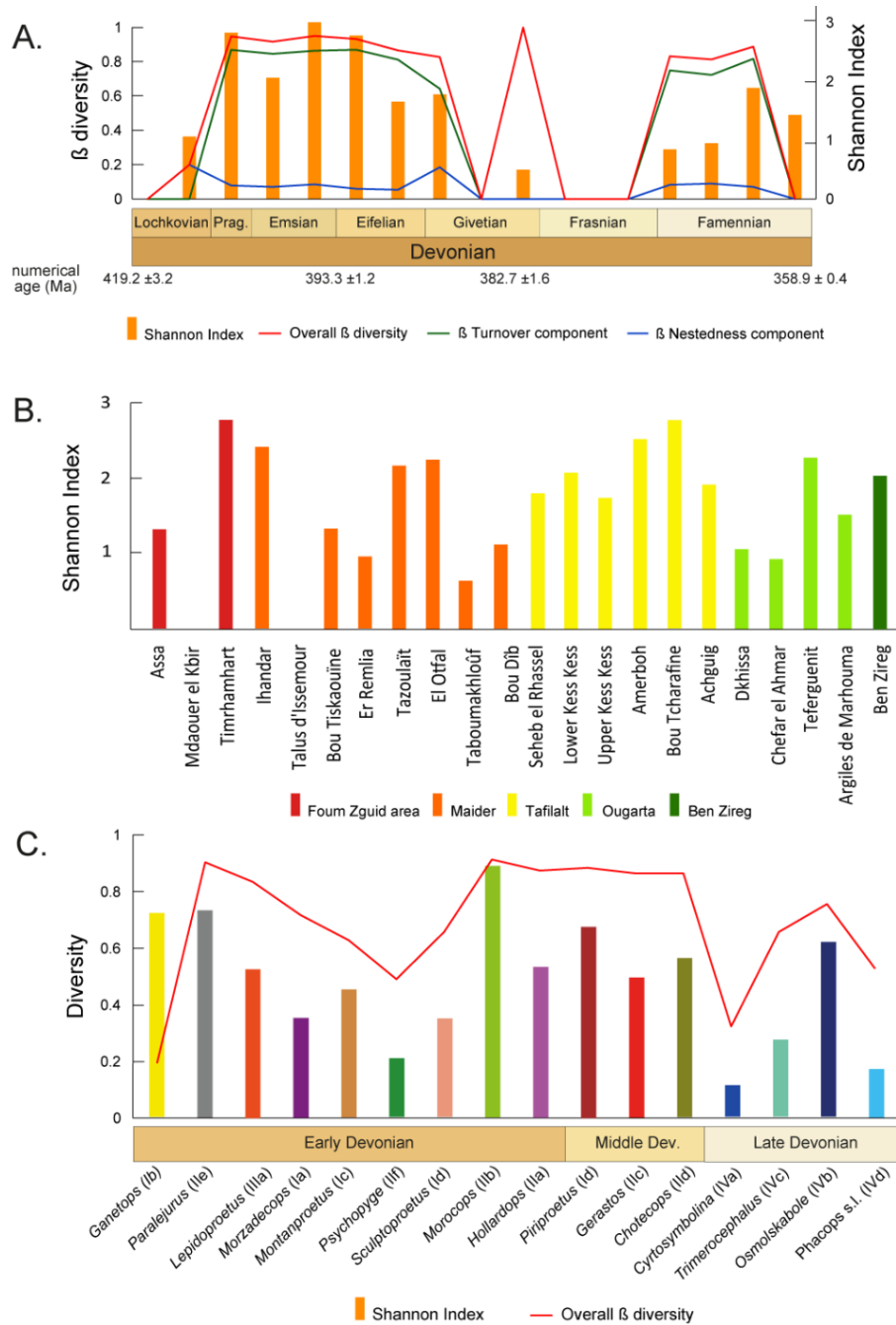


Fig. 9. Diversity indices. (A) Diversity through time: α diversity estimated with Shannon Index H' , Overall β Diversity and its components, i.e., β Turnover component and β Nestedness component determined with Sorensen dissimilarity. (B) α Diversity per from five areas. (C) α Diversity and Overall β Diversity per association. Ages from Cohen et al. (2013, updated).

4.3. Evolution of biodiversity indices through time

α and β diversity were low in the late Lochkovian with Shannon index H' of 1.06 and overall β diversity of 0.2 (Fig. 9A). Then, the diversity indices increased during the Pragian reaching a plateau of high diversity until the early Eifelian with Shannon index $H' > 2$ and overall β diversity > 0.9 . The diversity indices decreased progressively during the late Eifelian to the

early Givetian, before a sharp decrease from the middle Givetian to the end of the Frasnian with null or almost null values. In the early Famennian, both α and β diversity indices increased again. However, when the α diversity index stayed low compared to that of the Early and the Middle Devonian with a Shannon index H' of 0.84, overall β diversity reached values similar to the Early Devonian. In the late Famennian, α diversity increased to 1.89 before decreasing in the latest Famennian. During this period, overall β diversity evolved differently with a slight decrease in the middle Famennian followed by an increase in the late Famennian, the time of the highest disparity of the Late Devonian (Fig. 9A). Components related to compositional heterogeneity of β diversity show different trends. The β turnover component follows the overall β diversity trends whereas the β nestedness component always shows lower values (Fig. 9A) indicating that most of the β diversity corresponds to the replacement of genera by others in different localities (Balsega, 2010). Moreover, β nestedness component changed exactly oppositely to the overall β diversity in the Early and the Middle Devonian (Fig. 9A). Consequently, during periods of low diversity, the localities with smaller numbers of species were subsets of biotas found in localities with greater trilobite diversity.

Trilobite association of the Tafilalt remained diverse during nearly all the Devonian contrary to the Maïder and Ougarta where the associations contained in them were unevenly diverse (Fig. 9B). Although the presence of trilobites at Ben Zireg and Fom Zguid areas were not continuous through time, Shannon index H' was relatively high as in the other basins (Fig. 9B). These from the late Emsian and the Eifelian contained the most diverse trilobite faunas in all basins (Fig. 9B).

5. Palaeoenvironments of trilobite associations

It is widely known that trilobite associations vary between regions but the ecological drivers are largely unknown. HCA performed on the Devonian trilobite taxa of Morocco and Algeria enabled us to delineate twelve Early and/or Middle Devonian associations and four Late Devonian associations. The associations reflect distinctive taxonomic affinities and palaeoenvironmental preferences. Similar analyses on Devonian trilobites from the Ardenne Massif showed that trilobite associations were dependent on palaeobathymetric domains and sea-level variations (Crônier & Van Viersen, 2007). Subsequently, these associations (most particularly during the Givetian) were highlighted as equilibrated communities were able to maintain their organisation during rather strong and short environmental perturbations. These associations were able to flourish again during similar favourable environmental conditions. Only global events influenced the trilobite association (Bignon & Crônier, 2015).

During the Lochkovian, trilobites were rare in the study area. Only *Ganetops*, *Protacanthina* and to a lesser extent, *Morzadecops*, proliferated during the late Lochkovian in the Ougarta region (Ass. *Ila*). These asteropygines preferred the shallow siliciclastic environment of the Saoura Valley (Fig. 6; [Morzadec, 1997](#)) and similar environmental settings, also developing in the Iberian and Cantabric ranges and in the Armorican Massif ([Morzadec, 1992](#)). Subsequently, an increasing number of trilobites began to populate the region. Their remains are frequently found in the strata, whose carbonate content is also increasing. This suggests a lower sea-level and concerns distinct invertebrate faunas ([Frey et al., 2014](#)). In such environments, *Lepidoproetus* Association (*IIla*) flourished; proetids like *Lepidoproetus*, *Dalejeproetus* and *Podoliproetus* preferred these rather shallow environments with open marine conditions ([Johnson & Fortey, 2012](#)). The *Lepidoproetus* Association survived during the late Emsian of the Dra Valley in deeper water environments. Trilobites of this association are usually found in calcareous shales deposited above the photic zone but probably below the storm weather wave base ([Chatterton et al., 2006](#)). However, only *Hollandiella* was encountered in these deeper environments and in layers above the transgressive Daleje event ([House, 1985](#)).

During the Pragian, the *Paralejurus* Association (*IIId*) also established itself (Fig. 6). *Paralejurus* and *Reedops* were predominant in limestones at intermediate depth but also in shallower environments such as the bioherms of Hamar Laghdad ([McKellar & Chatterton, 2009](#)). *Reedops* was probably semi-infaunal or infaunal ([McKellar & Chatterton, 2009](#)) whereas [Schraut & Feist \(2004\)](#) excluded a semi-endobenthic life habit for *Paralejurus*. Consequently, these two genera were rarely found together notwithstanding some exceptions - *Paralejurus* co-occurred with *Reedops cephalotes hamlagdadianus* [Alberti 1983](#) but the latter species appears to have been ecologically more flexible with respect to the type of substrate ([Chlupáč, 1977](#)). During this period, the *Sculptoproetus* Association (*IIe*) developed and is often found in the nodular marly limestones from the north-eastern part of Jbel Issoumour ([Alberti, 1967b, 1969](#)), indicating a slightly deeper environment than those preferred Pragian associations. The *Sculptoproetus* Association evolved during the Emsian; *Sculptoproetus* abounds in marly limestones indicating an intermediate water depth environment (Fig. 6).

During the Emsian, *Morzadecops* first associated with other asteropygines during the Lochkovian, flourished and dominated the *Morzadecops* Association (*Ia*). *Morzadecops* occurs in marls and limestones interbedded with clay in moderately shallow water depth environments ([Klug et al., 2008](#)). The *Montanproetus* Association (*Ic*) also developed during the Emsian but it was mainly found in calcareous deposits in shallow carbonate environments (Fig. 6). The associated *Kayserops* preferred a more shallow environment ([Morzadec, 2001](#)). *Psychopyge* is

widely distributed in several marine basins during the Emsian. It was rarely associated with other genera (Fig. 4) and dominated the *Psychopyge* Association (*IIf*). *Psychopyge* are present in marls or limestones interbedded in thick marl deposits from relatively distal environments dominated by pelagic faunas (Morzadec, 1988).

Although the *Morocops* Association (*IIf*) was first encountered during the Pragian at the Maharch locality with the presence of *Cyphaspis* (Van Viersen & Holland, 2016), it proliferated in the late Emsian and the early Eifelian. This association was dominated by *Morocops*, which co-occurred with *Cyphaspis* and *Austerops*. The presence of *Austerops* could indicate a pioneer community (Khaldi et al., 2016). The *Morocops* Association also developed in the moderately deep-water environment of the Dra Valley (Chatterton et al., 2006) and the platform environment of Ougarta after the late Emsian transgression (Khaldi et al., 2016). It was also able to live in the epicontinental basin between fair weather and storm wave base of Hamar Laghdad (Brachert et al., 1992). Hence, the *Morocops* Association abounded in a water environment below the fair-weather wave base. At the same time, the *Piriproetus* Association (*Ia*) was encountered at the edge of the pelagic Tafilalt Platform in moderate depth below the fair-weather wave base (Figs. 6,7); Kaufmann, 1998; Chatterton et al., 2020). *Piriproetus* occurred in a facies dominated by marly limestones but they disappeared from this environment after the early Eifelian.

During the late Emsian, the *Hollardops* Association (*IIf*) also flourished and was dominated by *Hollardops*, *Timsaloproetus* and *Erbenochile*. These taxa proliferated in marls or limestones interbedded within marls. They were mostly present in Ougarta, an area considered relatively deep and dominated by shales (Ouali Mehadji et al., 2011) (Fig. 6). A similar environment developed in the western Dra Valley where *Timsaloproetus* was found (Chatterton et al., 2006). *Hollardops* enjoyed intermediate water depth below fair-weather wave base like in the Maïder and the Ougarta region (Chatterton & Gibb, 2010) but they disappeared with a more open marine environment (Morzadec, 2001). Finally, *Erbenochile* proliferated in relatively deep marine environments (Chatterton et al., 2006), which corroborates the moderately deep marine conditions such as an offshore transition for the *Hollardops* Association. The *Gerastos* Association (*IIf*) also flourished during the Emsian at Jbel Issoumour South-west (Fig. 6). In this balanced community (Fig. 4), *Morocops* or *Cyphaspis* did not prevail over *Gerastos* contrary to many late Emsian assemblages affiliated with the *Morocops* Association. Conversely, the *Gerastos* associations from the Middle Devonian were dominated by *Gerastos*, which was the only genus in many localities (Fig. 4). *Gerastos* is found in limestones from the Maïder where they found detritus for food in the shallow shelf marine environment (Gibb &

Chatterton, 2010).

The *Chotecops* Association (*IId*) was the only association to appear and expand during the Middle Devonian and was dominated by *Chotecops* associated with *Helmutia* and *Struveaspis*. The *Chotecops* Association was encountered in Ougarta and Tafilalt (Fig. 7) in marls or in thin limestone layers in marl deposits from the quiet environments of a distal platform or basin (Feist & Orth, 2000; Crônier et al., 2018a).

All the associations that appeared during the Early or Middle Devonian disappeared in the late Givetian. Only *Chlupacops*, a genus with reduced-eyed taxa was found in the limestones of deep marine environments in the Ougarta Basin (Feist et al., 2016).

After the Kellwasser event, trilobites were rare in the study area. The first trilobite after the crisis was *Cyrtosymbolina* in the early Famennian. The increasing depth of water during the Famennian (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) led to trilobites flourishing again, which meant we could use them to examine the relationships between different basins over time. During the early Famennian, only cyrtosymbolines proliferated in the shallow pelagic Tafilalt Platform in the *Cyrtosymbolina* Association (*IVa*). They became common in the photic offshore environments of North Africa and many other places (Lerosey-Aubril & Feist, 2012). Members of the *Cyrtosymbolina* Association occur mainly in limestones but also in marlstones and argillaceous limestones, such as shallow carbonate marine environments (Fig. 8).

In the Ougarta Basin, blind trilobites such as *Trimerocephalus*, *Trifoliops* and *Enygmapyge* occurred since the early Famennian. The *Trimerocephalus* Association (*IVc*) established in many localities of the Ougarta Basin (Fig. 8) in deep marine environments of the slopes and basins. They were collected from rare often nodular limestones indicating a weak water circulation (Benhamou et al., 2004; Crônier et al., 2013). *Trimerocephalus* also occurred at Korb-el-Atil in the Tafilalt Basin associated with *Osmolskabole* and *Phacops sensu lato* (Fig. 8) within a marine environment dominated by shales (Wendt & Belka, 1991). During the late Famennian, the *Trimerocephalus* Association is only found at Béchir, again in a deep marine environment, before its demise at the end of the Famennian.

The *Osmolskabole* Association (*IVb*) appeared during the middle Famennian in the limestones of the Tafilalt Platform (Fig. 8) because they appreciated the photic offshore environment. Consequently, this pelagic platform became convenient for the members of this association because of the sea-level rise (Wendt & Belka 1991). The *Osmolskabole* Association also flourished in the deeper marine environments of the slowly subsiding Tafilalt Basin (at Korb-el-Atil and Ouidane Chebbi localities), in argillaceous limestones. Nonetheless, this

association did not occur in the Maïder Basin because this area was deeper than the Tafilalt Basin (Wendt et al., 1984).

During the late Famennian, Cyrtosymbolines were still abundant in the Tafilalt Platform. However, the *Osmolskabole* Association was no longer present in the Tafilalt Basin, probably due to a transgression (Wendt & Belka, 1991; Becker et al., 2004). At the end of the Famennian, the *Osmolskabole* Association is still found in the limestones of the north Tafilalt Platform whereas the south became a deltaic area (Wendt et al., 1984). Indeed, trilobites did not appreciate brackish water although some attempts to colonize these environments happened in the clade history (Mángano et al., 2021). The *Osmolskabole* Association and cyrtosymbolines in general were restricted to moderate water depth environments from platform to slope, which are represented today by limestone deposits.

Finally, the *Phacops s.l.* Association (*IVd*) flourished in the Ougarta region (at Tamtert Zereg locality) during the Famennian, to the east of the location of the *Trimerocephalus* Association (Fig. 8) in nodular ‘griotte’ limestones corresponding to a basinal environment (Benhamou et al., 2004). The *Phacops s.l.* Association extended into the late Famennian with the continuous deepening of this area (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) and replaced *Trimerocephalus* Association (at Marhouma locality). The *Phacops s.l.* Association still abounds in nodular limestones alternating with claystones, or in marlstones, in moderate to deep marine environments such as basins. Samples with *Phacops s.l.* are generally slightly younger than those of *Trimerocephalus* even if these two genera may co-occur (Crônier et al., 2013). Therefore, a progressive replacement occurred in the Ougarta Basin in the deeper offshore environment and already recognised at the global (Crônier & François, 2014). At the end of the Famennian, a sea-level drop occurred and all the deep water trilobites disappeared from the studied area.

6. Connection between basins and their history through time

6.1. Lochkovian

Trilobite diversity was low in the study area in the Lochkovian (Fig. 9A). They only occurred in the Saoura Valley where trilobites populated the sediment surface in the late Lochkovian after a regional regression (Ouali Mehadji et al., 2011). Only asteropygines lived in these shallow siliciclastic environments (Morzadec, 1997). To the west, the eastern Anti-Atlas became too deep to allow benthic faunas to settle during the Lochkovian (Hollard, 1967) and thus, this environment was neither favourable for asteropygines (Morzadec, 1992), nor for other trilobites as they were completely absent from this area.

6.2. Pragian

The Pragian regression led to a higher carbonate content with more sand in the Saoura Valley where asteropygines no longer proliferated (Morzadec, 1997; Ouali Mehadji et al., 2011). Indeed, the composition of trilobite associations was linked to the sediment accumulation rate and the type of shelf (Bignon & Crônier, 2015) and no other trilobites replaced them. The eastern Anti-Atlas became more carbonate too (Hollard, 1963; Kaufmann, 1998). New trilobite communities were established (Hollard, 1967; Morzadec, 2001) in these favourable environments leading to a strong increase of their diversity in North Africa (Fig. 9A) simultaneously to the global Pragian diversification (Chlupáč, 1994, Bault et al., 2021). However, despite this high diversity three genera dominated the shallow water environments of the Anti-Atlas region: *Paralejurus*, *Reedops* and *Lepidoproetus*. These genera and some other genera, constituted two associations: the *Paralejurus* Association was dominant in the Maïder and the *Lepidoproetus* Association was dominant in the Tafilalt (Fig. 6). Nevertheless, the *Paralejurus* Association developed to the west in the Tafilalt and in the north of the Ougarta region at Ben Zireg and to the east near Foug Zguid. Thus, there was a strong connection between these different basins during the Pragian. This is due to a relatively homogeneous environment in the Anti-Atlas region at this time, considered as a homoclinal ramp (Kaufmann, 1998; Lubeseder et al., 2010). Exchanges also occurred with the neighbouring Bechar area, which was facilitated by the same carbonate platform environment (Ouali Mehadji et al., 2011) and with the south-west Foug Zguid area where *Reedops* and *Cyphaspis* were reported. All the Pragian trilobites populated a relatively shallow environment of various carbonate platforms. However, *Paralejurus* and its associated trilobites preferred slightly deeper environments than *Lepidoproetus*, which is why they rarely co-occurred. The shoal of Hamar Laghdad (Hollard, 1981, Brachert et al., 1992; Klug et al., 2018) showed a high diversity of trilobites.

6.3. Emsian

In the early Emsian, diversity decreased (Fig. 9A). While the Pragian dominant species almost disappeared from the studied area, other genera proliferated despite no important environmental changes in the Anti-Atlas (Kaufmann, 1998). *Morzadecops* spread over the entire eastern Anti-Atlas and *Sculptoproetus* lived in the Tafilalt. In the Ougarta region, a local transgression (Ouali Mehadji et al., 2011) led to a comeback of trilobites with the moderately deep water genus *Psychopyge* but no connection existed with the Anti-Atlas; the Ougarta region remained isolated from other basins to the west and to the north. The Bechar basin was also

excluded from the trilobite dispersal with *Prodrevermannia* the only genus occurring in that region (Alberti, 1983). *Morzadecops*, which preferred a shallow environment (Morzadec, 2001), could not proliferate in the Ougarta region. However, although *Sculptoproetus* lived in moderately deep-water (Chatterton et al., 2006), it was not found in the Ougarta region. Hence, the deep waters of the Tafilalt Basin between Ougarta and Anti-Atlas prevented the dispersal of shallow and moderately deep-water trilobites from one of these regions to the other.

In Morocco, the Maïder and Tafilalt platforms were still connected and the *Morzadecops* Association (*Ia*) flourished in both areas. However, the *Sculptoproetus* Association (*Id*) was restricted to the Tafilalt area while it appeared in the Maïder area during the Pragian. The Tafilalt area being typically shallower than the Maïder area (Wendt, 1995), trilobites migrated to shallower places but no transgression occurred at this time (Kaufmann, 1998). There were no more dispersal to the south-west as the Fom Zguid area became shallower (Jansen et al., 2004) where trilobites did not develop.

During the late Emsian Daleje transgression (Johnson et al., 1985; Kaufmann, 1998; House, 2002), the studied area became deeper (Kaufmann, 1998, Belka et al., 1999). Trilobites developed in this new environment leading to the highest α diversity and a high β diversity (Fig. 9A) simultaneously with the global diversity peak (Chlupáč, 1994; Adrain, 2008). Late Emsian trilobites constituted a stable equilibrium community. Some of the common trilobites of the Pragian persisted into the early Emsian, such as *Paralejurus*, *Reedops* and *Sculptoproetus*. However, no Pragian or early Emsian trilobite genus became common in the late Emsian; they were all declining and restricted to few areas. The only exception was *Psychopyge*, which invaded the Anti-Atlas. Thus, during this period of diversification, the genera quickly renewed themselves by showing innovations and novelties (Chlupáč, 1994). Numerous genera appeared in the late Emsian and among them with the phacopids *Morocops* and *Hollardops* respectively dominating the Anti-Atlas (Crônier et al., 2018b) and the Ougarta region. Connections between the different basins were strong, favoured by the relatively homogeneous environments in North Africa, moderately deep water, with an important proportion of muddy regions (now shales) covering the platforms (Hollard, 1967; Kaufmann, 1998; Jansen et al., 2004; Chatterton et al., 2006; Ouali Mehadji et al., 2011). Exchanges between Anti-Atlas and the deeper Ougarta region became possible: *Hollardops* and *Erbenochile* occurred in Ougarta, Maïder and Dra Valley (Morzadec, 2001; Chatterton et al., 2006; Chatterton & Gibb, 2010; Khaldi et al., 2016). *Psychopyge* were also found in both the eastern Anti-Atlas and the Ougarta region (Fig. 6). Although the Tafilalt and Maïder areas became different during the late Emsian in terms of both facies and fauna (Hollard, 1967), a strong connection was present between these two areas.

Sculptoproetus proliferated in the Maïder area, suggesting an invasion from the Tafilalt area. At the same time, *Morocops*, as well as *Cyphaspis*, flourished in the Tafilalt, Maïder and near Foug Zguid areas. Ben Zireg was also involved in the exchanges with *Montanproetus* existing in the Bechar Basin and the Maïder area. Nevertheless, it remains difficult to demonstrate the supply of trilobites from one basin to another without a finer temporal resolution. Although trilobite exchanges were numerous, some trilobites remained restricted to a basin such as *Gerastos* and *Piriproetus* in the Maïder Basin. Significant taxonomic turnovers occurred between the late Emsian localities as is highlighted by the high β diversity (Fig. 9). More important local environment variability in the eastern Anti-Atlas (Hollard, 1967) is a potential explanation for this high taxonomic turnover.

6.4. Eifelian

The transition between the Early and Middle Devonian was marked by the onset of tectonic events leading to a platform and basin topography (Wendt et al., 1984; Kaufmann, 1998; Lubeseder et al., 2010). This event is due to the Variscan orogeny, which disrupted the eastern Anti-Atlas. A deep basin (i.e., Maïder Basin) separated two platforms (i.e., Maïder and Tafilalt platforms). As most trilobites lived in shallow environments, they did not cross the basin to invade other localities. More specifically, the deep Maïder Basin acted as a natural barrier, which led to the development of distinct trilobite communities in the Middle Devonian. This barrier also effectively prevented the dispersion of these communities by pelagic or planktonic larvae, which had been identified in several Devonian trilobites (Speyer & Chatterton, 1989; Chatterton et al., 1990; Chatterton & Speyer, 1997). Indeed, these protaspides could not cross this deep basin because of unfavourable paleocurrents, paleoenvironmental conditions, or/and a too wide distance for their life duration. Consequently, in contrast to the Lower Devonian, trilobite distributions of the Eifelian show almost no connections between the Tafilalt and Maïder areas. To the west of the Maïder Basin, *Gerastos* and *Cyphaspis* evolved whereas *Piriproetus* then *Chotecops* developed in the Tafilalt (Fig. 7). The trilobites from the west of the Maïder Basin evolved in a relatively shallow environment (Gibb & Chatterton, 2010) and did not cross the deep Maïder Basin (Wendt et al., 1984). On the other hand, *Cyphaspis* occurred to the south-west at Foug Zguid (Van Viersen & Holland, 2016) showing a connection between the Maïder and the western Anti-Atlas areas. *Gerastos* that appeared in the late Emsian, proliferated in the Maïder during the Eifelian and covered the edges of the Maïder Platform including the western part at the Jbel Ou Driss locality (Fig. 7). *Gerastos* replaced *Morocops* during the Middle Devonian in the shallow neritic environments, while the distribution of this

genus decreased from the late Emsian to be restricted in some Maïder localities. To the eastern side of the Maïder Basin, a community of trilobites dominated by the genus *Piriproetus* (Ass. Id) expanded in the pelagic Tafilalt Platform. The trilobites from this association living in a moderately deep environment were unable to cross the Maïder Basin. While no connection existed to the west of Tafilalt, trilobite exchanges still occurred to the east. Indeed, *Chotecops*, present in deep environments (Feist & Orth, 2000; Crônier et al., 2018a), occurred in both Tafilalt and Ougarta areas. Variscan orogeny created a basin between the Tafilalt and the Ougarta areas but this basin seems shallower than the Maïder Basin (Kaufmann, 1998) thus enabling *Chotecops* to cross this basin to invade new localities but not *Piriproetus*. *Chotecops* probably never settled in the Maïder because this basin was too deep. Moreover, they did not flourish in the shallow environments of the Maïder Platform margins. *Austerops*, present in Ougarta, Maïder and Dra Valley, was the only genus living on both sides of the Maïder Basin (Chatterton et al., 2006; McKellar & Chatterton, 2009; Crônier et al., 2018a). Its presence in these areas was recorded since the late Emsian (Fig. 6).

In both Tafilalt and Maïder, the Eifelian faunas replaced those of the Emsian and the trilobite associations were influenced by the palaeobathymetry (Crônier & Van Viersen, 2007). The origination rate and trilobite changes were not particularly high at the Emsian/Eifelian boundary on an overall (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012). Thus, North-African faunal changes rather seemed attributed to topographic changes where some trilobite genera took advantage of this new heterogeneous environment.

6.5. Givetian

The overall Middle Devonian Choteč, Kačak and Taghanic events (House, 2002; Becker et al., 2016) had an impact on trilobites and their diversity at the global (Lerosey-Aubril & Feist, 2012) and from North Africa (Fig. 9A). Most of them disappeared during the Givetian and only three associations have been reported in the studied area: the *Gerastos* Association with *Gerastos* sometimes associated with *Cornuproetus* or *Cyphaspis* in the Maïder area; the *Chotecops* Association dominated by *Chotecops* and *Helmutia* in the Tafilalt area and the *Morocops* Association at Ras el Kebbar locality (Maïder). The same distinction between areas was identified during the Eifelian. However, the presence of *Gerastos* at the Jbel Ziata locality in the Tafilalt (Feist & Orth, 2000) associated with *Chotecops* showed that trilobite exchanges were rare but remained possible. The weak regressive regime during the early Givetian enabled such migrations from the Maïder to the Tafilalt areas (Lubeseder et al., 2003) as well as the proximity of the Maïder Platform with the Tafilalt Platform to the north of the Maïder Basin

(Kaufmann, 1998). All the trilobites occurred in the eastern Anti-Atlas, whereas the Fom Zguid area and the Ougarta Basin seem relatively depopulated. Unlike in the Ardenne Massif (North of France), the Kačak event did not lead to a replacement of faunas in North Africa (Bignon & Crônier, 2015) but instead to an extinction of existing faunas. However, like in the North of France, the environmental changes favoured *Dechenella* in the Tafilalt (Feist & Orth, 2000).

6.6. Frasnian

Overall, the Frasnian trilobite record is scarce (Feist, 1991; Lerosey-Aubril & Feist, 2012). In the studied North African area, the reduced-eyes *Chlupacops* was the only genus encountered in the Ougarta Basin in deep environments (Feist et al., 2016). This basin seems to have been disconnected from the others. The low trilobite diversity recorded during the Frasnian could be explained by unfavourably shallow environmental conditions in the eastern Anti-Atlas (Wendt et al., 1984, Wendt & Belka, 1991) whereas Feist (2002) described trilobites from an outer platform environment in the neighbouring Meseta Central in Morocco.

6.7. Famennian

After the Kellwasser crisis, some trilobites developed worldwide. While, cyrtosymbolines proliferated in the shallow outer platform (Lerosey-Aubril & Feist, 2012), in deeper environments such as basins, reduced-eyed and blind phacopids and proetids developed (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012). A similar process occurred in North Africa where cyrtosymbolines appeared during the early Famennian in the shallow Tafilalt Platform and constituted a pioneer community. At the same time, in the deeper Ougarta Basin, the number of blind phacopids increased. No trilobites have been found in the Maïder for this period. No dispersal routes seem to have existed between the different basins at that time: *Trimerocephalus* Association was encountered in the Ougarta Basin, while the *Cyrtosymbolina* Association was encountered in the Tafilalt area. Cyrtosymbolines could not cross the deep Maïder and Tafilalt basins as the Tafilalt Platform acts as a natural barrier to stop deep water trilobites coming from Ougarta. This trend remained through the Late Devonian. In contrast, the distal platform of Ben Zireg (Abbache et al., 2019) seems to have been a favourable environment to host trilobites but none have been found yet in the nodular limestones and shales. Trilobite studies based upon localities at Ben Zireg since Alberti (1983) remain scarce and this could explain the absence of trilobites in addition to the sedimentary gaps (Abbache et al., 2019). Trilobites were absent throughout the Famennian in the Maïder Basin, probably

deposited in deeper water than that of the Tafilalt Basin (Wendt et al., 1984; Kaufmann, 1998). Crônier & François (2014) suggested a depth superior to 60 m for blind genera (i.e., *Trimerocephalus*) and Feist et al. (2016) indicated an offshore environment near or beyond the limit of the photic zone. However, with its depth of 200 to 400 metres, the Maïder Basin had much deeper steep slopes according to stratigraphic studies (Wendt et al., 1984). The Tafilalt Platform also acted as a barrier to trilobite dispersal.

The sea-level rise of the middle Famennian (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) allowed the proliferation of deep-sea phacopids. They were present at that time in many Ougarta localities and a connection appeared between the Tafilalt and Ougarta areas. Exchanges were possible because the Tafilalt Basin and the Ougarta Basin were probably interconnected during the Late Devonian (Wendt et al., 1984; Wendt, 1985; Abbache et al., 2019). However, dispersal apparently only occurred from the Ougarta Basin to the Tafilalt area, i.e., from deeper to shallower environments. Indeed, this unidirectional supply of biodiversity suggests that only the deep-living taxa of Ougarta were able to cross the deep basin between the Ougarta and the Tafilalt. The moderately deep-water taxa *Phacops s.l.* and *Trimerocephalus* present in the Ougarta region were able to colonise the margins of the quite deep Tafilalt Basin. Shallower areas also enabled the development of other trilobite communities with new cyrtosymbolines appearing in the Tafilalt Platform dominated by the *Osmolskabole* genus (Alberti, 1973, 1974, 1975a, 1976a, 1976b; Lerosey-Aubril & Feist, 2005; Lerosey-Aubril & Feist, 2006). Because of the deepening of this area, they were adapted to intermediate water depths and could have settled in the margins of this relatively shallow Tafilalt Basin (Wendt et al., 1984) although they were still unable to cross a deep basin to establish themselves in the Ougarta region. Moreover, in the intermediate water/depth, other taxa developed during the middle Famennian. These were the large eyed *Phacops s.l.*, which proliferated in the deeper part of the shallow Tafilalt Platform, associated with *Trimerocephalus* or *Osmolskabole*. On the other hand, *Phacops s.l.* only occurred in the shallower part of Ougarta region to the south-east.

During the late Famennian, this connection was disrupted and the Tafilalt and Ougarta areas are represented by two separate communities (Fig. 8). Despite the deepening of the Tafilalt basin at this time, no trace of deep-water phacopids has been found there although they were still present in the Ougarta Basin. Two explanations are possible - first, that they were present but still not sampled and secondly, that a natural barrier, which has still not been identified between the two basins prevented any trilobite exchange. This kind of natural barrier could have resulted from the deepening between Ougarta and Tafilalt areas, preventing any crossing

of trilobites, or, alternatively, from a very shallow barrier, formed in the context of Variscan orogeny, which was not favourable to Famennian trilobites (Hollard, 1974, Wendt et al., 1984). Unfortunately, this area was covered by Cretaceous deposits (Benhamou et al., 2004) thus preventing any information on the evolution of this basin. Cyrtosymbolines were restricted to the shallowest part of Tafilalt, to the North. During this period of highstand sea-level (Wendt & Belka, 1991), the rest of the Tafilalt was probably too deep to host them. In contrast, *Trimerocephalus* has been recorded in the Ougarta region for this time in just one locality, while *Phacops s.l.* dominated the rest of this area. These phacopids tended to replace *Trimerocephalus* in the late Famennian (Crônier & François, 2014).

Finally, at the end of the Famennian, a regression occurred leading to a deltaic environment with sandstone deposits in the eastern Anti-Atlas and Ougarta region (Wendt et al., 1984; Kaiser et al., 2011; Abbache et al., 2019). This environment was unfavourable for many benthic organisms and all deep-sea trilobites disappeared from these areas. Only two cyrtosymbolines (i.e., *Pusillabole* and *Pseudowaribole*) remained in the shallow water environment of the northern Tafilalt and were apparently unable to migrate to the Ougarta Basin, which was probably too deep (Fig. 8). It is difficult to understand the facies distribution of the Tafilalt because of the scarce outcrops and the potential reworking due to debris flows (Wendt et al., 1984).

Originations and migrations always occurred from the shallower part of Tafilalt and Ougarta region. In the Tafilalt, trilobites appeared in the shallowest part of the Tafilalt Platform, located to the north (Wendt & Belka, 1991) before becoming a deeper basin in the south. Trilobite migrations seemed to have started in its south-eastern part of the Ougarta Basin. *Trimerocephalus* Association from the early Famennian and *Phacops s.l.* Association from the middle Famennian appeared respectively at the Marhouma and Tamtert Zereg localities (Fig. 8). These localities corresponded to an epicontinental platform (Benhamou et al., 2004) and represented the shallowest part of the Ougarta Basin. Then, following their occurrences, each genus invaded the deepest north-western part and dominated the basin (Fig. 8). However, an influence from the south-west was unlikely because the environment in the Gourara area was deep with basinal deposits (Benhamou et al., 2004; Abbache et al., 2019).

6.8. Tectonic impact on trilobite faunas

During the Early Devonian, the Anti-Atlas area had a rather homogeneous environment (Lubeseder et al., 2010). In this context, faunal changes were linked to global environmental changes with first, the Pragian regression, which led to environmental changes driving faunal

changes (Chlupáč, 1994; Morzadec, 1997, 2001). Similar changes occurred in Bohemia with the development of *Reedops* and *Odontochile* (Chlupáč et al., 1985). Then, the Daleje transgression (Kaufmann, 1998; House, 2002) affected the North African trilobites with the development of new faunas dominated among others by *Morocops* and *Hollandops*, adapted to slightly deeper environments (Fig. 6). The same trend occurred worldwide, with diversifications and innovations, particularly in offshore facies (Chlupáč, 1994). From the Middle Devonian, the Variscan orogeny started to influence the regional topography (Wendt et al., 1984; Kaufmann, 1998) and global events (sea-level changes and continental drift) were no longer the only cause of biodiversity changes. Obviously, the Middle Devonian events influenced the trilobite faunas, both quantitatively (Bault et al. 2021) and qualitatively (Fig. 7). Similarly, an important turnover occurred with the Kellwasser events (Lerosey-Aubril & Feist, 2012) and consequently, the Famennian trilobites had nothing in common with their predecessors in North Africa (Fig. 4). However, from the Eifelian, there were faunal differences between nearby areas (Fig. 7). These differences were well marked in Morocco and Algeria with strong differences between Maïder and Tafilalt whereas in other places such as the Ardenne Massif, the faunas were still subject only to global changes (Bignon & Crônier, 2015). The basin and platform topography affected the trilobites because of their bathymetric preferences (Morzadec, 2001; Chatterton et al., 2006). Rapid changes and instability made unpredictable regional conditions indicating that North African trilobite communities conform to Gleasonian models where 'species-individualistic' responses to environmental changes became prevalent in community ecology (Gleason, 1927). Regular local and/or global changes hampered the ecological stasis spotted in other communities (Brett et al., 1996).

Unlike topography, the type of sedimentation had a low impact on North African trilobites, except for those due to global changes at the Lochkovian-Pragian boundary. Moreover, the associations seemed less dependant on the sedimentation type laterally. For instance, *Gerastos* has been found both in thick-layered limestones and in calcareous mudstones interbedded with shales (Gibb & Chatterton, 2010). This kind of equilibrium community has been already noted in the Middle Devonian trilobites of the Ardenne Massif (Bignon & Crônier, 2015). Indeed, the *Dechenella* association raised and flourished when carbonate platform environments appeared at the end of the Eifelian. This community was able to maintain its organization during several dismantling episodes of the platform during the Givetian, corresponding to a mixed carbonate-siliciclastic ramp. Only the global Taghanic event of the late Givetian (House, 1985) broke the stability of this community. A similar signal has currently been highlighted in Morocco regarding the stability of trilobite organization despite environmental variations restricted in

local and temporal terms (Hollard, 1963, 1967; Bultynck & Walliser, 2000; Lubeseder et al., 2010).

7. Conclusions

During the Devonian, the Anti-Atlas Range and its Algerian extensions were located on the Saharan Platform, a passive continental margin of Gondwana. This area underwent several ecological changes due to regional and global events with many sea-level changes, anoxic/hypoxic events and tectonic events occurring throughout the Devonian. All these changes affected the composition of trilobite communities and their diversity.

Trilobites were not well dispersed between the different areas of Northern Africa because of spatial and temporal environmental changes. Devonian trilobites can be assigned to 16 associations with 12 of these associations existing during the Early and Middle Devonian and four exclusively during the Famennian. Each of these trilobite associations flourished in a specific environment, which was favourable for some genera but less so for others. In siliciclastic environments, asteropygines prospered in the Ougarta region during the Lochkovian, while the Pragian regression allowed the diversification of many trilobites in shallow water environments. Both trilobite diversity and the number of associations further increased during the Emsian. During this period, the different basins were well interconnected. Faunal exchanges were facilitated by the absence of strong ecological or topographical barriers and further favoured by a relatively homogeneous environment. The Variscan orogeny modified the palaeogeographic setting during the Middle Devonian towards a platform and basin topology. Geographical barriers formed and trilobite associations became restricted to smaller areas with poor connections between them. This regional tectonic context coupled with more widespread Middle Devonian events affected trilobites, which were almost eradicated from this area in the Frasnian. After the Kellwasser events, trilobites once again flourished regionally and globally although not to the diversity levels of the Emsian or Eifelian. During the same period, cyrtosymboline associations proliferated in shallow platform environments, while phacopid associations proliferated in deeper water environments. Finally, new sea-level and sedimentological changes in the latest Famennian led to the disappearance of numerous trilobites in the Northern African area under study.

Acknowledgments

The authors thank the reviewers Christian Klug (Switzerland) and Brian D. E. Chatterton (Canada), and the editor for their constructive remarks, which improved the manuscript. This

work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic time’, to the ECOS Sud-MINCYT (Argentina) A17A01, and to the French CNRS UMR 8198 Evo-Eco-Paleo (Université de Lille). The authors thank the Région Hauts-de-France, the Ministère de l’Enseignement Supérieur et de la Recherche (CPER Climibio) and the Université de Lille for their financial support.

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Supplemental figures

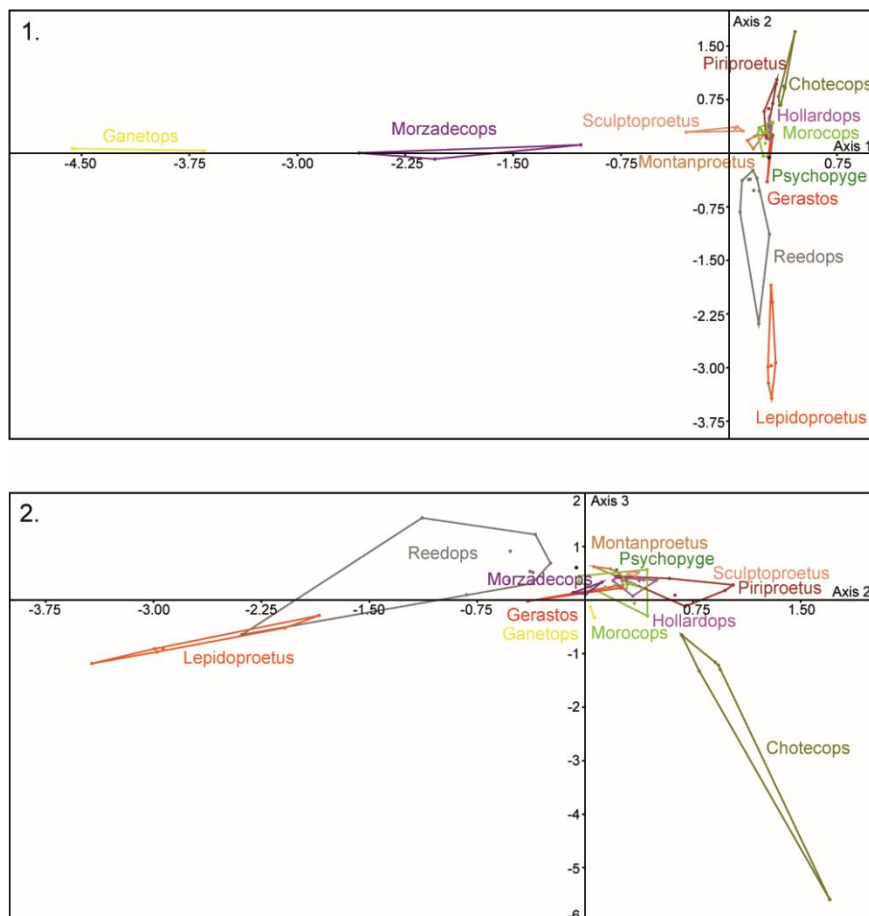


Fig. A. Scatter plot of North African samples according to Correspondence Analysis (CA) for the Early and Middle Devonian. (1) CA1 and CA2 showing a Pinocchio effect, and (2) CA2 and CA3 showing an arch effect.

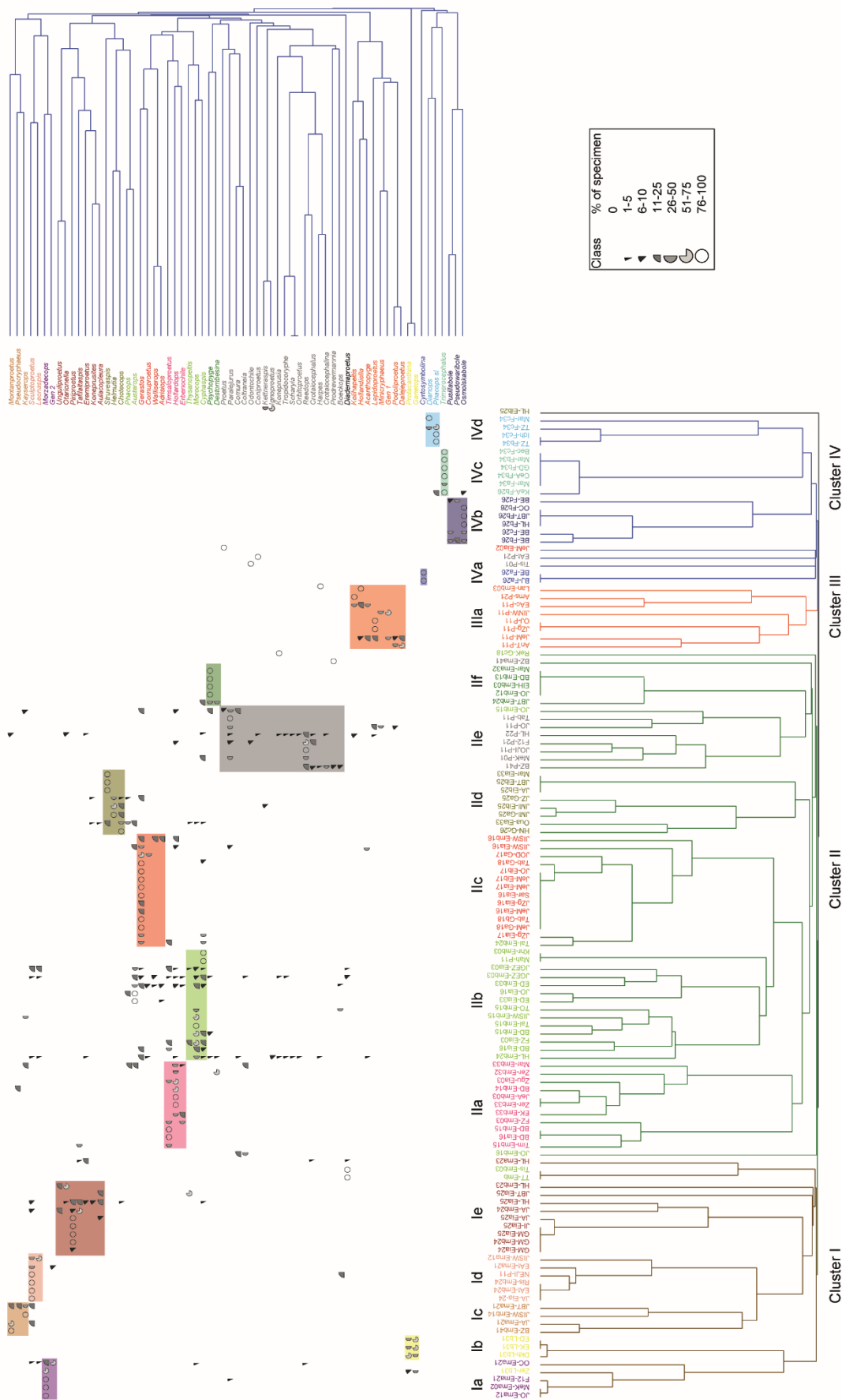


Fig. B. Dendrogram with R and Q modes from hierarchical cluster analysis (HCA) using the average linkage method as correlation setting and the Pearson correlation index as similarity index (Hammer & Harper, 2008). 67 taxa (genera) are clustered according to 123 analysed samples from the Devonian of North Africa. Four clusters and 16 associations are identified. Occurrences of genera in samples are given in proportion of the total number of genera in the sample.

Lochkovian

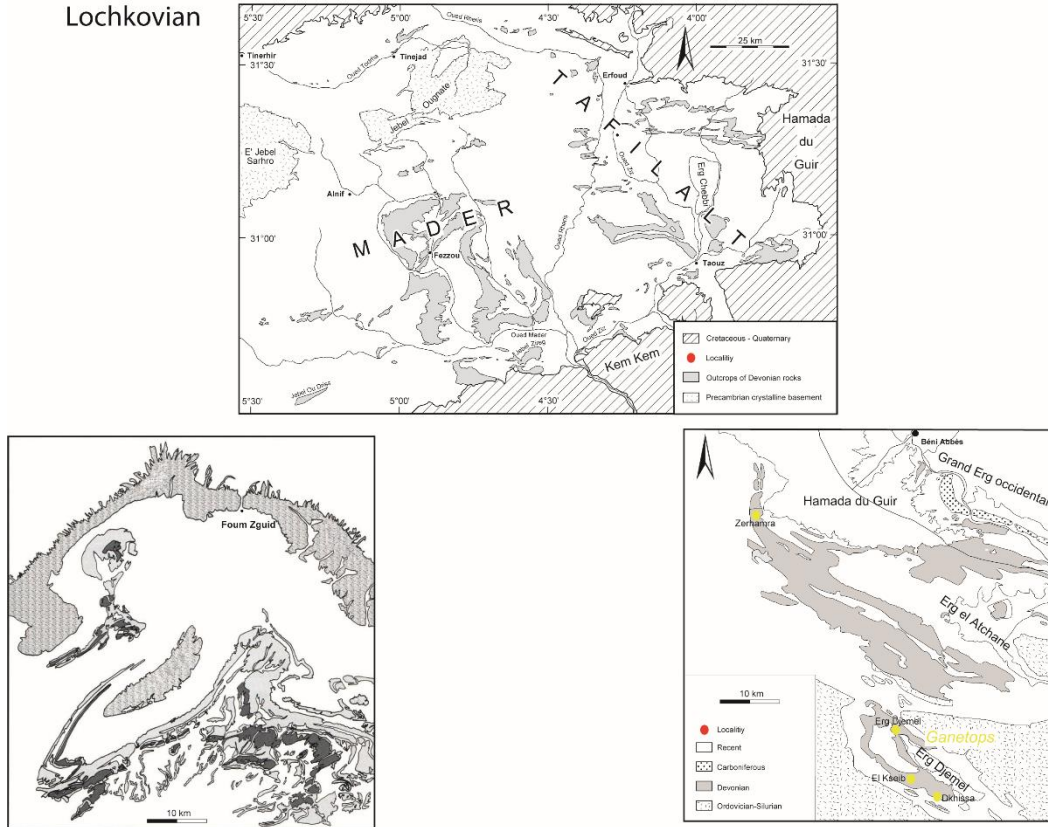


Fig. C. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Lochkovian.

Pragian

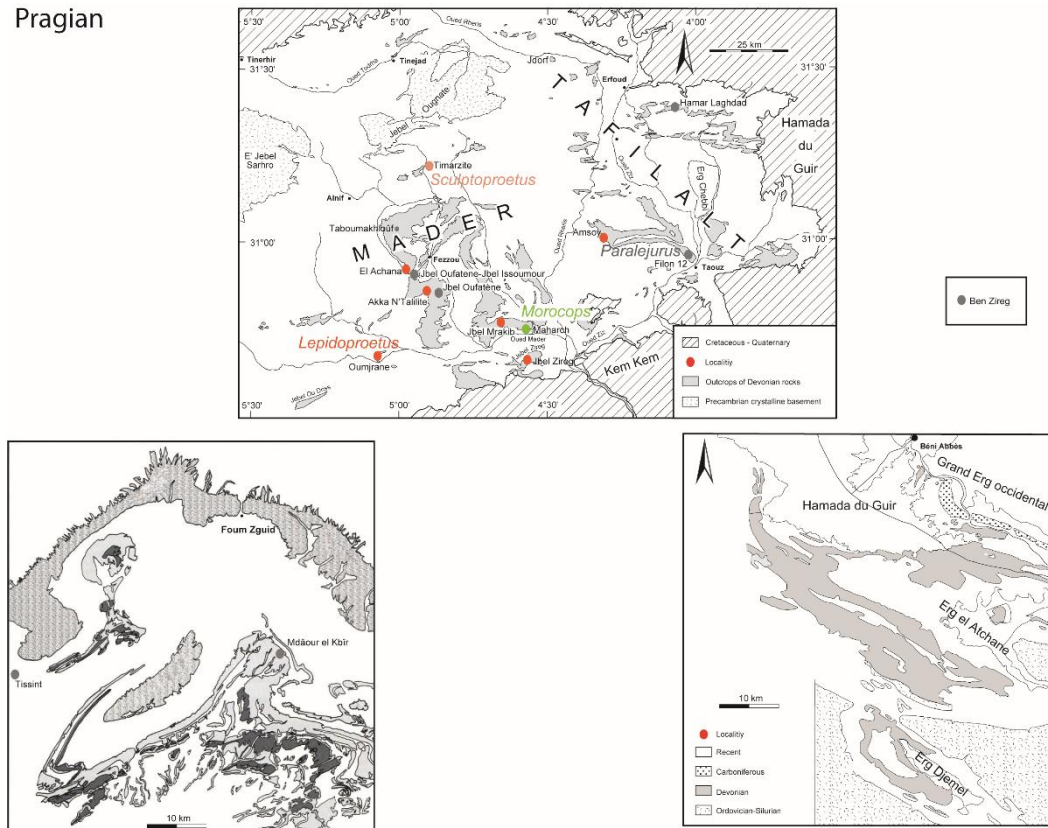
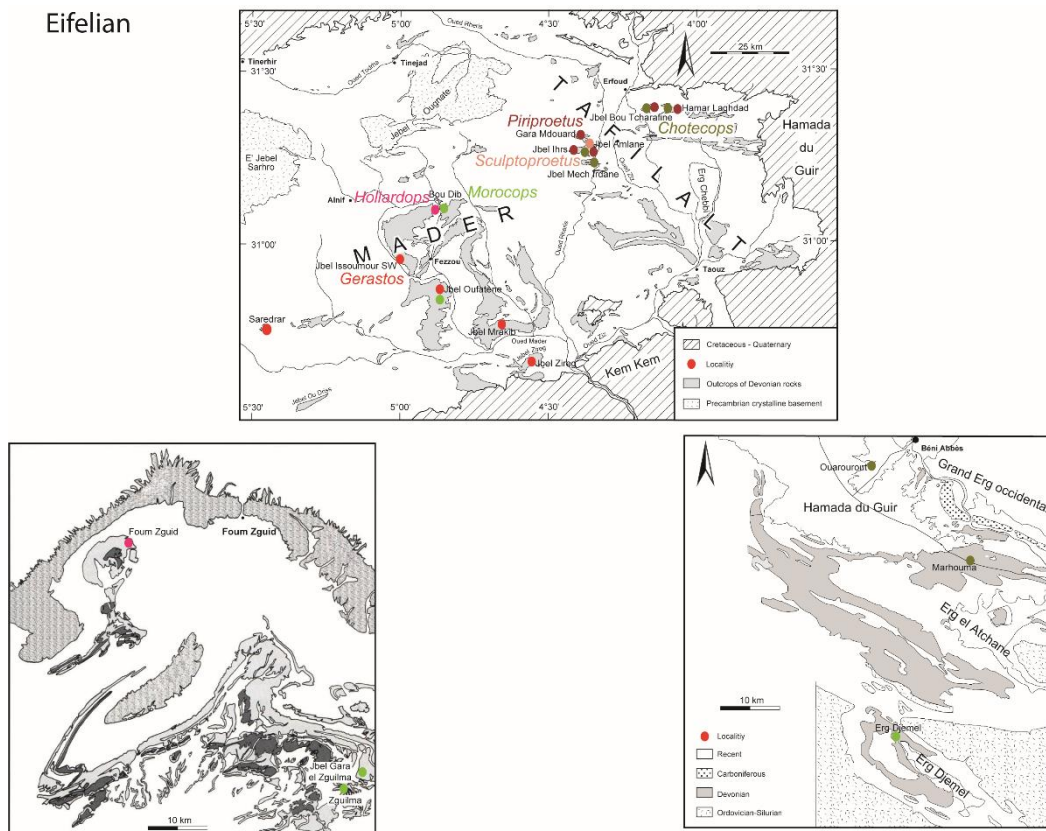
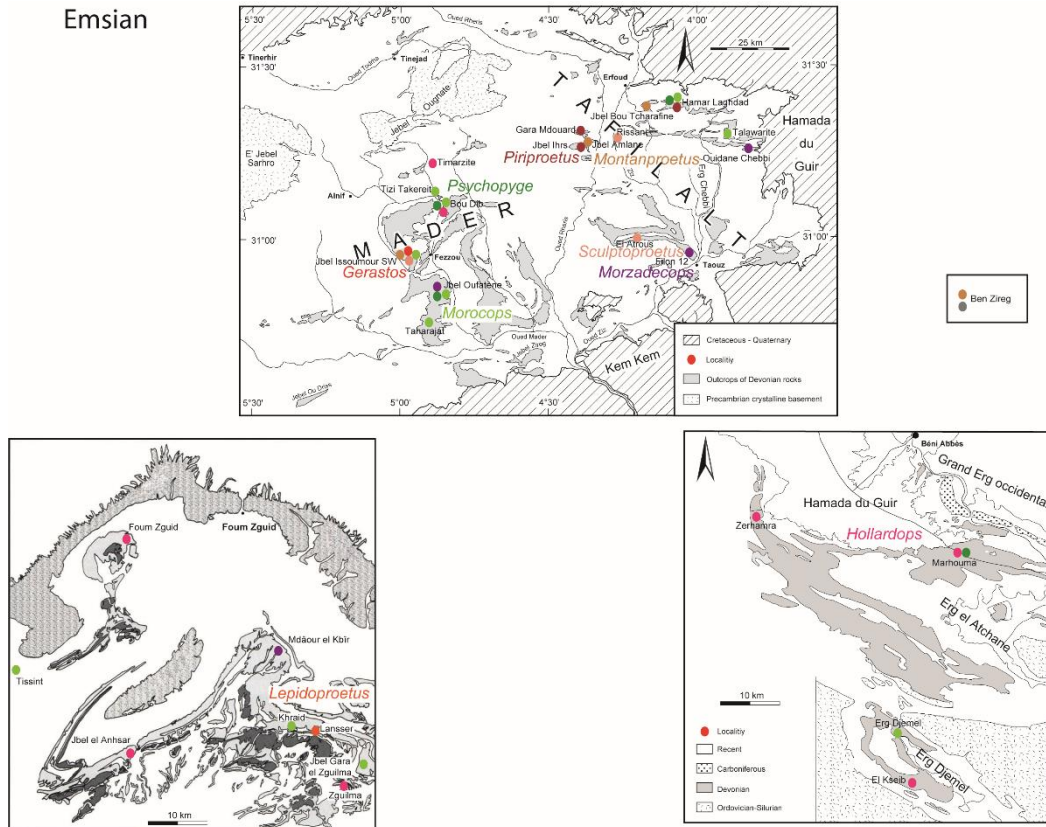


Fig. D. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Pragian.



Givetian

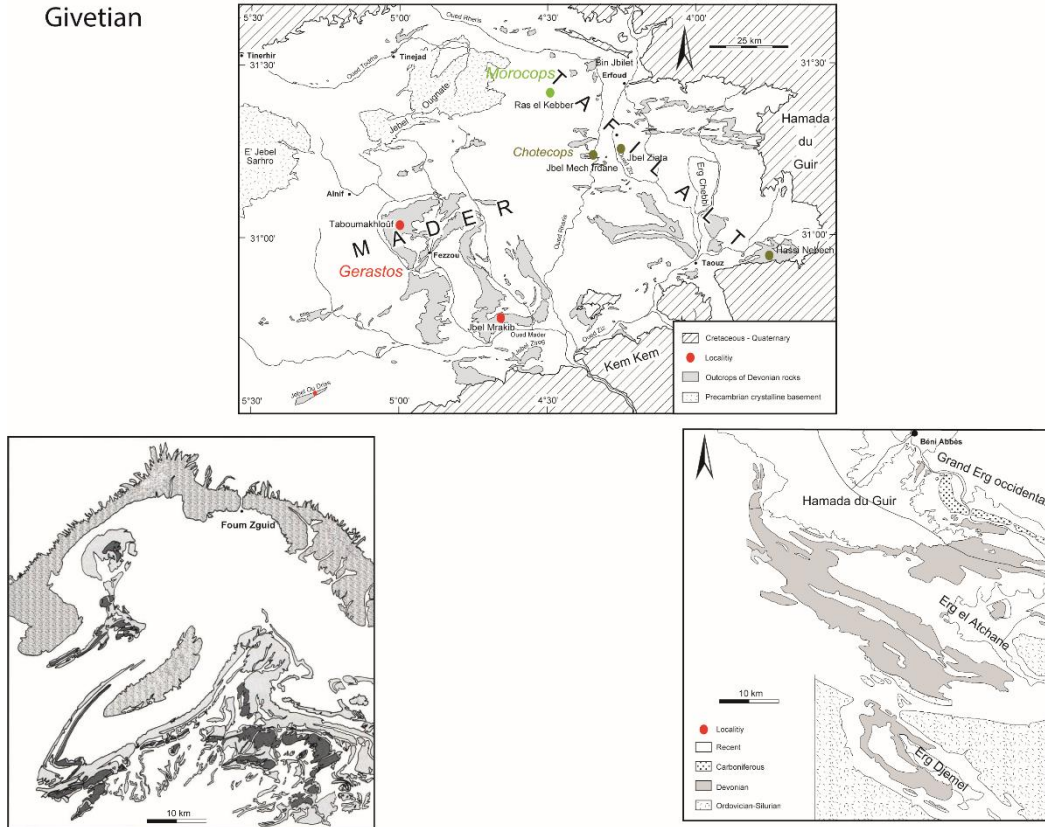


Fig. G. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Givetian.

Famennian

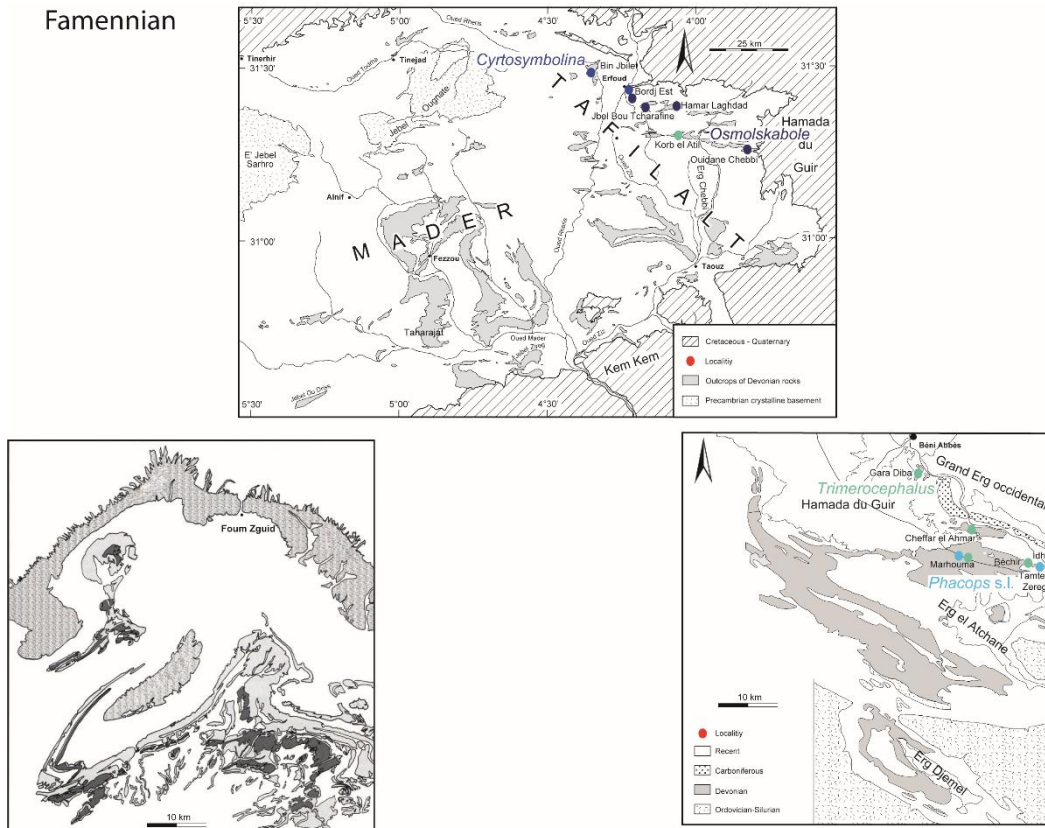


Fig. H. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Famennian.

CONCLUSION

Alors qu'elle a commencé avec succès il y a plus de 500 millions d'années au Cambrien, l'histoire évolutive des trilobites s'est perpétuée pendant 250 millions d'années jusqu'à leur disparition lors de la crise de la fin du Permien. Avant cette extinction définitive, plusieurs autres extinctions sont venues perturber ces arthropodes au cours du temps. Cette thèse s'est focalisée sur la seconde partie de l'histoire des trilobites, après l'extinction fini-ordovicienne qui a conduit à la perte de nombreux genres et de plusieurs ordres. Le but a été de comprendre comment les changements environnementaux ont influencé les trilobites afin de mieux comprendre leurs effets sur la biodiversité en général. Les trilobites ont été choisis comme modèle car ils représentent un support de choix en paléontologie, étant abondants et diversifiés en termes de formes et d'écologie. Ils ont connu un succès évolutif au Paléozoïque au cours duquel ils ont survécu à de nombreux événements. Ils abondent dans les terrains du Dévonien d'Afrique du Nord, région très étudiée pour son contenu paléontologique et géologique, offrant une bonne opportunité de recherche. Le Dévonien constitue également une période d'étude idéale en tant que période marquée par d'importants changements écologiques et environnementaux.

Le premier aspect de la biodiversité estimée a été la diversité taxonomique. Pour mieux comprendre les tendances régionales, il a fallu identifier les dynamiques mondiales et élargir la gamme temporelle en partant du Silurien et en allant jusqu'au Permien à l'aide d'une analyse factorielle. Au début du Dévonien, les faunes présentes étaient celles qui ont survécu à la précédente extinction de masse à la transition Ordovicien-Silurien. Ces faunes vont être supplantées par d'autres trilobites lors de la diversification du Dévonien inférieur. Après un pic de diversité à l'Emsien, une succession d'événements environnementaux incluant des changements abrupts du niveau marin et des périodes d'anoxie affectèrent les trilobites. Leur diversité va considérablement diminuer et quelques taxons vont tirer bénéfices de cette période de crise. Une dernière faune de trilobites va se développer à partir du Carbonifère, mais celle-ci ne sera composée que de l'ordre Proetida et n'atteindra jamais les niveaux de diversité précédents. Les événements du Dévonien auront donc eu un impact néfaste et durable sur les trilobites. Les trilobites d'Afrique du Nord montrent les mêmes tendances qu'à l'échelle mondiale. Grâce à des données de bonne qualité, il a été possible d'analyser les dynamiques avec une résolution temporelle relativement fine, au sous-étage. Pour estimer la diversité, il a été possible d'utiliser des méthodes à la pointe permettant de corriger un maximum les biais

paléontologiques. Les résultats montrent que la diversité était assez faible au début du Dévonien, mais très vite, elle augmenta lors de deux phases de diversification : au Praguien et à l'Emsien supérieur. Le déclin des trilobites d'Afrique du Nord a été plus soudain à l'échelle régionale qu'à l'échelle mondiale, une importante extinction ayant eu lieu à l'Eifelien. La diversité était donc très faible au Givétien et au Frasnien. La richesse taxonomique a augmenté au Frasnien supérieur et l'extinction de masse du Kellwasser à la limite Frasnien–Famennien s'est plutôt avérée être une phase de *turnover* faunique. L'Afrique du Nord riche en fossiles de différentes faunes a offert l'opportunité unique de comparer les tendances de diversité entre les trilobites benthiques et une faune nectonique, les ammonoïdes, étudiée dans le cadre d'une thèse aux approches similaires (Allaire, 2017 thèse non publiée). Cette comparaison a montré que le necton et le benthos d'une même région pouvaient avoir des dynamiques distinctes et être impactés différemment par les changements environnementaux.

La deuxième partie de ce travail s'est focalisée sur les changements morphologiques des trilobites du Dévonien d'Afrique du Nord. Pour appréhender les variations de forme de ces arthropodes, des séries de points homologues ont été capturées sur des illustrations 2D puis utilisées à l'aide d'analyses Procruste. Des indices de disparité morphologique ont également été utilisés pour caractériser au mieux les variations. Trois structures ont été choisies pour être étudiées car elles concentrent la variation morphologique chez les trilobites : le céphalon, sa partie centrale le cranidium, et le pygidium. Les principales différences mises en évidence entre les individus sont la forme de la glabelle et la position de la suture faciale pour le céphalon et l'élongation du pygidium. La présence ou non d'épines constitue également une divergence importante entre les différents taxons. L'espace morphologique résultant n'a pas été occupé uniformément au Dévonien. En effet, au début du Dévonien inférieur, cet espace était quasiment inoccupé. Ce n'est qu'au Praguien que de nouvelles innovations ont eu lieu chez les trilobites d'Afrique du Nord, en particulier avec l'apparition d'épines de différentes natures. Cette tendance s'est confirmée à l'Emsien mais la plupart des formes ont disparu au Dévonien moyen pour ne plus réapparaître ensuite. Les analyses mettent en avant une extinction sélective, marginale ou latérale. Les formes déjà présentes à la fin du Silurien sont celles qui ont le mieux supporté les changements environnementaux et qui ont subsisté jusqu'à la fin du Dévonien. Ces formes ont montré une meilleure compatibilité/adaptabilité aux changements d'environnements ou de mode de vie, les aidant à persister au cours du temps. Les deux seuls ordres à avoir survécu jusqu'au Dévonien supérieur avaient un espace morphologique étendu et des morphologies adaptées à une large gamme d'écologie, ce qui a sans doute joué un rôle dans leur survie. Un focus sur les phacopidés, une famille emblématique du Dévonien a permis de confirmer que les

innovations ont été réalisées au Dévonien inférieur et que c'est surtout le Givétien qui a conduit à la disparition de nombreuses morphologies. Contrairement à de nombreux clades, les trilobites du Dévonien ont eu des dynamiques de diversité et de disparité relativement couplées. Cela est notamment dû à l'intensité des extinctions dévoniennes qui sont venues interrompre leur diversification.

Outre l'aspect temporel, la configuration spatiale a été étudiée pour une partie de l'Afrique du Nord. En se basant sur quelques bassins riches en trilobites et bien connus du point de vue de la paléogéographie, des associations fauniques ont été déterminées avec des analyses de partitionnement et de correspondance. 16 associations avec des affinités temporelles, géographiques et environnementales ont été identifiées en Afrique du Nord au Dévonien. En analysant leur répartition et évolution, les études réalisées ont mis en évidence le rôle de la paléogéographie sur la biodiversité en favorisant les migrations ou au contraire, en les empêchant. En effet, l'orogénèse varisque a modifié la région à partir du Dévonien moyen impactant fortement les trilobites et accélérant leur déclin en créant des barrières géographiques. Des hauts fonds, des bassins profonds ou des environnements différents ont ainsi empêché des échanges fauniques.

L'Afrique du Nord était donc une région où les trilobites vivaient au Silurien et au début du Dévonien, mais sans y être particulièrement abondants. Ce n'est qu'à partir du Praguien que le nombre de trilobites a explosé à la suite de l'expansion d'environnements peu profonds, favorables à l'établissement de faunes benthiques (Fig. 1). Ces conditions avantageuses perdurèrent jusqu'à l'Emsien. De nombreux échanges et migrations ont eu lieu et l'invasion de ces nouveaux environnements a suscité la mise en place des innovations morphologiques chez les trilobites. La plupart des familles et sous-familles de trilobites ont ainsi participé à cette grande phase de diversification. Le pic de diversité taxonomique et morphologique a été atteint à la fin du Dévonien inférieur mais dès le début du Dévonien moyen, les conditions se sont dégradées pour les trilobites. Les changements rapides et répétés du niveau marin et les phases d'anoxies successives ont grandement affecté les faunes nord-africaines au point que la plupart des genres de trilobites ont disparu au Givétien. L'Afrique du Nord a été particulièrement touchée puisqu'une combinaison de changements environnementaux a accéléré le déclin des trilobites. L'orogénèse varisque et des événements tectoniques qu'elle a induits se sont superposés aux événements marins, morcelant le paysage à partir de l'Eifelien et le rendant ainsi moins avantageux pour le benthos. L'extinction de masse du Frasnien–Famennien est venu accabler une faune déjà meurtrie et a eu davantage d'effets à grande échelle avec des extinctions au niveau des ordres. Si la disparité morphologique est restée faible pendant cette

période, il y a néanmoins eu des innovations avec la prolifération de formes aveugles ou à vision réduite. Cette tendance est en partie une adaptation à la vie marine en profondeur en réponse à une augmentation du niveau marin. Cette faculté d'adaptation des trilobites a permis une récupération écologique au Famennien avec une légère augmentation de la diversité mais l'événement Hangenberg est venu affecter cette faune déjà fragilisée à la fin du Dévonien, conduisant à l'extinction de l'un des deux derniers ordres de trilobites à l'échelle mondiale et à la quasi-disparition des trilobites en Afrique du Nord. Les trilobites du Dévonien d'Afrique du Nord constituent donc un bon *proxy* pour comprendre les effets des changements environnementaux sur la biodiversité et ont permis de démontrer que ces changements peuvent avoir des effets variables et que la combinaison d'événements néfastes peut être dévastatrice.

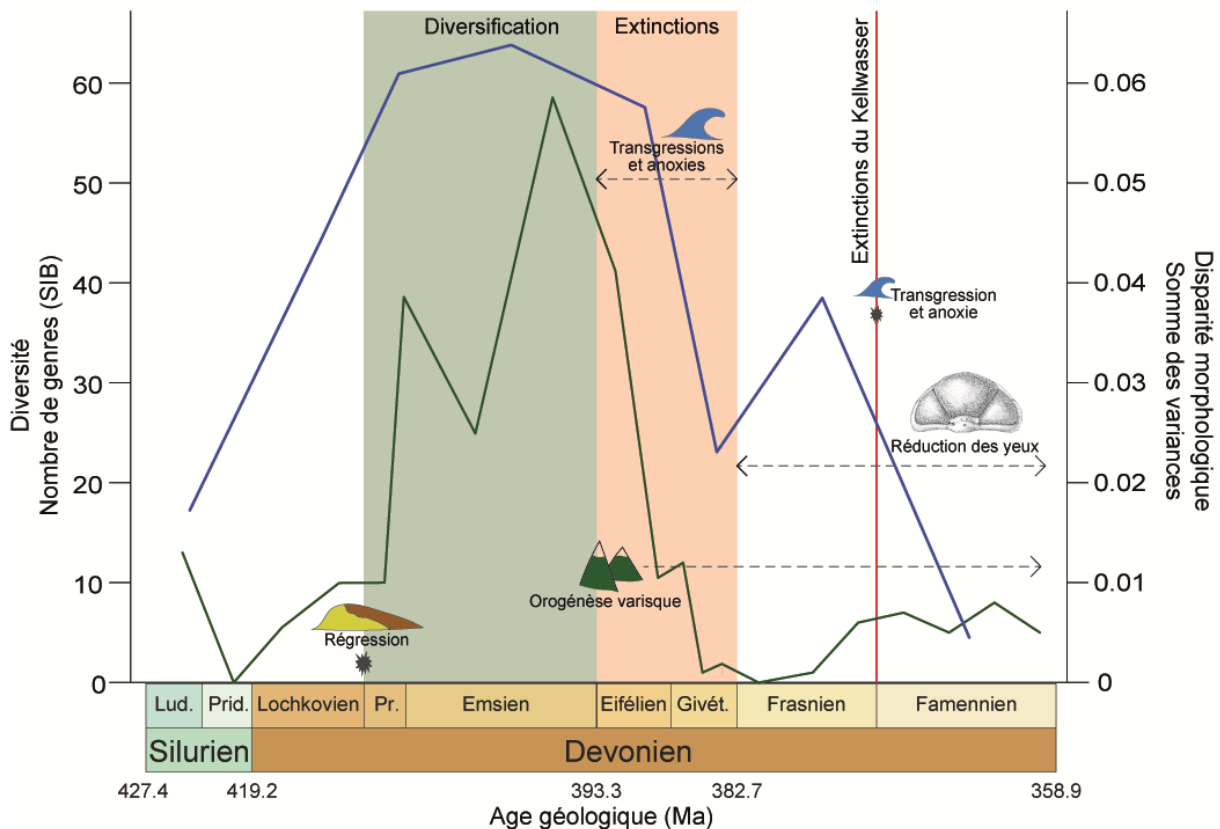


Figure 1 : Schéma synthétique de l'évolution de la diversité taxonomique (vert) et morphologique (bleu) des trilobites du Siluro-Dévonien d'Afrique du Nord

PERSPECTIVES

Bien que plusieurs aspects de la biodiversité aient été analysés dans le cadre de cette thèse, il reste de nombreuses pistes à étudier pour améliorer notre compréhension des facteurs mis en jeu. Nous l'avons vu, le Dévonien est une période marquée par d'importants changements écologiques et environnementaux : de nouveaux clades apparaissent et les modes de vie se

diversifient (Klug et al., 2010 ; Capel et al., 2021). L'influence d'autres taxons sur les trilobites, et inversement, n'a été que brièvement abordée. Cette influence peut s'exercer en termes de compétition entre deux taxons partageant la même niche ou de relation proie/prédateur. Ce dernier aspect mérite un intérêt particulier puisqu'il n'existe que très peu d'articles traitant des chaînes trophiques (Fig. 2) du Paléozoïque dans la littérature. Certes, il reste très compliqué de connaître les véritables liens trophiques au Dévonien mais les quelques recherches réalisées (Mark-Kurik, 1995 ; Brett and Walker, 2002 ; Babcock, 2003 ; Brett, 2003 ; Kriwet et al., 2008) permettent d'avancer des théories plus ou moins étayées et certaines preuves directes semblent exister. Les dépôts sédimentaires d'Afrique du Nord renferment de nombreux fossiles de différents taxons – y compris ceux à corps mous. L'Afrique du Nord représente ainsi un endroit idéal pour faire un état de l'art sur toutes les faunes dévoniennes retrouvées. A l'échelle locale, plusieurs récifs sont bien conservés et permettent de faire une étude des relations trophiques à l'échelle d'un écosystème réduit. En se basant sur des études réalisées sur des écosystèmes cénozoïques (Roopnarine et al., 2007) on pourrait identifier l'effet de l'apparition ou de la disparition d'un ou plusieurs prédateurs (ou proies) sur l'écosystème entier ou les trilobites en particulier.

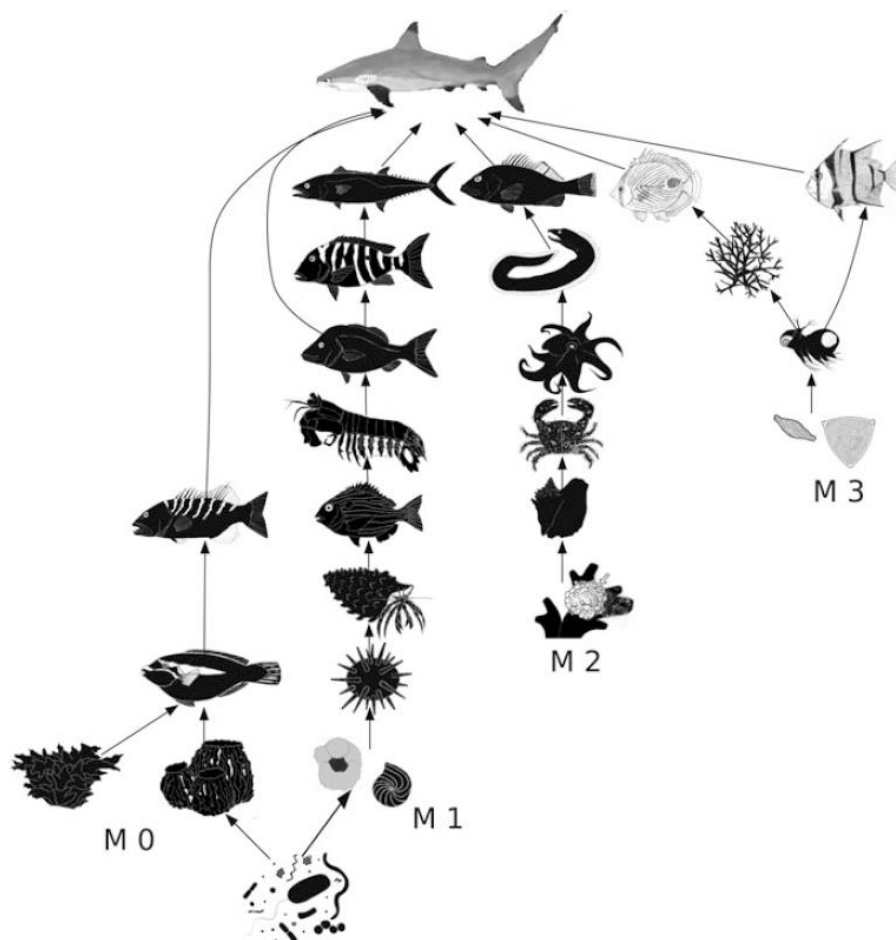


Figure 2 : Représentation d'une chaîne alimentaire marine actuelle (Roopnarine et Dineen, 2018)

L’Afrique du Nord est une des régions les plus riches en fossiles de trilobites du Dévonien. Cependant, des restes de ces arthropodes ont également été découverts ailleurs dans le monde (Amérique du Nord, Amérique du Sud, Asie, Australie...) et notamment en Europe. A cette période, le nord de l’Europe actuelle appartenait au continent Laurentia alors que la partie sud était disséminée en une multitude d’îles au milieu de l’océan Rhéique (Fig. 3). L’Europe étant située en face de l’Afrique et au Gondwana, cela offre ainsi une opportunité d’augmenter notre étude et d’analyser d’autres interactions trilobites-environnement. Les trilobites européens étant proches taxonomiquement de ceux d’Afrique du Nord avec beaucoup de genres communs, cela permettrait d’identifier les relations paléobiogéographiques à une plus grande échelle que celle abordée dans ce manuscrit. Cela permettrait notamment de comprendre les liens entre différents continents et d’identifier les grandes routes de migration. La fermeture de l’océan Rhéique et la collision des continents Laurentia et Baltica se mettant en place au Dévonien (Scotese, 2021), on pourrait même étudier l’effet de la tectonique des plaques sur la richesse taxonomique. Les trilobites d’Europe permettraient également de corriger certains biais obtenus en Afrique du Nord comme le manque de données au Givétien–Frasnien puisque l’Europe a un enregistrement relativement continu sur cette période avec de nombreux affleurements au Dévonien moyen et supérieur (Chlupáč, 1992 ; Bignon et Crônier, 2015 par exemple). L’Europe étant une des régions les plus étudiées en géologie, tout comme l’Afrique du Nord, comparer les données de ces deux régions offrirait l’opportunité de mieux comprendre les effets des changements environnementaux à l’échelle inter-régionale. Enfin, la création d’une base de

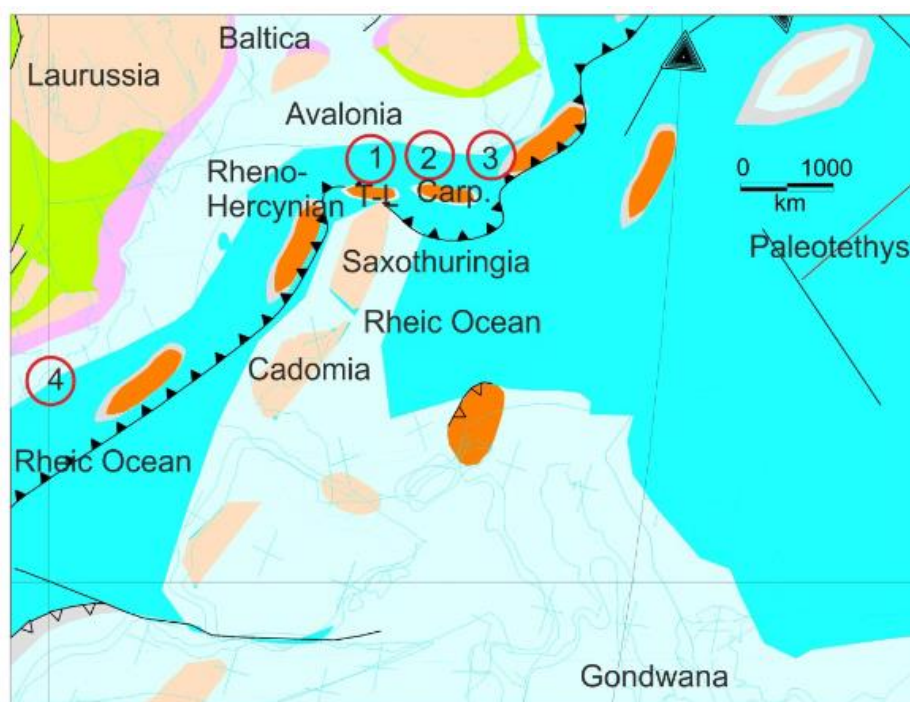


Figure 3 : Paléogéographie de l’Europe au Dévonien supérieur (Golonka et Gaweda, 2012).

données fondée sur les gisements européens permettrait de mettre à jour les données de diversité, la base de données mondiale (la Paleobiology database) étant incomplète.

Les analyses morphologiques effectuées lors de ce travail soulèvent également de nouvelles questions sur la relation trilobites-environnement. Cela concerne surtout les effets des changements environnementaux de la deuxième partie du Dévonien qui ont considérablement affecté les trilobites. Sur les deux ordres (Phacopida et Proetida) présents tout au long du Dévonien, seul l'ordre des Proetida subsistera au Carbonifère. Les Phacopida disparaîtront en même temps que de nombreux taxons à la frontière Dévonien–Carbonifère, marquée par une crise écologique importante : l'évènement du Hangenberg (Lerosey-Aubril et Feist, 2012 ; Kaiser et al., 2015). Cet évènement n'a que peu été évoqué dans ce manuscrit car les données d'Afrique du Nord pour la fin du Famennien sont relativement pauvres et il semble n'y avoir que peu de trilobites au début du Carbonifère. On peut se demander pourquoi cette crise semble n'avoir épargné aucun trilobite dans la région alors que la récupération post-Kellwasser avait été relativement importante. De la même manière, le fait que les Phacopida aient survécu pendant tout le Dévonien mais pas lors de l'évènement Hangenberg interroge. La flexibilité morphologique mise en avant dans l'article 3 (« Trilobite biodiversity trends in the Devonian of North Africa ») n'a-t-elle pas suffi pour permettre d'échapper à l'extinction ? Qu'avaient les Proetida en plus des Phacopida pour survivre ? D'autres questions se posent aussi sur le Kellwasser. En effet, si au Dévonien moyen, la diversité taxonomique et la disparité morphologique ont fortement diminué, il semble que la disparité soit la plus affectée lors de la crise du Frasnien–Famennien. Au niveau de la diversité, il y a eu beaucoup d'extinctions mais ces extinctions ont été compensées par un grand nombre d'apparitions, au point que cette crise soit plutôt une phase de *turnover* qu'une phase de diminution de diversité. Il faudrait confirmer ce postulat avec des données plus globales et comprendre ces changements, pour celle qui reste une des cinq extinctions de masse de l'histoire.

Enfin, toujours dans l'objectif de mieux comprendre les dynamiques géographiques, une étude à l'échelle mondiale fondée sur la Paleobiology database pourrait venir compléter les travaux effectués dans l'article 1 (« Post-Ordovician trilobite diversity and macroevolutionary history »). Cette base de données étant incomplète, de potentiel biais pourrait survenir, liés notamment au manque de données dans certaines régions du globe. Néanmoins, la Paleobiology database constitue un outil pratique avec un grand nombre de données facilement accessibles. Cette étude permettrait donc de voir les grandes voies de migration et les provinces biogéographiques et ainsi de mieux replacer les dynamiques observées en Afrique du Nord dans un cadre global.

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BASES DE DONNEES

Article 2 :

ID	Family	Genus	Species	Type	Cephalon	Type	Paper	Figures	Pygidium	Type	Paper	Figures	Eyes	FAD	LAD
1	Phacopidae	Acernaspis	Acernaspis orestes	Type	GSC 2472	Lectotype	Chatterton & Ludvigsen 2004	27.7	GSC 2472	Lectotype	Chatterton & Ludvigsen 2004	27.8		Rhuddanian	Telychian
2	Phacopidae	Acuticryphops	Acuticryphops acuticeps	Type	WAM 07.286		Feist et al., 2009	5e	WAM 07.290		Feist et al., 2009	5n		Frasnian	Frasnian
3	Phacopidae	Adastocephalum	Adastocephalum teleotypicum	Type			Mitchell 1919	16.2						Lochkovian?	Lochkovian?
4	Phacopidae	Adrisiops	Adrisiops weugii	Type	NHMM 2016.007	Holotype	VanViersen 2017a	7D	NHMM 2016.007	Holotype	VanViersen 2017a	7D		Emsian	Eifelian
5	Phacopidae	Afrops	Afrops larvifer	Type	SH	Holotype	Alberti 1983	7.87					Blind	Pragian	Pragian
6	Phacopidae	Ainasuella	Ainasuella ainasuensis	Type	No information		Maksimova 1978	2.1a			Maksimova 1978	2.1b		Lochkovian	Lochkovian
7	Phacopidae	Altaesajania	Altaesajania primitiva	Type	No information		Maksimova 1978	2.3.a			Maksimova 1978	2.3b	Blind	Lochkovian?	Emsian?
8	Phacopidae	Ananaspis	Ananaspis fecunda fecunda	Type	NM 9324		Chlupac 1977	4.1	NML 9325		Chlupac 1977	4.12		Ludlow	Pridoli
9	Phacopidae	Angulophacops	Angulophacops angulatus	Type	No information		Maksimova 1968	20.2	No information		Maksimova 1968	20.4	Blind?	Emsian	Emsian
10	Phacopidae	Arduennops	Arduennops michelsi	Type	SMF 24603	Holotype	Franke 2010	15.1c	SMF 32032		Basse 2006	9.80		Lochkovian	Emsian
11	Phacopidae	Atopophacops	Atopophacops apiculata	Type	Tr355		Zhou & Campbell 1990	5.4	Tr358		Zhou & Campbell 1990	5.7		Emsian?	Givetian?
12	Phacopidae	Austerops	Austerops kermi	Type	UA 6884	Holotype	McKellar & Chatterton 2009	8.3	UA 6884	Holotype	McKellar & Chatterton 2009	8.4		Emsian	Eifelian
13	Phacopidae	Babinops	Babinops minor	Type	WAM 07.273	Holotype	Feist et al., 2009	4t	WAM 07.275		Feist et al., 2009	422		Famennian	Famennian
14	Phacopidae	Boeckops	Boeckops stelcki	Type	UA 6897	Holotype	McKellar & Chatterton 2009	11.4	UA 6897	Holotype	McKellar & Chatterton 2009	11.9		Lochkovian	Eifelian
15	Phacopidae	Burtonops	Burtonops cristatus	Type	No information		Becker et al., 2017	4d						Lochkovian	Emsian
16	Phacopidae	Chlupacops	Chlupacops laticeps	Type	UM-IP 712	Holotype	Feist et al., 2016	3B	UM-IP 713		Feist et al., 2016	3F		Frasnian	Frasnian
17	Phacopidae	Chotecops	Chotecops hoseri	Type	MU-G-Sr.Tr.A4/Ph123		Crónier et al., 2018	5m	MU-G-Sr.Tr.A4/Ph123		Crónier et al., 2018	5n		Emsian	Frasnian
18	Phacopidae	Cryphops	Cryphops cryptophthalmus	Type	SMF 57513		Crónier & Feist 2000	1.1a						Famennian	Famennian
19	Phacopidae	Denckmannites	Denckmannites volborthi	Type	Ich 3441		Chlupac 1977	6.6	Ich 3432		Chlupac 1977	6.15		Ludlow	Pragian
20	Phacopidae	Dianops	Dianops vicarius	Type	MUA 1094 011		Crónier et al., 2013	5b	MUA/1094/010		Crónier et al. 2013	5.0	Blind	Famennian	Famennian
21	Phacopidae	Dienstina	Dienstina diens	Type			Brauckmann & Brauckmann 1986	6.5a			Brauckmann & Brauckmann 1986	6.5b		Famennian	Famennian
22	Phacopidae	Drotops	Drotops megalomanicus	Type	SMF 49340	Holotype	Struve 1995	1.1a	SMF 49357		Struve 1995	1.2b		Eifelian	Givetian
23	Phacopidae	Ductina	Ductina ductifrons	Type			Basse & Müller 2000	3.19			Basse & Müller 2000	3.21	Blind?	Famennian	Famennian
24	Phacopidae	Echinidnops	Echinidnops taphomimus	Type	CEGH-UNC 26130		Rustan & Balseiro 2016	3.7	CEGH-UNC 24082	Holotype	Rustan & Balseiro 2016	2.5		Lochkovian	Lochkovian
25	Phacopidae	Echinophacops	Echinophacops mirabilis	Type	Tr 229		Zhou 1983	2a	Tr231		Zhou 1983	2c		Upper Silurian	Emsian
26	Phacopidae	Eldredgeops	Eldredgeops rana milleri	Type	AMNH 28896		Burton & Eldredge 1974	47.7	RSM GY 1979.11.3		Miller & Clarkson 1980	1.7		Eifelian	Frasnian
27	Phacopidae	Enigmapyge	Enigmapyge marhoumensis	Type	Do not exist				UM-IP 727	Holotype	Feist et al., 2016	5A		Famennian	Famennian
28	Phacopidae	Eocryphops	Eocryphops albertii	Type	NHM It 19284	Holotype	Holloway 2005	1P	NHM It 27131		Holloway 2005	1M		Emsian	Eifelian
29	Phacopidae	Eophacops	Eophacops bulliceps	Type	Ich 4546		Chlupac 1977	3.1	JV 98		Chlupac 1977	3.14		Wenlock	Pridoli
30	Phacopidae	Geesops	Geesops schlotheimi	Type	NHMM 2016.006		VanViersen et al., 2017	7A	DI/00/004 (Ed3n1)		Khaldi et al. 2016	4p		Emsian	Givetian
31	Phacopidae	Houseops	Houseops canningensis	Type	WAM 07.266	Holotype	Feist et al., 2008	3n	WAM 07.270		Feist et al., 2008	3v		Frasnian	Famennian
32	Phacopidae	Hypsiariops	Hypsiariops vagabundus	Type	SMF 49402	Holotype	Struve 1995	8.23a	SMF 49368		Struve 1995	8.24c		Eifelian	Givetian
33	Phacopidae	Illaenula	Illaenula struvei	Type	SMF 55933	Paratype	Basse & Müller 2000	2.15	SMF 55933	Holotype	Basse & Müller 2000	2.15	Blind?	Eifelian	Eifelian
34	Phacopidae	Kainops	Kainops microps	Type	ANU 35207	Holotype	Chatterton et al., 1979	107.1	ANU 35217	Paratype	Chatterton et al., 1979	107.18		Lochkovian	Emsian
35	Phacopidae	Liolophops	Liolophops sublevatus	Type	SMF 24518	Paratype	Struve 1970	6.24a			Ernst & Bohaty 2010	13		Eifelian	Givetian
36	Phacopidae	Lochkovella	Lochkovella misera	Type	NML 9332		Chlupac 1977	7.9	NMIT 394		Chlupac 1977	7.15		Ludlow	Lochkovian
37	Phacopidae	Morocops	Morocops granulos	Type	UA 13295	Holotype	Chatterton et al., 2006	1.2	UA 13295	Holotype	Chatterton et al., 2006	1.5		Emsian	Eifelian
38	Phacopidae	Nandanaspis	Nandanaspis laevigatus	Type	GT-464		Yin et al., 1978	192.11	GT-464		Yin et al., 1978	192.11	Blind?	Eifelian	Eifelian
39	Phacopidae	Nephranomma	Nephranomma sweeti	Type	P307225		Sandford 2003	4.1	P307303		Sandford 2003	3.15		Pragian	Emsian
40	Phacopidae	Nephranops	Nephranops incisus	Type	SMF 97026		Feist 2019	4D	SMF 97027		Feist 2019	4F	Blind	Frasnian	Famennian
41	Phacopidae	Nyterops	Nyterops hollandi	Type	IRSBNa12430	Holotype	VanViersen 2007	1.1			Megrean and Taghon 2014	1		Eifelian	Givetian
42	Phacopidae	Omegops	Omegops tilabadenis	Type	GUGM 1359	Holotype	Pour et al., 2018	4A	GUGM 1359	Holotype	Pour et al., 2018	4G		Famennian	Famennian
43	Phacopidae	Orygmats	Orygmats yanyeani	Type	P136135	Holotype	Sandford 2000	18A	P136137	Paratype	Sandford 2000	18J		Ludlow	Ludlow
44	Phacopidae	Paciphacops	Paciphacops logani	Type	YPM 6594-4		Campbell 1977	12.4c	YPM 6594		Campbell 1977	12.1a		Lochkovian	Eifelian
45	Phacopidae	Pedinopariops	Pedinopariops insequens	Type	No information		Crónier et al., 2015	3J	IRSNB a12671	Holotype	Van Viersen et al. 2009	1.1		Eifelian	Givetian
46	Phacopidae	Phacopidella	Phacopidella glöckeri	Type	NML 8917		Chlupac 1977	1.1	NMIT 379		Chlupac 1977	1.11		Wenlock	Wenlock
47	Phacopidae	Phacops s.l.	Phacops tamertensis	Type	MUA 1094 001	Holotype	Crónier et al., 2013	3i	MUA/1094/002		Crónier et al. 2013	5U		Frasnian	Famennian
48	Phacopidae	Plagiolaria	Plagiolaria senex	Type	SH	Holotype	Alberti 1983	8.90	KSGR VI_670/334	Holotype	Crónier and Tsmeyrek 2011	3A		Pragian	Eifelian
49	Phacopidae	Portlockia	Portlockia sublaevis	Type		Holotype	McCoy 1846	4.13		Holotype	McCoy 1846	4.13	Blind?	Pragian	Pragian
50	Phacopidae	Prokops	Prokops prokopi	Type	No information		Crónier et al., 2015	3A	P307117		Sandford 2004	3s		Lochkovian	Emsian
51	Phacopidae	Pulvinocephalus	Pulvinocephalus steinachensis	Type	SMF-X540d	Holotype	Feist 2019	6A	SMF-X540e		Feist 2019	6G	Blind	Famennian	Famennian
52	Phacopidae	Rabienops	Rabienops wedeckind	Type			Feist et al. 2020	4d			Feist et al. 2020	4e		Famennian	Famennian
53	Phacopidae	Reedops	Reedops bronni	Type	UA 6843	Plésiotype	McKellar & Chatterton 2009	1.9	UA 6844		McKellar & Chatterton 2009	1.8		Lochkovian	Eifelian
54	Phacopidae	Rhinophacops	Rhinophacops schizoloma	Type	Tr-240		Atsushi & Kaneko 1990	2.10a	JP 10003		Atsushi & Kaneko 1990	2.3a		Emsian	Emsian
55	Phacopidae	Signatops	Signatops signatus	Type	NMIT 391a		Chlupac 1977	28.1			Chlupac 1977	28.1		Eifelian	Eifelian
56	Phacopidae	Somatrikelon		Type										Eifelian	Eifelian
57	Phacopidae	Spinicryphops	Spinicryphops lemkei	Type	SMF X 564e	Holotype	Crónier & Feist 2000	2.11						Famennian	Famennian
58	Phacopidae	Struveaspis	Struveaspis marocanica	Type	MU-G-SR.Tr.S7/Ph003		Crónier et al., 2018	3b	JC 104	Paratype	Corbacho 2014	1.4		Eifelian	Eifelian
59	Phacopidae	Struveops	Struveops schlosseri	Type	SMF 57520		Crónier & Feist 2000	2.13	SMF 57525		Crónier & Feist 2000	2.18	Blind	Famennian	Famennian
60	Phacopidae	Struvephacops	Struvephacops werneri	Type	SMF 24417	Holotype	Struve 1995	Abb 11						Lochkovian	Emsian
61	Phacopidae	Tangbailaspis	Tangbailaspis beijiagensis	Type			Zhang 1983	183.13							
62	Phacopidae	Teichertops	Teichertops soetenicus	Type	SMF 24467	Holotype	Struve 1970	4.13a	SMF 58034a		Basse 2006	45.447		Eifelian	Givetian
63	Phacopidae	Toxophacops	Toxophacops cristata	Type	Tr339	Holotype	Zhou & Campbell 1990	3.7A	Tr345		Zhou & Campbell 1990	3.9A		Emsian	Emsian
64	Phacopidae	Trifoliops	Trifoliops trifoliops	Type	UM-IP 722		Feist et al., 2016	5E	UM-IP 723		Feist et al., 2016	5F	Blind	Famennian	Famennian
65	Phacopidae	Trimerocephalus	Trimerocephalus caecus	Type	MUA 1094 007		Crónier et al., 2013	3a	MUA 1094 007		Crónier et al., 2013	3b	Blind	Famennian	Famennian
66	Phacopidae	Trimerocephaloides	Trimerocephaloides sinevisus	Type	WAM 07.277	Holotype	Feist et al., 2009	4i	WAM 07.278		Feist et al., 2009	4k	Blind	Frasnian	Famennian
67	Phacopidae	Viaehacops	Viaehacops stummi	Type	AMNH 28902	Holotype	Eldredge 1973	20A	UMMP 47207		Eldredge 1973	20E		Lochkovian	Eifelian
68	Phacopidae	Weyerites	Weyerites woclumeriae	Type	SMF 57512		Crónier & Feist 2000	Fig-text	M.B.T. 3731		Crónier et al. 1999	2.1		Famennian	Famennian
69	Phacopidae	Zaplaops	Zaplaops zaplensis	Type	MACN-PI-2354	Holotype	Baldis & Blasco 1976	3.4						Ludlow?	Pridoli?
70	Phacopidae	Zhusiengops	Zhusiengops ejinensis	Type	Tr373	Holotype	Zhou & Campbell 1990	4.1a	Tr375		Zhou & Campbell 1990	4.4a		Emsian	Eifelian
71	Phacopidae	Phacops	Phacops ourouroutensis	Type	MU-G-Sr.Tr.S7/Ph0	Holotype	Crónier et al., 2018	6h-k	MU-G-Sr.Tr.S7/Ph0	Holotype	Crónier et al., 2018	6j		Eifelian	Givetian
72	Phacopidae	Feistops	Feistops mongolensis	Type	MUST-RCSR-TRI-01	Holotype	Crónier et al. 2020	4.1	MUST-RCSR-TRI-01	Paratype	Crónier et al. 2020	4.10		Famennian	Famennian
73	Phacopidae	Megraneops	Megraneops renaeae	Type	IRSBNa13216	Holotype	Van Viersen and Vanherle 2018	10e	IRSBNa13216	Holotype	Van Viersen and Vanherle 2018	10d		Frasnian	Frasnian
74	Pterygometo	Calyptaulax	Calyptaulax callirhachis	Type	U.A. 1412		Chatterton and Ludvigsen 1976	16.1	U.A. 1417		Chatterton and Ludvigsen 1976	16.10		Late Ordovician	Late Ordovician
75	Phacopidae	Rhinoreedops	Rhinoreedops rhinoceras	Type	No information	Holotype	Maksimova 1978	3.9	No information	Holotype	Maksimova 1978	3.9		Eifelian	Eifelian
76	Phacopidae	Phacopidae	Sambremeussaspis fossesensis	Type	I.R.Sc.N.B. a2511	Holotype	Lespérance and Sheehan 1983	3.4	I.R.Sc.N.B. a2514	Paratype	Lespérance and Sheehan 1988			Late Ordovician	Late Ordovician

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Order	Family	Genus	Species	ID	Vision	Depth	Diet	Figures	Specimen	Paper	Scale	Stage	Analysis
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	0	Large eyes	Middle shelf	Predator/Scavenger	7.2		Morzadec 2001	=0,00608	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	1	Large eyes	Middle shelf	Predator/Scavenger	7.5		Morzadec 2001	=0,00448	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	2	Large eyes	Middle shelf	Predator/Scavenger	60	GFCL401	Khaldi 2016	=0,037036	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	3	Large eyes	Middle shelf	Predator/Scavenger	8.3		Morzadec 2001	=0,02113	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops burtandmimiae	4	Large eyes	Middle shelf	Predator/Scavenger	9.8		Morzadec 2001	=0,00849	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops aithassainorum	5	Large eyes	Middle shelf	Predator/Scavenger	17.2	UA13440	Chatterton 2006	=0,116013	Eifelian	Cephalon
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	6	Large eyes	Inner shelf	Predator/Scavenger	14.5		Morzadec 2001	=0,010730	Eifelian	Cephalon
Phacopida	Acastidae	Pilletina	Pilletina marokkensis	7	Large eyes	Shallow	Predator/Scavenger	12.1a	SMF 53876	Schraut 2000c	=0,083331	Pragian	Cephalon
Phacopida	Acastidae	Pilletina	Pilletina marokkensis	8	Large eyes	Shallow	Predator/Scavenger	12.2a	SMF 53866	Schraut 2000c	=0,100289	Pragian	Cephalon
Phacopida	Acastidae	Pilletina	Pilletina marokkensis	9	Large eyes	Shallow	Predator/Scavenger	12.3a	SMF 53859	Schraut 2000c	=0,099431	Pragian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge elegans	10	Large eyes	Middle shelf	Predator/Scavenger	13.4		Morzadec 2001	=0,042040	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	11	Large eyes	Middle shelf	Predator/Scavenger	22.6		Chatterton 2006	=0,176156	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	12	Large eyes	Middle shelf	Predator/Scavenger	23.4	UA13371	Chatterton 2006	=0,128859	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	13	Large eyes	Middle shelf	Predator/Scavenger	23.6	UA13372	Chatterton 2006	=0,116441	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge hammerorum	14	Large eyes	Middle shelf	Predator/Scavenger	25.5	UA13375	Chatterton 2006	=0,129346	Emsian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge prorotundifrons iberica	15	Large eyes	Shallow	Predator/Scavenger	11.1a	SMF 53879	Schraut 2000c	=0,122202	Pragian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge prorotundifrons iberica	16	Large eyes	Shallow	Predator/Scavenger	11.2a	SMF 53790	Schraut 2000c	=0,077768	Pragian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge prorotundifrons iberica	17	Large eyes	Shallow	Predator/Scavenger	11.4a	SMF 53943	Schraut 2000c	=0,129336	Pragian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge prorotundifrons iberica	18	Large eyes	Shallow	Predator/Scavenger	42.10	CGMTA 209	Alberti 1969	=0,008503	Pragian	Cephalon
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	19	Large eyes	Middle shelf	Predator/Scavenger	15.1a		Morzadec 2001	=0,030418	Emsian	Cephalon
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	20	Large eyes	Middle shelf	Predator/Scavenger	15.3e		Morzadec 2001	=0,028726	Emsian	Cephalon
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura ignorata	21	Large eyes	Middle shelf	Particle feeding	36;15	CGMTA 158	Alberti 1969	=0,017829	Eifelian	Cephalon
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura ignorata	22	Large eyes	Middle shelf	Particle feeding	36;16	SMF 23381	Alberti 1969	=0,020068	Eifelian	Cephalon
Proetida	Aulacopleuridae	Chamaeleospis	Chamaeleospis lkomalii	23	Large eyes	Middle shelf	Particle feeding	6a_24	UA 11821	Lerosy-Aubril 2008	=0,014619	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis walteri	24	Large eyes	Middle shelf	Particle feeding	1b_24	IRSNB a12875	Van Viersen 2014	=0,056453		Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis eximia	25	Large eyes	Middle shelf	Particle feeding	6e_24	IRSNB a13010	Van Viersen 2016	=0,022982	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis bluhmi	26	Large eyes	Middle shelf	Particle feeding	7a_24	IRSNB a13003	Van Viersen 2016	=0,027387	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis sp A	27	Large eyes	Middle shelf	Particle feeding	7z_24	MU-G-Sr.Tr.A4/Pr098	Crônier-Abbache 2018	=0,054509	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis kippingi	28	Large eyes	Middle shelf	Particle feeding	14d_24	IRSNB a13012	Van Viersen 2016	=0,026307	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis fouxguideensis	29	Large eyes	Middle shelf	Particle feeding	16b_24	IRSNB a12996	Van Viersen 2016	=0,014805	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis sp. I	30	Large eyes	Middle shelf	Particle feeding	19c_24	IRSNB a13008	Van Viersen 2016	=0,037031	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis heisingi	31	Large eyes	Middle shelf	Particle feeding	21b_24	IRSNB a13011	Van Viersen 2016	=0,014919	Pragian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis cf. eberhardci	32	Large eyes	Middle shelf	Particle feeding	23d_24	IRSNB a13001	Van Viersen 2016	=0,020404	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis agayuara	33	Large eyes	Middle shelf	Particle feeding	42.1_24	UA13397	Chatterton 2006	=0,071700	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis sp A	34	Large eyes	Middle shelf	Particle feeding	45.3_24	UA13399	Chatterton 2006	=0,047565	Eifelian	Cephalon

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Proetida	Aulacopleuridae	Otarionella	Otarionella magnifica	35	Large eyes	Inner shelf	Particle feeding	35.2a_24	CGMTA 154	Alberti 1969	=0,017824	Pragian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	36	Small eyes	Deep	Predator/Scavenger	8.8_24	UA13332	Chatterton 2006	=0,062162	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	37	Small eyes	Deep	Predator/Scavenger	9.13_24	UA13340	Chatterton 2006	=0,062081	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	38	Small eyes	Deep	Predator/Scavenger	6	SGMRA 9	Alberti 1966a	=0,016353	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	39	Small eyes	Deep	Predator/Scavenger	7	SMF 23017	Alberti 1966a	=0,009982	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	40	Small eyes	Deep	Predator/Scavenger	18.4	CGMTA 336	Alberti 1970a	=0,021200	Emsian	Cephalon
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	41	Large eyes	Inner shelf	Predator/Scavenger	5.1a_24	SMF 53914	Schraut 2000c	=0,085764	Pragian	Cephalon
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	42	Large eyes	Inner shelf	Predator/Scavenger	5.2a_24	SMF 53830	Schraut 2000c	=0,158112	Pragian	Cephalon
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	43	Large eyes	Inner shelf	Predator/Scavenger	5.4a_24	SMF 53917	Schraut 2000c	=0,152597	Pragian	Cephalon
Lichida	Odontopleuridae	Kettneraspis	Kettneraspis prescheri	44	Large eyes	Deep	Predator/Scavenger	2a	IRSNB a1713	Van Viersen 2015	=0,035584	Pragian	Cephalon
Lichida	Odontopleuridae	Leonaspis	Leonaspis maura	45	Large eyes	Middle shelf	Predator/Scavenger	40.10a_24	CGMTA 165	Alberti 1969	=0,015812		Cephalon
Lichida	Odontopleuridae	Leonaspis	Leonaspis haddanei	46	Large eyes	Middle shelf	Predator/Scavenger	50.10_24		Chatterton 2006	=0,042728	Eifelien	Cephalon
Lichida	Odontopleuridae	Leonaspis	Leonaspis haddanei	47	Large eyes	Middle shelf	Predator/Scavenger	51.4_24		Chatterton 2006	=0,033465	Emsian	Cephalon
Phacopida	Phacopidae	Acuticryphops	Acuticryphops acuticeps	48	Small eyes	Middle shelf	Predator/Scavenger	3a_24	UM2-RF 220	Feist 2002	=0,045903	Frasnian	Cephalon
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	49	Large eyes	Middle shelf	Predator/Scavenger	4i_24	Di/UO/016	Khalidi 2016	=0,040645	Emsian	Cephalon
Phacopida	Phacopidae	Adrisiops	Adrisiops weugi	50	Large eyes	Middle shelf	Predator/Scavenger	7d_24		Van Viersen 2017	=0,006894	Emsian	Cephalon
Phacopida	Phacopidae	Anaspis	Anaspis fecunda	51	Large eyes	Middle shelf	Predator/Scavenger	11.2a_24	SMF 23512	Alberti 1970a	=0,017109	Ludlow-Pridoli	Cephalon
Phacopida	Phacopidae	Austerops	Austerops legrandi	52	Large eyes	Middle shelf	Predator/Scavenger	7a_24	GFCL399	Khalidi 2016	=0,047610	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	53	Large eyes	Middle shelf	Predator/Scavenger	3.9a_24		Schraut 2000c	=0,073473	Eifelien	Cephalon
Phacopida	Phacopidae	Chlupacops	Chlupacops laticeps	54	Large eyes	Deep	Predator/Scavenger	3a_24	UM-IP 712	Feist 2016	=0,076866	Frasnian	Cephalon
Phacopida	Phacopidae	Chlupacops	Chlupacops laticeps	55	Large eyes	Deep	Predator/Scavenger	3b_24	UM-IP 712	Feist 2016	=0,037629	Frasnian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops salamandroides	56	Large eyes	Middle shelf	Predator/Scavenger	3s_24	MU-G-Sr.Tr.S6/Ph186	Crónier-Abbache 2018	=0,018987	Eifelien	Cephalon
Phacopida	Phacopidae	Eophacops	Eophacops bulliceps	57	Large eyes	Middle shelf	Predator/Scavenger	1.10_24		Alberti 1966c	=0,008450	Ludlow-Pridoli	Cephalon
Phacopida	Phacopidae	Hypsiariops	Hypsiariops africanus	58	Large eyes	Middle shelf	Predator/Scavenger	47.9_24	USNM 174072	Burton 1974	=0,140125	Eifelien	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	59	Large eyes	Inner shelf	Predator/Scavenger	1.2_24	UA 13295	Chatterton 2006	=0,070609	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	60	Large eyes	Inner shelf	Predator/Scavenger	1.7_24	UA 13297	Chatterton 2006	=0,061025	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	61	Large eyes	Inner shelf	Predator/Scavenger	1.8_24	UA 13294	Chatterton 2006	=0,075561	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	62	Large eyes	Inner shelf	Predator/Scavenger	2.9_24	UA 13301	Chatterton 2006	=0,090746	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops torkozensis	63	Large eyes	Inner shelf	Predator/Scavenger	3.4a_24	SMF 53627	Schraut 2000c	=0,076227	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops torkozensis	64	Large eyes	Inner shelf	Predator/Scavenger	5d_24	NHMM 2016 002	Van Viersen 2017	=0,038757	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops forteyi	65	Large eyes	Inner shelf	Predator/Scavenger	5g_24	NHMM 2016 003	Van Viersen 2017	=0,048760	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops spinifer	66	Large eyes	Inner shelf	Predator/Scavenger	6a_24	NHMM 2016 004	Van Viersen 2017	=0,050759	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops spinifer	67	Large eyes	Inner shelf	Predator/Scavenger	6f_24	NHMM 2016 005	Van Viersen 2017	=0,042729	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops sparsinodosus struvei	68	Large eyes	Inner shelf	Predator/Scavenger	8j_24	SMF 57109	Schraut 2000a	=0,011602	Eifelien	Cephalon
Phacopida	Phacopidae	Morocops	Morocops sparsinodosus struvei	69	Large eyes	Inner shelf	Predator/Scavenger	8m_24	SMF 57110	Schraut 2000a	=0,017740	Eifelien	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	70	Large eyes	Inner shelf	Predator/Scavenger	18a		Becker 2018	=0,038449	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	71	Large eyes	Inner shelf	Predator/Scavenger	2b	PIMUZ 35146	Crónier-Oudot 2018	=0,013089	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	72	Large eyes	Inner shelf	Predator/Scavenger	2i	PIMUZ 35147	Crónier-Oudot 2018	=0,005593	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	73	Large eyes	Inner shelf	Predator/Scavenger	2k	PIMUZ 35148	Crónier-Oudot 2018	=0,009191	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	74	Large eyes	Inner shelf	Predator/Scavenger	2n	PIMUZ 35149	Crónier-Oudot 2018	=0,018315	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	75	Large eyes	Inner shelf	Predator/Scavenger	2o	PIMUZ 35150	Crónier-Oudot 2018	=0,025772	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops forteyi	76	Large eyes	Inner shelf	Predator/Scavenger	2t	PIMUZ 35152	Crónier-Oudot 2018	=0,016835	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops sp A	77	Large eyes	Inner shelf	Predator/Scavenger	2w	PIMUZ 35153	Crónier-Oudot 2018	=0,029238	Emsian	Cephalon

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Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	78	Large eyes	Inner shelf	Predator/Scavenger	3a_24	PIMUZ 35154	Crônier-Oudot 2018	=0,008944	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	79	Large eyes	Inner shelf	Predator/Scavenger	3d	PIMUZ 35155	Crônier-Oudot 2018	=0,011085	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	80	Large eyes	Inner shelf	Predator/Scavenger	3g	PIMUZ 35156	Crônier-Oudot 2018	=0,007072	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	81	Large eyes	Inner shelf	Predator/Scavenger	3k	PIMUZ 35157	Crônier-Oudot 2018	=0,004153	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	82	Large eyes	Inner shelf	Predator/Scavenger	3l	PIMUZ 35159	Crônier-Oudot 2018	=0,008547	Emsian	Cephalon
Phacopida	Phacopidae	PHACOPINAE	Indet	83	Large eyes	Middle shelf	Predator/Scavenger	1.1a	Nr 25	Richter 1943	=0,035142	Eifelian	Cephalon
Phacopida	Phacopidae	PHACOPINAE	Indet	84	Large eyes	Middle shelf	Predator/Scavenger	1.3a	Nr 8	Richter 1943	=0,035142		Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops tafuipernensis	85	Large eyes	Deep	Predator/Scavenger	2.a_24	UM2/CCp002	Crônier 2001	=0,015029	Famennian	Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops tafuipernensis	86	Large eyes	Deep	Predator/Scavenger	2.g_24	UM2/CCp004	Crônier 2001	=0,019872	Famennian	Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops tafuipernensis	87	Large eyes	Deep	Predator/Scavenger	3.e_24	UM2/CCp007	Crônier 2001	=0,014306	Famennian	Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops zeregensis	88	Large eyes	Deep	Predator/Scavenger	3i_24	MUA/1094/001	Crônier 2013	=0,034246	Famennian	Cephalon
Phacopida	Phacopidae	Phacops	Phacops ourouroutensis ourouroutensis	89	Large eyes	Middle shelf	Predator/Scavenger	4z_24	MU-G-Sr.T r.S4/Ph054	Crônier-Abbache 2018	=0,078920	Eifelian	Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops sensu lato sp B	90	Large eyes	Deep	Predator/Scavenger	5f_24	Di/UO/033	Khalidi 2016	=0,102020	Emsian	Cephalon
Phacopida	Phacopidae	Phacops sl	Phacops zeregensis	91	Large eyes	Deep	Predator/Scavenger	5q_24	MUA/1094/002	Crônier 2013	=0,032461	Famennian	Cephalon
Phacopida	Phacopidae	Phacops	Omegops accipitrinus	92	Large eyes	Middle shelf	Predator/Scavenger	1.2a	Nr 27	Richter 1943	=0,023333	Famennian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops bronni	93	Large eyes	Inner shelf	Predator/Scavenger	1.4_24	UA 6844	McKellar 2009	=0,013314	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadi nus	94	Large eyes	Inner shelf	Predator/Scavenger	2.8_24	UA 6861	McKellar 2009	=0,023057	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops intermedius chlupaci	95	Large eyes	Inner shelf	Predator/Scavenger	4.10a_24	SMF 57095	Schraut 2000c	=0,088333	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops maurulus	96	Large eyes	Inner shelf	Predator/Scavenger	15.6a_24	SMF 23514	Alberti 1970a	=0,026488	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops platilegnor	97	Large eyes	Inner shelf	Predator/Scavenger	15.10a_24	CGMTA 316	Alberti 1970a	=0,026488	Pragian	Cephalon
Phacopida	Phacopidae	Struveaspis	Struveaspis bignoni	98	Large eyes	Middle shelf	Predator/Scavenger	1.2_24		Corbacho 2014	=0,025252	Eifelian	Cephalon
Phacopida	Phacopidae	Struveaspis	Struveaspis bignoni	99	Large eyes	Middle shelf	Predator/Scavenger	1.4_24		Corbacho 2014	=0,037726	Eifelian	Cephalon
Phacopida	Phacopidae	Struveaspis	Struveaspis sp A	100	Large eyes	Middle shelf	Predator/Scavenger	1a_24	SGMRA 8	Alberti 1966a	=0,016162	Eifelian	Cephalon
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	101	Large eyes	Middle shelf	Predator/Scavenger	5b_24	Di/UO/035	Crônier-Abbache 2018	=0,029999	Eifelian	Cephalon
Phacopida	Phacopidae	Chotecops	Chotecops occidomaurus	102	Large eyes	Middle shelf	Predator/Scavenger	6.60a_24	CGMTA	Alberti 1981a	=0,080854	Eifelian	Cephalon
Proetida	Proetidae	Dalejeoproetus	Dalejeoproetus sagaouii	103	Large eyes	Inner shelf	Predator/Scavenger	4.1_24	NHM It 28946	Johnson 2012	=0,013300	Pragian	Cephalon
Proetida	Proetidae	Dalejeoproetus	Dalejeoproetus sagaouii	104	Large eyes	Inner shelf	Predator/Scavenger	4.6_24	NHM It 28947	Johnson 2012	=0,037207	Pragian	Cephalon
Proetida	Proetidae	Dalejeoproetus	Dalejeoproetus owensi	105	Large eyes	Inner shelf	Predator/Scavenger	5.1_24	NHM It 28950	Johnson 2012	=0,046180	Pragian	Cephalon
Proetida	Proetidae	Dalejeoproetus	Dalejeoproetus owensi	106	Large eyes	Inner shelf	Predator/Scavenger	5.3_24	NHM It 28951	Johnson 2012	=0,037324	Pragian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus mohamedi	107	Large eyes	Deep	Predator/Scavenger	34.6_24	UA 13382	Chatterton 2006	=0,050598	Eifelian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	108	Large eyes	Deep	Predator/Scavenger	35.8_24		Chatterton 2006	=0,084885	Emsian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	109	Large eyes	Deep	Predator/Scavenger	36.6_24		Chatterton 2006	=0,082452	Emsian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	110	Large eyes	Deep	Predator/Scavenger	37.12_24		Chatterton 2006	=0,110567	Emsian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus holzapfeli praecursor	111	Large eyes	Deep	Predator/Scavenger	16.1a	SMF 53620	Schraut 2000c	=0,092640	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	112	Large eyes	Inner shelf	Predator/Scavenger	1.1_24	UA13526	Gibb 2010	=0,012382	Eifelian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	113	Large eyes	Inner shelf	Predator/Scavenger	2.5_24	UA13464	Gibb 2010	=0,010204	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	114	Large eyes	Inner shelf	Predator/Scavenger	2.12_24	UA13466	Gibb 2010	=0,010751	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	115	Large eyes	Inner shelf	Predator/Scavenger	4.8_24	UA13530	Gibb 2010	=0,008948	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	116	Large eyes	Inner shelf	Predator/Scavenger	4.9_24	UA13530	Gibb 2010	=0,008948	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos aintawilus	117	Large eyes	Inner shelf	Predator/Scavenger	6.3_24	UA13454	Gibb 2010	=0,003722	Eifelian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos aintawilus	118	Large eyes	Inner shelf	Predator/Scavenger	5.4_24	UA13532	Gibb 2010	=0,004842	Eifelian	Cephalon

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Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	119	Large eyes	Inner shelf	Predator/Scavenger	6.12_24	UA13650	Chatterton 2010	=0,040846	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos hammii	120	Large eyes	Inner shelf	Predator/Scavenger	7.10_24		Gibb 2010	=0,009415	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos lisanrasus	121	Large eyes	Inner shelf	Predator/Scavenger	8.3_24		Gibb 2010	=0,009162	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos lisanrasus	122	Large eyes	Inner shelf	Predator/Scavenger	8.8_24		Gibb 2010	=0,005776	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos ainrasifus	123	Large eyes	Inner shelf	Predator/Scavenger	9.8_24		Gibb 2010	=0,014590	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos discombobulatus	124	Large eyes	Inner shelf	Predator/Scavenger	11.11_24		Gibb 2010	=0,006762	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos cuvieri malisus	125	Large eyes	Inner shelf	Predator/Scavenger	13.9_24		Gibb 2010	=0,006350	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos taqus	126	Large eyes	Inner shelf	Predator/Scavenger	16.2_24		Gibb 2010	=0,007241	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos malisjildus	127	Large eyes	Inner shelf	Predator/Scavenger	17.1_24		Gibb 2010	=0,004468	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos raribus	128	Large eyes	Inner shelf	Predator/Scavenger	19.3_24		Gibb 2010	=0,005780	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos emmetus	129	Large eyes	Inner shelf	Predator/Scavenger	22.5_24		Gibb 2010	=0,004581	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos emmetus	130	Large eyes	Inner shelf	Predator/Scavenger	22.6_24		Gibb 2010	=0,005844	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos emmetus	131	Large eyes	Inner shelf	Predator/Scavenger	23.8_24		Gibb 2010	=0,007994	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos izius	132	Large eyes	Inner shelf	Predator/Scavenger	24.3_24		Gibb 2010	=0,006982	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos izius	133	Large eyes	Inner shelf	Predator/Scavenger	24.9_24		Gibb 2010	=0,006946	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos izius	134	Large eyes	Inner shelf	Predator/Scavenger	25.7_24		Gibb 2010	=0,008754	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos izius	135	Large eyes	Inner shelf	Predator/Scavenger	25.10_24		Gibb 2010	=0,009129	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	136	Large eyes	Inner shelf	Predator/Scavenger	37.5_24	UA13276	Chatterton 2006	=0,065026	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	137	Large eyes	Inner shelf	Predator/Scavenger	39.8_24	UA13278	Chatterton 2006	=0,055102	Emsian	Cephalon
Proetida	Proetidae	Kegelella	Kegelella listei bouregregus	138	Large eyes	Middle shelf	Predator/Scavenger	3.2b_24	SMF 23032	Alberti 1969	=0,019092	Pragian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	139	Large eyes	Shallow	Predator/Scavenger	6.1_24	NHM It 28954	Johnson 2012	=0,041042	Pragian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus spendens	140	Large eyes	Shallow	Predator/Scavenger	6.11_24	NHM It 28956	Johnson 2012	=0,028721	Pragian	Cephalon
Proetida	Proetidae	Piriproetus	Piriproetus amblyops oulmesanicus	141	Blind	Deep	Predator/Scavenger	4.10a_24	SMF23471	Alberti 1970a	=0,008407	Eifelien	Blind
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	142	Large eyes	Inner shelf	Predator/Scavenger	7.3_24	NHM It 28957	Johnson 2012	=0,037131	Pragian	Cephalon
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	143	Large eyes	Inner shelf	Predator/Scavenger	7.6_24	NHM It 28958	Johnson 2012	=0,037131	Pragian	Cephalon
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	144	Large eyes	Inner shelf	Predator/Scavenger	7.11_24	NHM It 28959	Johnson 2012	=0,037131	Pragian	Cephalon
Proetida	Proetidae	Podoliproetus	Podoliproetus sinespina	145	Large eyes	Inner shelf	Predator/Scavenger	8.3_24	NHM It 28960	Johnson 2012	=0,036862	Pragian	Cephalon
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	146	Large eyes	Inner shelf	Predator/Scavenger	8.11_24	NHM It 28961	Johnson 2012	=0,022910	Pragian	Cephalon
Proetida	Proetidae	Proetina	Proetina ihmadii	147	Large eyes	Inner shelf	Predator/Scavenger	9.5_24	NHM It 28962	Johnson 2012	=0,018273	Pragian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	148	Large eyes	Middle shelf	Predator/Scavenger	40.10_24	UA13269	Chatterton 2006	=0,046287	Eifelien	Cephalon
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp B	149	Large eyes	Middle shelf	Predator/Scavenger	40.13_24	UA13262	Chatterton 2006	=0,038369	Eifelien	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	150	Large eyes	Middle shelf	Predator/Scavenger	4.1_24	UA13272	Gibb 2007	=0,005109	Eifelien	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	151	Large eyes	Middle shelf	Predator/Scavenger	5.2_24	UA13256	Gibb 2007	=0,011598	Eifelien	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	152	Large eyes	Middle shelf	Predator/Scavenger	5.3_24	UA13269	Gibb 2007	=0,007741	Eifelien	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	153	Large eyes	Middle shelf	Predator/Scavenger	5.7_24	UA13269	Gibb 2007	=0,015086	Eifelien	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus elguerrouji	154	Large eyes	Middle shelf	Predator/Scavenger	9.11_24	UA13260	Gibb 2007	=0,010911	Eifelien	Cephalon
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	155	Large eyes	Inner shelf	Predator/Scavenger	33.5_24	CGMT	Alberti 1969	=0,008475	Lochkovian	Cephalon
Proetida	Tropidocoryphe	Tropidocoryphidae	Tropidocoryphe amuri	156	Large eyes	Middle shelf	Predator/Scavenger	41.4_24	UA13394	Chatterton 2006	=0,053329	Emsian	Cephalon
Phacopida	Acastidae	Coltranea	Coltranea berbera	157	Large eyes	Middle shelf	Predator/Scavenger	10.2		Morzadec 2001	=0,027925	Emsian	Cephalon
Phacopida	Acastidae	Coltranea	Coltranea effelesa	158	Large eyes	Middle shelf	Predator/Scavenger	12.1	UA 13351	Chatterton 2006	=0,089724	Emsian	Cranidium
Phacopida	Acastidae	Comura	Comura butyncki	159	Large eyes	Middle shelf	Predator/Scavenger	12.2a		Morzadec 2001	=0,027972	Emsian	Cephalon
Phacopida	Acastidae	Comura	Comura butyncki	160	Large eyes	Middle shelf	Predator/Scavenger	12.3a		Morzadec 2001	=0,042423	Emsian	Cephalon

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Phacopida	Acastidae	Destombesina	Destombesina ougartensis	161	Large eyes	Middle shelf	Predator/Scavenger	3.6a		Morzadec 1997	=0,006728	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	162	Large eyes	Middle shelf	Predator/Scavenger	3.10a		Morzadec 1997	=0,005262	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	163	Large eyes	Middle shelf	Predator/Scavenger	7.1a		Morzadec 2001	=0,010405	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	164	Large eyes	Middle shelf	Predator/Scavenger	7.7		Morzadec 2001	=0,00448	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	165	Large eyes	Middle shelf	Predator/Scavenger	7.8		Morzadec 2001	=0,00448	Emsian	Cephalon
Phacopida	Acastidae	Destombesina	Destombesina tafalaltensis	166	Large eyes	Middle shelf	Predator/Scavenger	7.11		Morzadec 2001	=0,003526	Emsian	Cephalon
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	167	Large eyes	Deep	Predator/Scavenger	3.6	UA13645	Chatterton 2010	=0,060774		Cranidium
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	168	Large eyes	Deep	Predator/Scavenger	4.11	UA13647	Chatterton 2010	=0,056921		Cranidium
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	169	Large eyes	Deep	Predator/Scavenger	4.13	UA13648	Chatterton 2010	=0,078486		Cranidium
Phacopida	Acastidae	Greenops	Indet	170	Large eyes	Middle shelf	Predator/Scavenger	6.2a		Morzadec 1997	=0,014105	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops lemaitreae	171	Large eyes	Middle shelf	Predator/Scavenger	4.1b		Morzadec 1997	=0,007053	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops lemaitreae	172	Large eyes	Middle shelf	Predator/Scavenger	4.2a		Morzadec 1997	=0,008989	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops lemaitreae	173	Large eyes	Middle shelf	Predator/Scavenger	4.3a		Morzadec 1997	=0,008285	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops lemaitreae	174	Large eyes	Middle shelf	Predator/Scavenger	4.4a		Morzadec 1997	=0,014061	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops lemaitreae	175	Large eyes	Middle shelf	Predator/Scavenger	4.7		Morzadec 1997	=0,005273	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	176	Large eyes	Middle shelf	Predator/Scavenger	6.1a		Morzadec 1997	=0,008360	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	177	Large eyes	Middle shelf	Predator/Scavenger	6.3a		Morzadec 1997	=0,023627	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	178	Large eyes	Middle shelf	Predator/Scavenger	6.4		Morzadec 1997	=0,017041	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	179	Large eyes	Middle shelf	Predator/Scavenger	6.6a		Morzadec 1997	=0,013700	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	180	Large eyes	Middle shelf	Predator/Scavenger	6m	Di/UO/010	Khalidi 2016	=0,053760	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	181	Large eyes	Middle shelf	Predator/Scavenger	7.1a		Morzadec 1997	=0,010470	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	182	Large eyes	Middle shelf	Predator/Scavenger	7.2a		Morzadec 1997	=0,013857	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	183	Large eyes	Middle shelf	Predator/Scavenger	7.3a		Morzadec 1997	=0,013857	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	184	Large eyes	Middle shelf	Predator/Scavenger	7.4a		Morzadec 1997	=0,020849	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	185	Large eyes	Middle shelf	Predator/Scavenger	7.6a		Morzadec 1997	=0,027985	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops boudibensis	186	Large eyes	Middle shelf	Predator/Scavenger	8.1a		Morzadec 2001	=0,013887	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops boudibensis	187	Large eyes	Middle shelf	Predator/Scavenger	8.2		Morzadec 2001	=0,010580	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	188	Large eyes	Middle shelf	Predator/Scavenger	8.5a		Morzadec 1997	=0,020620	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	189	Large eyes	Middle shelf	Predator/Scavenger	8.6a		Morzadec 2001	=0,027957	Emsian	Cephalon
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	190	Large eyes	Middle shelf	Predator/Scavenger	8.7a		Morzadec 1997	=0,020620	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	191	Large eyes	Middle shelf	Predator/Scavenger	9.5a		Morzadec 2001	=0,021051	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops aithassainorum	192	Large eyes	Middle shelf	Predator/Scavenger	18.4		Chatterton 2006	=0,050655	Eifelian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	193	Large eyes	Middle shelf	Predator/Scavenger	20.8		Chatterton 2006	=0,049175	Emsian	Cranidium
Phacopida	Acastidae	Hollardops	Hollardops mesocristata	194	Large eyes	Middle shelf	Predator/Scavenger	3z	Di/UO/010	Crônier Oudot 2018	=0,014367	Emsian	Cranidium
Phacopida	Acastidae	Kayserops	Kayserops megalpina	195	Large eyes	Shallow	Predator/Scavenger	4.5a		Morzadec 2001	=0,041981	Emsian	Cephalon
Phacopida	Acastidae	Kayserops	Kayserops marocanensis	196	Large eyes	Shallow	Predator/Scavenger	5.1a_24		Morzadec 2001	=0,028409	Emsian	Cephalon
Phacopida	Acastidae	Kayserops	Kayserops marocanensis	197	Large eyes	Shallow	Predator/Scavenger	5.2a_24		Morzadec 2001	=0,028409	Emsian	Cephalon
Phacopida	Acastidae	Kayserops	Kayserops tamrherta	199	Large eyes	Shallow	Predator/Scavenger	19.3		Chatterton 2006	=0,042244	Emsian	Cranidium
Phacopida	Acastidae	Kayserops	Kayserops tamrherta	200	Large eyes	Shallow	Predator/Scavenger	19.8		Chatterton 2006	=0,044376	Emsian	Cephalon
Phacopida	Acastidae	Kayserops	Kayserops tamrherta	201	Large eyes	Shallow	Predator/Scavenger	19.9		Chatterton 2006	=0,045418	Emsian	Cranidium
Phacopida	Acastidae	Kayserops	Kayserops tamrherta	202	Large eyes	Shallow	Predator/Scavenger	19.10		Chatterton 2006	=0,044376	Emsian	Cranidium
Phacopida	Acastidae	Kayserops	Kayserops tamrherta	203	Large eyes	Shallow	Predator/Scavenger	20.7		Chatterton 2006	=0,051276	Emsian	Cephalon

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Phacopida	Acastidae	Kayserop	Kayserop tammrherta	204	Large eyes	Shallow	Predator/Scavenger	21.2		Chatterton 2006	=0,072840	Emsian	Cephalon
Phacopida	Acastidae	Kayserop	Kayserop tammrherta	205	Large eyes	Shallow	Predator/Scavenger	21.7		Chatterton 2006	=0,066804	Emsian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina issoumourensis	206	Large eyes	Shallow	Predator/Scavenger	3.1a		Morzadec 2001	=0,028528	Pragian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina issoumourensis	207	Large eyes	Shallow	Predator/Scavenger	3.2a		Morzadec 2001	=0,028528	Pragian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina maderensis	208	Large eyes	Shallow	Predator/Scavenger	3.4a		Morzadec 2001	=0,021050	Pragian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	209	Large eyes	Shallow	Predator/Scavenger	6.1a		Morzadec 2001	=0,021183	Pragian	Cranidium
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	210	Large eyes	Shallow	Predator/Scavenger	6.2a		Morzadec 2001	=0,021183	Pragian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	211	Large eyes	Shallow	Predator/Scavenger	6.3		Morzadec 2001	=0,021183	Pragian	Cranidium
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	212	Large eyes	Shallow	Predator/Scavenger	6.4		Morzadec 2001	=0,021183	Pragian	Cephalon
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	213	Large eyes	Inner shelf	Predator/Scavenger	14.3		Morzadec 2001	=0,021161	Eifelien	Cephalon
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	214	Large eyes	Inner shelf	Predator/Scavenger	14.7		Morzadec 2001	=0,021161	Eifelien	Cephalon
Phacopida	Acastidae	Morzadecops	Morzadecops zguidensis	215	Large eyes	Inner shelf	Predator/Scavenger	4.1a		Morzadec 2001	=0,020901	Emsian	Cephalon
Phacopida	Acastidae	Morzadecops	Morzadecops zguidensis	216	Large eyes	Inner shelf	Predator/Scavenger	4.2		Morzadec 2001	=0,020901	Emsian	Cephalon
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus minimus	217	Large eyes	Shallow	Predator/Scavenger	1.2a		Morzadec 2001	=0,008462	Pragian	Cephalon
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus minimus	218	Large eyes	Shallow	Predator/Scavenger	1.3		Morzadec 2001	=0,005248	Pragian	Cranidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus minimus	219	Large eyes	Shallow	Predator/Scavenger	1.4a		Morzadec 2001	=0,008462	Pragian	Cephalon
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus sarirus	220	Large eyes	Shallow	Predator/Scavenger	2.1a		Morzadec 2001	=0,010281	Pragian	Cranidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus quaterspinus	222	Large eyes	Shallow	Predator/Scavenger	2.3a		Morzadec 2001	=0,013517	Pragian	Cephalon
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus sp 2	223	Large eyes	Shallow	Predator/Scavenger	5.7		Morzadec 2001	=0,010095	Emsian	Cranidium
Phacopida	Acastidae	Psychopyge	Psychopyge termierorum	225	Large eyes	Middle shelf	Predator/Scavenger	13.1a		Morzadec 2001	=0,021144	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	226	Large eyes	Middle shelf	Predator/Scavenger	13.5a		Morzadec 2001	=0,039807	Emsian	Cephalon
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	227	Large eyes	Middle shelf	Predator/Scavenger	24.3		Chatterton 2006	=0,164636	Emsian	Cranidium
Phacopida	Acastidae	Psychopyge	Psychopyge hammerorum	228	Large eyes	Middle shelf	Predator/Scavenger	26.5		Chatterton 2006	=0,069324	Emsian	Cranidium
Phacopida	Acastidae	Saharops	Saharops bensaidi	229	Large eyes	Shallow	Predator/Scavenger	14.1a		Morzadec 2001	=0,041660	Emsian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge maura	230	Large eyes	Shallow	Predator/Scavenger	10.1a		Morzadec 2001	=0,042420	Emsian	Cephalon
Phacopida	Acastidae	Treveropyge	Treveropyge prorotundifrons iberica	231	Large eyes	Shallow	Predator/Scavenger	11.3a	SMF 53791	Schraut 2000c	=0,053068	Pragian	Cranidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	232	Large eyes	Middle shelf	Predator/Scavenger	15.2a		Morzadec 2001	=0,020595	Emsian	Cephalon
Phacopida	Acastidae	Walliserops	Walliserops hammii	233	Large eyes	Middle shelf	Predator/Scavenger	29.6		Chatterton 2006	=0,049998	Emsian	Cephalon
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	234	Large eyes	Middle shelf	Predator/Scavenger	31.1		Chatterton 2006	=0,093520	Emsian	Cephalon
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura beyrichi africana	235	Large eyes	Middle shelf	Particle feeding	9.17a		Alberti1970a	=0,005291	Eifelien	Cranidium
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura beyrichi africana	236	Large eyes	Middle shelf	Particle feeding	9.18		Alberti1970a	=0,005224	Eifelien	Cranidium
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleurella mauretunica	237	Large eyes	Middle shelf	Particle feeding	5.50a	CGMTA	Alberti1981a	=0,024430	Eifelien	Cranidium
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura bohémica	238	Large eyes	Middle shelf	Particle feeding	5.51	SMF 36276	Alberti1981a	=0,029450	Eifelien	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis akkae	239	Large eyes	Middle shelf	Particle feeding	3.d	Di/UO/010	Feist 2018	=0,010988	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis hamlagdadicus	240	Large eyes	Middle shelf	Particle feeding	5.52a	CGMTA	Alberti 1981a	=0,024515	Eifelien	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis boutscharafinense	241	Large eyes	Middle shelf	Particle feeding	5.53	CGMTA	Alberti 1981a	=0,023553	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis boutscharafinense	242	Large eyes	Middle shelf	Particle feeding	5.54	SMF 36275	Alberti 1981a	=0,015380	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lierli	243	Large eyes	Middle shelf	Particle feeding	6.75a	CGMTA	Alberti 1983	=0,010709	Pragian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lierli	244	Large eyes	Middle shelf	Particle feeding	6.76	SMF 36567	Alberti 1983	=0,010709	Pragian	Cranidium

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Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis sp A	245	Large eyes	Middle shelf	Particle feeding	7w	MU-G- Sr.T r.A4 /Pr1 44	Crônier Abbache 2018	=0,062446	Eifelien	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lerougei	246	Large eyes	Middle shelf	Particle feeding	11a	IRSNB a13016	Van Viersen 2016	=0,023803	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lerougei	247	Large eyes	Middle shelf	Particle feeding	11b	IRSNB a13014	Van Viersen 2016	=0,012345	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lerougei	248	Large eyes	Middle shelf	Particle feeding	12c	IRSNB a12998	Van Viersen 2016	=0,024383	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lerougei	249	Large eyes	Middle shelf	Particle feeding	12f	IRSNB a12999	Van Viersen 2016	=0,024089	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lerougei	250	Large eyes	Middle shelf	Particle feeding	13c	IRSNB a13000	Van Viersen 2016	=0,023808	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis kippingi	251	Large eyes	Middle shelf	Particle feeding	15c	IRSNB a12997	Van Viersen 2016	=0,019996	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis juergenholla ndi	252	Large eyes	Middle shelf	Particle feeding	17a	IRSNB a13013	Van Viersen 2016	=0,021945	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis smeenki	253	Large eyes	Middle shelf	Particle feeding	18d	IRSNB a13009	Van Viersen 2016	=0,037031	Eifelien	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis maharchensis	254	Large eyes	Middle shelf	Particle feeding	20g	IRSNB a13007	Van Viersen 2016	=0,029399	Pragian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis khraidensis	255	Large eyes	Middle shelf	Particle feeding	24c	IRSNB a13004	Van Viersen 2016	=0,037012	Emsian	Cephalon
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis khraidensis	256	Large eyes	Middle shelf	Particle feeding	25a	IRSNB a13006	Van Viersen 2016	=0,044636	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis tadachachten sis	257	Large eyes	Middle shelf	Particle feeding	26c	IRSNB a13002	Van Viersen 2016	=0,022221	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis hamidi	258	Large eyes	Middle shelf	Particle feeding	46.2	UA 13402	Chatterton 2006	=0,024009	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis hamidi	259	Large eyes	Middle shelf	Particle feeding	46.12	UA 13409	Chatterton 2006	=0,026604	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lata	260	Large eyes	Middle shelf	Particle feeding	b.25		Alberti 1967b	=0,039842	Pragian	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	261	Large eyes	Middle shelf	Particle feeding	36.1a	CGMTA 159	Alberti 1969	=0,005620	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	262	Large eyes	Middle shelf	Particle feeding	36.2a	SMF 23383	Alberti 1969	=0,005620	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	263	Large eyes	Middle shelf	Particle feeding	36.3	SMF 23384	Alberti 1969	=0,005966	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	264	Large eyes	Middle shelf	Particle feeding	36.4a	SMF 23386	Alberti 1969	=0,004734	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion novellum	265	Large eyes	Middle shelf	Particle feeding	36.7	SMF 23215	Alberti 1969	=0,008397	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion novellum	266	Large eyes	Middle shelf	Particle feeding	36.8	CGMTA 206	Alberti 1969	=0,007699	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion neptis	267	Large eyes	Middle shelf	Particle feeding	36.9a	CGMTA 160	Alberti 1969	=0,004853	Pragian	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion neptis	268	Large eyes	Middle shelf	Particle feeding	36.10	SMF 23387	Alberti 1969	=0,004589	Pragian	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion ambiguum	269	Large eyes	Middle shelf	Particle feeding	36.11a	CGMTA 153	Alberti 1969	=0,006397		Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	270	Large eyes	Middle shelf	Particle feeding	b.28	CGMTA 159	Alberti 1967b	=0,006939	Ludlow-Pridoli	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion neptis	271	Large eyes	Middle shelf	Particle feeding	b.29	CGMTA 160	Alberti 1967b	=0,006379	Pragian	Cranidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion ambiguum	272	Large eyes	Middle shelf	Particle feeding	b.30	CGMTA 161	Alberti 1967b	=0,008395		Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis boutscharafi nense	273	Large eyes	Middle shelf	Particle feeding	34.7a	SMF 23444	Alberti 1969	=0,007100	Emsian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis akkae	274	Large eyes	Middle shelf	Particle feeding	34.1a	CGMTA-AK 112	Alberti 1969	=0,010349	Pragian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis valida	275	Large eyes	Middle shelf	Particle feeding	34.2a	CGMTA 198	Alberti 1969	=0,012955	Pragian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lata	276	Large eyes	Middle shelf	Particle feeding	34.5a	CGMTA 152	Alberti 1969	=0,008909	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella bensaidi	277	Large eyes	Inner shelf	Particle feeding	6.77	CGMTA	Alberti 1983	=0,005137	Eifelien	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella proavus	278	Large eyes	Inner shelf	Particle feeding	9.14a	CGMT	Alberti 1970a	=0,015661	Lochkovian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella magnifica	279	Large eyes	Inner shelf	Particle feeding	35.1a	SMF 23373	Alberti 1969	=0,019122	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella magnifica	280	Large eyes	Inner shelf	Particle feeding	35.3a	SMF 23374	Alberti 1969	=0,022707	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella magnifica	281	Large eyes	Inner shelf	Particle feeding	35.4a	SMF 23375	Alberti 1969	=0,022260	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella sidiarounium	282	Large eyes	Inner shelf	Particle feeding	35.5a	CGMTA 200	Alberti 1969	=0,009356	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella tafalaltense	283	Large eyes	Inner shelf	Particle feeding	35.6a	SMF 23377	Alberti 1969	=0,009356	Emsian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella tafalaltense	284	Large eyes	Inner shelf	Particle feeding	35.7a	CGMTA 157	Alberti 1969	=0,011646	Emsian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella magnifica	285	Large eyes	Inner shelf	Particle feeding	b.26	SMF 23375	Alberti 1967b	=0,028250	Pragian	Cranidium
Proetida	Aulacopleuridae	Otarionella	Otarionella tafalaltense	286	Large eyes	Inner shelf	Particle feeding	b.27	CGMTA 157	Alberti 1967b	=0,015093	Emsian	Cranidium

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Proetida	Aulacopleuridae	Scharya	Scharya maura	287	Large eyes	Middle shelf	Particle feeding	9.1a	CGMTA 299	Alberti 1970a	=0,003913	Emsian	Cranidium
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	288	Small eyes	Deep	Predator/Scavenger	9.5	UA 13330	Chatterton 2006	=0,082800	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	289	Small eyes	Deep	Predator/Scavenger	12.10	UA 13343	Chatterton 2006	=0,036985	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	290	Small eyes	Deep	Predator/Scavenger	18.3a	CGMTA 335	Alberti 1970a	=0,019067	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	291	Small eyes	Deep	Predator/Scavenger	18.5a*	SMF 23566	Alberti 1970a	=0,022038	Emsian	Cephalon
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	292	Small eyes	Deep	Predator/Scavenger	18.6a	SMF 23567	Alberti 1970a	=0,023200	Emsian	Cephalon
Phacopida	Calymenidae	Gravicalymene	Gravicalymene hamlagadica	293	Large eyes	Middle shelf	Predator/Scavenger	6.57a	CGMTA	Alberti 1981a	=0,092157	Pragian	Cranidium
Phacopida	Calymenidae	Gravicalymene	Gravicalymene hamlagadica	294	Large eyes	Middle shelf	Predator/Scavenger	6.58	SMF 36283	Alberti 1981a	=0,084178	Pragian	Cranidium
Phacopida	Calymenidae	Gravicalymene	Gravicalymene maura	295	Large eyes	Middle shelf	Predator/Scavenger	42.1a	CGMTA 164	Alberti 1969	=0,017787	Pragian	Cranidium
Phacopida	Cheiruridae	Cheirurus	Cheirurus obtusatus	296	Blind	Middle shelf	Predator/Scavenger	39.11	CGMTA 207	Alberti 1969	=0,007724	Ludlow-Pridoli	Cranidium
Phacopida	Cheiruridae	Crotalocephalides	Crotalocephalides africanus	297	Large eyes	Middle shelf	Predator/Scavenger	39.1a	SMF 23401	Alberti 1969	=0,051668	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalides	Crotalocephalides africanus	298	Large eyes	Middle shelf	Predator/Scavenger	39.2a	CGMTA 162	Alberti 1969	=0,031148	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalides	Crotalocephalides africanus	299	Large eyes	Middle shelf	Predator/Scavenger	a.19	SMF 23401	Alberti 1967a	=0,056025	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus benziregensis	300	Large eyes	Middle shelf	Predator/Scavenger	1.1a	SMF 36569	Alberti 1983	=0,031526	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus benziregensis	301	Large eyes	Middle shelf	Predator/Scavenger	1.2	SH	Alberti 1983	=0,031526	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus benziregensis	302	Large eyes	Middle shelf	Predator/Scavenger	1.5	SMF 36581	Alberti 1983	=0,029187	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus tiftetensis	303	Large eyes	Middle shelf	Predator/Scavenger	2.1a	SMF 57067	Schraut 2000c	=0,098363	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus auster	304	Large eyes	Middle shelf	Predator/Scavenger	10.6a	CGMTA 307	Alberti 1970a	=0,032459	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus auster	305	Large eyes	Middle shelf	Predator/Scavenger	10.8a	SMF 23510	Alberti 1970a	=0,030701	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus	306	Large eyes	Middle shelf	Predator/Scavenger	38.1a	CGMT	Alberti 1969	=0,035594	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus	307	Large eyes	Middle shelf	Predator/Scavenger	38.2	SMF 23447	Alberti 1969	=0,016341	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus	308	Large eyes	Middle shelf	Predator/Scavenger	38.3a	CGMT	Alberti 1969	=0,014603	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus	309	Large eyes	Middle shelf	Predator/Scavenger	38.4a	SMF 23448	Alberti 1969	=0,020722	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina gibbus	310	Large eyes	Middle shelf	Predator/Scavenger	38.5	CGMTA 173	Alberti 1969	=0,019998	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalina	Crotalocephalina sp B	311	Large eyes	Middle shelf	Predator/Scavenger	38.10	SMF 23449	Alberti 1969	=0,024375	Lochkovian	Blind
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus pauper saharensis	312	Large eyes	Middle shelf	Predator/Scavenger	7.78	SH	Alberti 1983	=0,004549	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus pauper saharensis	313	Large eyes	Middle shelf	Predator/Scavenger	7.79	SMF 36593	Alberti 1983	=0,033313	Pragian	Cranidium
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus meridianus	314	Large eyes	Middle shelf	Predator/Scavenger	37.1a	CGMTA 201	Alberti 1969	=0,021165	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus meridianus	315	Large eyes	Middle shelf	Predator/Scavenger	37.2a	CGMT	Alberti 1969	=0,030662	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus maurus	316	Large eyes	Middle shelf	Predator/Scavenger	38.6a	CGMTA 161	Alberti 1969	=0,026459	Pragian	Blind
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus maurus	317	Large eyes	Middle shelf	Predator/Scavenger	38.7a	SMF 23391	Alberti 1969	=0,013498	Pragian	Blind
Phacopida	Cheiruridae	Ktenoura	Ktenoura strux	318	Large eyes	Inner shelf	Predator/Scavenger	10.1a	CGMTA 305	Alberti 1970a	=0,029930	Ludlow-Pridoli	Cranidium
Harpetida	Harpetidae	Harpes	Indet	319	Small eyes	Middle shelf	Predator/Scavenger	2.20	SH	Alberti 1983	=0,019083	Pragian	Cranidium
Harpetida	Harpetidae	Harpes	Harpes neogracilis	320	Small eyes	Middle shelf	Predator/Scavenger	2l	UM-RF 220	Feist 2002	=0,020642	Frasnian	Cranidium
Harpetida	Harpetidae	Lioharpes	Lioharpes wendti	321	Small eyes	Middle shelf	Predator/Scavenger	4.a	UM-IP 729	Feist 2018	=0,015871	Emsian	Cranidium
Harpetida	Harpetidae	Lioharpes	Lioharpes wendti	322	Small eyes	Middle shelf	Predator/Scavenger	4.c	UM-IP 728	Feist 2018	=0,013158	Emsian	Cranidium
Harpetida	Harpetidae	Lioharpes	Lioharpes wendti	323	Small eyes	Middle shelf	Predator/Scavenger	4.d	UM-IP 730	Feist 2018	=0,019223	Emsian	Cranidium

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Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	324	Large eyes	Middle shelf	Predator/Scavenger	1.3	MGSB 79489	Corbacho Kier 2013	=0,014005	Pragian	Cephalon
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	325	Large eyes	Middle shelf	Predator/Scavenger	2.1	MGSB 79489	Corbacho Kier 2013	=0,009940	Pragian	Cephalon
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	326	Large eyes	Middle shelf	Predator/Scavenger	2.2	MGSB 79486	Corbacho Kier 2013	=0,019526	Pragian	Cranidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	327	Large eyes	Middle shelf	Predator/Scavenger	2.4	MMB 109	Corbacho Kier 2013	=0,006289	Pragian	Cranidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	328	Large eyes	Middle shelf	Predator/Scavenger	3.2	MMB 105	Corbacho Kier 2013	=0,020660	Pragian	Cranidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	329	Large eyes	Middle shelf	Predator/Scavenger	3.3	MMB 106	Corbacho Kier 2013	=0,013158	Pragian	Cranidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	330	Large eyes	Middle shelf	Predator/Scavenger	3.4	MMB 107	Corbacho Kier 2013	=0,011062	Pragian	Cephalon
Lichida	Lichidae	Akantharges	Akantharges mbareki	332	Large eyes	Middle shelf	Predator/Scavenger	3.2	JC 95	Corbacho Lopez 2013	=0,043472	Eifelien	Blind
Lichida	Lichidae	Ceratarges	Ceratarges ziregensis	333	Large eyes	Inner shelf	Predator/Scavenger	1a	NHMM 2011 001	Van Viersen 2011	=0,035453	Eifelien	Cranidium
Lichida	Lichidae	Ceratarges	Ceratarges koumalii	334	Large eyes	Inner shelf	Predator/Scavenger	2d	NHMM 2011 002	Van Viersen 2011	=0,034227	Eifelien	Cephalon
Lichida	Odontopleuridae	Ceratocephala	Ceratocephala hoernesii	335	Large eyes	Middle shelf	Predator/Scavenger	3.e_24	UM-IP 786	Feist 2018	=0,011293	Emsian	Cranidium
Lichida	Odontopleuridae	Ceratocephala	Ceratocephala hoernesii	336	Large eyes	Middle shelf	Predator/Scavenger	3.h	UM-IP 789	Feist 2018	=0,014083	Emsian	Cranidium
Lichida	Odontopleuridae	Ceratocephala	Ceratocephala vesiculosa	337	Large eyes	Middle shelf	Predator/Scavenger	19.10a	CGMTA 344	Alberti 1970a	=0,013172	Eifelien	Cranidium
Lichida	Odontopleuridae	Isoprusia	Isoprusia laportei	340	Large eyes	Middle shelf	Predator/Scavenger	3.m	UM-IP 804	Feist 2018	=0,005747	Emsian	Cranidium
Lichida	Odontopleuridae	Isoprusia	Isoprusia laportei	341	Large eyes	Middle shelf	Predator/Scavenger	41.11a	SMF 23421	Alberti 1969	=0,012586		Cranidium
Lichida	Odontopleuridae	Isoprusia	Isoprusia laportei	342	Large eyes	Middle shelf	Predator/Scavenger	41.12	CGMTA 168	Alberti 1969	=0,005682		Cranidium
Lichida	Odontopleuridae	Isoprusia	Isoprusia laportei	343	Large eyes	Middle shelf	Predator/Scavenger	41.13a	ISCR	Alberti 1969	=0,017139		Cranidium
Lichida	Odontopleuridae	Kettneraspis	Kettneraspis pigra	344	Large eyes	Deep	Predator/Scavenger	41.3	SMF 23450	Alberti 1969	=0,013512	Eifelien	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi leonhardi	345	Large eyes	Middle shelf	Predator/Scavenger	19.6a	CGMTA 368	Alberti 1970a	=0,011621	Ludlow-Pridoli	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi grouensis	346	Large eyes	Middle shelf	Predator/Scavenger	19.7a	CGMTA 342	Alberti 1970a	=0,007742	Ludlow-Pridoli	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	347	Large eyes	Middle shelf	Predator/Scavenger	40.2a	SMF 23408	Alberti 1969	=0,011859	Pragian	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	348	Large eyes	Middle shelf	Predator/Scavenger	40.3a	SMF 23409	Alberti 1969	=0,011859	Pragian	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	349	Large eyes	Middle shelf	Predator/Scavenger	40.4	SMF 23410	Alberti 1969	=0,012694	Pragian	Cranidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	350	Large eyes	Middle shelf	Predator/Scavenger	40.5	CGMTA 167	Alberti 1969	=0,013203	Pragian	Cranidium
Phacopida	Phacopidae	Acuticryphops	Acuticryphops acuticeps	351	Small eyes	Middle shelf	Predator/Scavenger	3.c	UM2-RF 221	Feist 2002	=0,011087	Frasnian	Blind
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	352	Large eyes	Middle shelf	Predator/Scavenger	4.g		Khalidi 2016	=0,041317	Emsian	Cephalon
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	353	Large eyes	Middle shelf	Predator/Scavenger	4.n		Khalidi 2016	=0,087706	Emsian	Cranidium
Phacopida	Phacopidae	Adrisiops	Adrisiops boudjemaai	354	Large eyes	Middle shelf	Predator/Scavenger	5.n		Khalidi 2016	=0,128163	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	355	Large eyes	Middle shelf	Predator/Scavenger	4.2	UA 13306	Chatterton 2006	=0,061248	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	Austerops sp D	356	Large eyes	Middle shelf	Predator/Scavenger	4b		Crônier Abbache 2018	=0,054536	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	Austerops sp B	357	Large eyes	Middle shelf	Predator/Scavenger	4s		Crônier Abbache 2018	=0,042840	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	Austerops sp B	358	Large eyes	Middle shelf	Predator/Scavenger	4u		Crônier Abbache 2018	=0,061212	Eifelien	Cranidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	359	Large eyes	Middle shelf	Predator/Scavenger	5.1	UA 13311	Chatterton 2006	=0,058588	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	360	Large eyes	Middle shelf	Predator/Scavenger	5.2	UA 13313	Chatterton 2006	=0,065006	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	361	Large eyes	Middle shelf	Predator/Scavenger	5.3	UA 13307	Chatterton 2006	=0,059082	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	362	Large eyes	Middle shelf	Predator/Scavenger	5.4	UA 13357	Chatterton 2006	=0,087816	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	363	Large eyes	Middle shelf	Predator/Scavenger	5.6	UA 13312	Chatterton 2006	=0,050395	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	Austerops speculator punctatus	364	Large eyes	Middle shelf	Predator/Scavenger	6.1	UA 6878	McKellar 2009	=0,015433	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	Austerops speculator punctatus	365	Large eyes	Middle shelf	Predator/Scavenger	6.3	UA 6882	McKellar 2009	=0,015433	Eifelien	Cephalon

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Phacopida	Phacopidae	Austerops	<i>Austerops speculator speculator</i>	366	Large eyes	Middle shelf	Predator/Scavenger	6.a		Khaldi 2016	=0,056176	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	367	Large eyes	Middle shelf	Predator/Scavenger	6.e		Khaldi 2016	=0,043858	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	368	Large eyes	Middle shelf	Predator/Scavenger	6.i		Khaldi 2016	=0,063271	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	369	Large eyes	Middle shelf	Predator/Scavenger	7.2	UA 13322	Chatterton 2006	=0,059993	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	370	Large eyes	Middle shelf	Predator/Scavenger	7.3	UA 13317	Chatterton 2006	=0,041059	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	371	Large eyes	Middle shelf	Predator/Scavenger	7.5	UA 13325	Chatterton 2006	=0,043587	Eifelien	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	372	Large eyes	Middle shelf	Predator/Scavenger	7.8	UA 13324	Chatterton 2006	=0,053775	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	373	Large eyes	Middle shelf	Predator/Scavenger	7.9	UA 13319	Chatterton 2006	=0,067651	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops legrandi</i>	374	Large eyes	Middle shelf	Predator/Scavenger	7.d		Khaldi 2016	=0,060957	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops legrandi</i>	375	Large eyes	Middle shelf	Predator/Scavenger	7.k		Khaldi 2016	=0,026454	Emsian	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	376	Large eyes	Middle shelf	Predator/Scavenger	8.3	UA 6884	McKellar 2009	=0,013968	Eifelien	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	377	Large eyes	Middle shelf	Predator/Scavenger	8.7	UA 6889	McKellar 2009	=0,013275	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	378	Large eyes	Middle shelf	Predator/Scavenger	8.9	UA 6888	McKellar 2009	=0,011414	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	379	Large eyes	Middle shelf	Predator/Scavenger	9.2	UA 6885	McKellar 2009	=0,011945	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	380	Large eyes	Middle shelf	Predator/Scavenger	9.9	UA 6887	McKellar 2009	=0,011945	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops salamandar</i>	381	Large eyes	Middle shelf	Predator/Scavenger	10.1	UA 6892	McKellar 2009	=0,010181	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops salamandar</i>	382	Large eyes	Middle shelf	Predator/Scavenger	10.6	UA 6893	McKellar 2009	=0,012318	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops salamandar</i>	383	Large eyes	Middle shelf	Predator/Scavenger	10.9	UA 6894	McKellar 2009	=0,011295	Eifelien	Cephalon
Phacopida	Phacopidae	Austerops	<i>Austerops speculator speculator</i>	384	Large eyes	Middle shelf	Predator/Scavenger	12.i.a	ISCR	Alberti 1970a	=0,018431	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops speculator speculator</i>	385	Large eyes	Middle shelf	Predator/Scavenger	12.2.a	ISCR	Alberti 1970a	=0,018431	Emsian	Cranidium
Phacopida	Phacopidae	Austerops	<i>Austerops speculator speculator</i>	386	Large eyes	Middle shelf	Predator/Scavenger	12.3.a	ISCR	Alberti 1970a	=0,019762	Emsian	Cranidium
Harpetida	Harpetidae	Harpes	<i>Harpes hamarlaghda densis</i>	387	Small eyes	Middle shelf	Predator/Scavenger	6b	PIMUZ 35192	Crônier Oudot 2018	=0,010941	Emsian	Cranidium
Harpetida	Harpetidae	Harpes	<i>Harpes hamarlaghda densis</i>	388	Small eyes	Middle shelf	Predator/Scavenger	6h	PIMUZ 35194	Crônier Oudot 2018	=0,004433	Emsian	Cranidium
Harpetida	Harpetidae	Harpes	<i>Harpes hamarlaghda densis</i>	389	Small eyes	Middle shelf	Predator/Scavenger	6m	PIMUZ 35196	Crônier Oudot 2018	=0,008929	Emsian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops maidericus</i>	390	Large eyes	Middle shelf	Predator/Scavenger	2.15a	CGMTA	Alberti 1983	=0,028007	Pragian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops algericus</i>	391	Large eyes	Middle shelf	Predator/Scavenger	2.16a	SH	Alberti 1983	=0,028007	Pragian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops algericus</i>	392	Large eyes	Middle shelf	Predator/Scavenger	2.17a	SH	Alberti 1983	=0,031526	Pragian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops slimanensis</i>	393	Large eyes	Middle shelf	Predator/Scavenger	4.38	SMF 36582	Alberti 1983	=0,008749	Lochkovian	Cephalon
Phacopida	Phacopidae	Boeckops	<i>Boeckops sp C</i>	394	Large eyes	Middle shelf	Predator/Scavenger	5k		Khaldi 2016	=0,029761	Emsian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops maidericus</i>	395	Large eyes	Middle shelf	Predator/Scavenger	8.96a	SMF 36621	Alberti 1983	=0,029187	Pragian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops stelcki</i>	396	Large eyes	Middle shelf	Predator/Scavenger	11.4	UA 6897	McKellar 2009	=0,016854	Emsian	Cephalon
Phacopida	Phacopidae	Boeckops	<i>Boeckops slimanensis</i>	397	Large eyes	Middle shelf	Predator/Scavenger	16.9a	CGMTA 323	Alberti 1970a	=0,018561	Lochkovian	Cranidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops slimanensis</i>	398	Large eyes	Middle shelf	Predator/Scavenger	16.10a	CGMTA 322	Alberti 1970a	=0,012725	Lochkovian	Cephalon
Phacopida	Phacopidae	Denckmanites	<i>Denckmannites miser</i>	399	Small eyes	Deep	Predator/Scavenger	16.1a	CGMTA 321	Alberti 1970a	=0,019372	Lochkovian	Blind
Phacopida	Phacopidae	Dianops	<i>Dianops vicarius</i>	400	Blind	Deep	Predator/Scavenger	5b	MUA/1094/011	Crônier 2013	=0,032677	Famennian	Cranidium
Phacopida	Phacopidae	Dianops	<i>Dianops vicarius</i>	401	Blind	Deep	Predator/Scavenger	5e	MUA/1094/012	Crônier 2013	=0,035713	Famennian	Cranidium
Phacopida	Phacopidae	Dianops	<i>Dianops vicarius</i>	402	Blind	Deep	Predator/Scavenger	5j	MUA/1094/013	Crônier 2013	=0,032679	Famennian	Cranidium
Phacopida	Phacopidae	Dianops	<i>Dianops typhlops</i>	403	Blind	Deep	Predator/Scavenger	5m	MUA/1094/010	Crônier 2013	=0,037309	Famennian	Cranidium
Phacopida	Phacopidae	Dianops	<i>Indet</i>	404	Blind	Deep	Predator/Scavenger	6h	MUA/1094/004	Crônier 2013	=0,034719	Famennian	Cranidium
Phacopida	Phacopidae	Dianops	<i>Dianops algeriensis</i>	405	Blind	Deep	Predator/Scavenger	6p	MUA/1094/014	Crônier 2013	=0,043477	Famennian	Cranidium
Phacopida	Phacopidae	Drotops	<i>Drotops megalomanicus megalomanicus</i>	406	Large eyes	Shallow	Predator/Scavenger	1.1a	SMF 349340	Struve 1995	=0,058274	Givetian	Cephalon

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Phacopida	Phacopidae	Drotops	Drotops megalomanicus megalomanicus	407	Large eyes	Shallow	Predator/Scavenger	1.2a	SMF 49357	Struve 1995	=0,066009	Givetian	Cranidium
Phacopida	Phacopidae	Drotops	Drotops megalomanicus subornatus	408	Large eyes	Shallow	Predator/Scavenger	1.3	SMF 49354	Struve 1995	=0,065495	Givetian	Cranidium
Phacopida	Phacopidae	Drotops	Drotops megalomanicus megalomanicus	409	Large eyes	Shallow	Predator/Scavenger	2.4a	SMF 349341	Struve 1995	=0,058755	Givetian	Cranidium
Phacopida	Phacopidae	Drotops	Drotops megalomanicus megalomanicus	410	Large eyes	Shallow	Predator/Scavenger	2.5	MB.T. 1948	Struve 1995	=0,059784	Givetian	Cranidium
Phacopida	Phacopidae	Drotops	Drotops armatus	411	Large eyes	Shallow	Predator/Scavenger	6.14a	Kat-Nr. 1011	Struve 1995	=0,099663	Givetian	Cephalon
Phacopida	Phacopidae	Drotops	Drotops armatus	412	Large eyes	Shallow	Predator/Scavenger	5.12a		Struve 1995	=0,057550	Givetian	Cephalon
Phacopida	Phacopidae	Drotops	Drotops armatus	413	Large eyes	Shallow	Predator/Scavenger	4.11a	SMF 49480/S GPIMH Nr. 3652	Struve 1995	=0,048508	Givetian	Cephalon
Phacopida	Phacopidae	Drotops	Drotops armatus	414	Large eyes	Shallow	Predator/Scavenger	6.15a		Struve 1995	=0,064712	Givetian	Cranidium
Phacopida	Phacopidae	Drotops	Drotops megalomanicus megalomanicus	415	Large eyes	Shallow	Predator/Scavenger	Abb21	MB.T. 1934	Struve 1995	=0,058154	Givetian	Cranidium
Phacopida	Phacopidae	Eldredgeops	Eldredgeops tindoufensis	416	Large eyes	Inner shelf	Predator/Scavenger	47.3	USNM 174073	Burton 1974	=0,104998	Eifelian	Cranidium
Phacopida	Phacopidae	Eophacops	Eophacops bulliceps	417	Large eyes	Middle shelf	Predator/Scavenger	11.4	CGMTA 332	Alberti 1970a	=0,009095	Ludlow-Pridoli	Cephalon
Phacopida	Phacopidae	Eophacops	Eophacops bulliceps	418	Large eyes	Middle shelf	Predator/Scavenger	11.5	CGMTA 333	Alberti 1970a	=0,011284	Ludlow-Pridoli	Cranidium
Phacopida	Phacopidae	Houseops	Houseops cryphoides	419	Small eyes	Deep	Predator/Scavenger	3m	MUA/1094/006	Crônier 2013	=0,046727	Famennian	Cranidium
Phacopida	Phacopidae	Hypsipariops	Hypsipariops vagabundus	420	Large eyes	Middle shelf	Predator/Scavenger	8.23a	SMF 49402	Struve 1995	=0,059176	Givetian	Cephalon
Phacopida	Phacopidae	Hypsipariops	Hypsipariops vagabundus	421	Large eyes	Middle shelf	Predator/Scavenger	8.24a	SMF 49368	Struve 1995	=0,059923	Givetian	Cranidium
Phacopida	Phacopidae	Hypsipariops	Hypsipariops vagabundus	422	Large eyes	Middle shelf	Predator/Scavenger	9.28a	SMF 49403	Struve 1995	=0,059724	Givetian	Cephalon
Phacopida	Phacopidae	Hypsipariops	Hypsipariops vagabundus	423	Large eyes	Middle shelf	Predator/Scavenger	9.30a	SMF 49370	Struve 1995	=0,059062	Givetian	Cranidium
Phacopida	Phacopidae	Hypsipariops	Hypsipariops vagabundus	424	Large eyes	Middle shelf	Predator/Scavenger	48.4	In 57166	Burton 1974	=0,104829	Givetian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	425	Large eyes	Inner shelf	Predator/Scavenger	2.5	UA 13299	Chatterton 2006	=0,081844	Emsian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops granulops	426	Large eyes	Inner shelf	Predator/Scavenger	2.8	UA 13302	Chatterton 2006	=0,132123	Emsian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops tafalitanus	427	Large eyes	Inner shelf	Predator/Scavenger	2.12a	CGMTA	Alberti 1983	=0,024871	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops lebesus	428	Large eyes	Inner shelf	Predator/Scavenger	3.1	UA 13303	Chatterton 2006	=0,094946	Eifelian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops lebesus	429	Large eyes	Inner shelf	Predator/Scavenger	3.5	UA 13304	Chatterton 2006	=0,044970	Eifelian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops lebesus	430	Large eyes	Inner shelf	Predator/Scavenger	3.8	UA 13305	Chatterton 2006	=0,074292	Eifelian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	431	Large eyes	Inner shelf	Predator/Scavenger	3a	Di/UO/028	Khaldi 2016	=0,073521	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	432	Large eyes	Inner shelf	Predator/Scavenger	3e	Di/UO/027	Khaldi 2016	=0,048075	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	433	Large eyes	Inner shelf	Predator/Scavenger	3i	Di/UO/034	Khaldi 2016	=0,098020	Emsian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops granulops	434	Large eyes	Inner shelf	Predator/Scavenger	3m	GFCL 405	Khaldi 2016	=0,076887	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops chattertoni	435	Large eyes	Inner shelf	Predator/Scavenger	4d	Di/UO/002	Khaldi 2016	=0,040317	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops sp F	436	Large eyes	Inner shelf	Predator/Scavenger	7k	MU-G- Sr.T r.A4 /Ph1 11	Crônier Abbache 2018	=0,090867	Eifelian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops sparsinodosus struvei	437	Large eyes	Inner shelf	Predator/Scavenger	8p	SMF 57112	Schraut 2000a	=0,041375	Eifelian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops ovatus	438	Large eyes	Inner shelf	Predator/Scavenger	13.1	UA 6909	McKellar 2009	=0,029954	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops ovatus	439	Large eyes	Inner shelf	Predator/Scavenger	13.5	UA 6910	McKellar 2009	=0,012607	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops ovatus	440	Large eyes	Inner shelf	Predator/Scavenger	13.8	UA 6913	McKellar 2009	=0,013091	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops forteyi	441	Large eyes	Inner shelf	Predator/Scavenger	15.1	UA 6926	McKellar 2009	=0,018943	Emsian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops forteyi	442	Large eyes	Inner shelf	Predator/Scavenger	15.4	UA 6932	McKellar 2009	=0,019821	Emsian	Cephalon
Phacopida	Phacopidae	Morocops	Morocops granulops	443	Large eyes	Inner shelf	Predator/Scavenger	2A3	PIMUZ 27077	Klug 2009	=0,008504	Emsian	Cranidium
Phacopida	Phacopidae	PHACOPINAE	Indet	444	Large eyes	Middle shelf	Predator/Scavenger	2.11a	CGMTA	Alberti 1983	=0,028007	Eifelian	Cranidium
Phacopida	Phacopidae	PHACOPINAE	Indet	445	Large eyes	Middle shelf	Predator/Scavenger	2.13a	CGMTA	Alberti 1983	=0,028007	Pragian	Cranidium
Phacopida	Phacopidae	Phacops	Phacops sensu lato sp A	446	Large eyes	Middle shelf	Predator/Scavenger	3n	Di/UO/032	Khaldi 2016	=0,062480	Emsian	Cranidium

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Phacopida	Phacopidae	Phacops	Phacops sensu lato sp B	447	Large eyes	Middle shelf	Predator/Scavenger	5b	Di/UO/035	Khalidi 2016	=0,101956	Emsian	Cephalon
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	448	Large eyes	Middle shelf	Predator/Scavenger	6b	MU-G-Sr.T r.S7/Ph032	Crônier Abbache 2018	=0,039986	Eifelien	Cranidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	449	Large eyes	Middle shelf	Predator/Scavenger	6e	MU-G-Sr.T r.S4/Ph064	Crônier Abbache 2018	=0,046869	Eifelien	Cephalon
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	450	Large eyes	Middle shelf	Predator/Scavenger	6i	MU-G-Sr.T r.S7/Ph001	Crônier Abbache 2018	=0,062486	Eifelien	Cranidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	451	Large eyes	Middle shelf	Predator/Scavenger	6m	MU-G-Sr.T r.S7/Ph036	Crônier Abbache 2018	=0,090867	Eifelien	Cranidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	452	Large eyes	Middle shelf	Predator/Scavenger	6p	MU-G-Sr.T r.S4/Ph050	Crônier Abbache 2018	=0,081051	Eifelien	Cephalon
Phacopida	Phacopidae	Phacops	Phacops sp E	453	Large eyes	Middle shelf	Predator/Scavenger	7b	MU-G-Sr.T r.A4/Ph124	Crônier Abbache 2018	=0,066650	Eifelien	Cephalon
Phacopida	Phacopidae	Phacops	Phacops sp E	454	Large eyes	Middle shelf	Predator/Scavenger	7f	MU-G-Sr.T r.A4/Ph074	Crônier Abbache 2018	=0,088197	Eifelien	Cranidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensoides	455	Large eyes	Middle shelf	Predator/Scavenger	7n	MU-G-Sr.T r.A2/Ph156	Crônier Abbache 2018	=0,046869	Eifelien	Cranidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensoides	456	Large eyes	Middle shelf	Predator/Scavenger	7r	MU-G-Sr.T r.A2/Ph165	Crônier Abbache 2018	=0,065156	Eifelien	Cephalon
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensoides	457	Large eyes	Middle shelf	Predator/Scavenger	7t	MU-G-Sr.T r.A2/Ph166	Crônier Abbache 2018	=0,078920	Eifelien	Cranidium
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	458	Large eyes	Middle shelf	Predator/Scavenger	48.5	ULL 256 d 49	Burton 1974	=0,060076	Eifelien	Cranidium
Phacopida	Phacopidae	Plagiolaria	Plagiolaria senex	459	Small eyes	Deep	Predator/Scavenger	8.90a	SH	Alberti 1983	=0,019434	Pragian	Cranidium
Phacopida	Phacopidae	Plagiolaria	Plagiolaria senex	460	Small eyes	Deep	Predator/Scavenger	8.91	SH	Alberti 1983	=0,021832	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops chlupaci	461	Large eyes	Middle shelf	Predator/Scavenger	4.31a	SH	Alberti 1983	=0,029187	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops chlupaci	462	Large eyes	Middle shelf	Predator/Scavenger	4.32a	SH	Alberti 1983	=0,026021	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops chlupaci	463	Large eyes	Middle shelf	Predator/Scavenger	4.33	SH	Alberti 1983	=0,031526	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops chlupaci	464	Large eyes	Middle shelf	Predator/Scavenger	4.35	SH	Alberti 1983	=0,026021	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	465	Large eyes	Middle shelf	Predator/Scavenger	18.1a	CGMTA 329	Alberti 1970a	=0,016029	Lochkovian	Cephalon
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	466	Large eyes	Middle shelf	Predator/Scavenger	18.2a	CGMTA 330	Alberti 1970a	=0,022725	Lochkovian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis	467	Large eyes	Middle shelf	Predator/Scavenger	4.40	SH	Alberti 1983	=0,014140	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis	468	Large eyes	Middle shelf	Predator/Scavenger	8.88a	SH	Alberti 1983	=0,009214	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	469	Large eyes	Middle shelf	Predator/Scavenger	16.14a	CGMTA 328	Alberti 1970a	=0,012259	Pragian	Cranidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	470	Large eyes	Middle shelf	Predator/Scavenger	16.15	SMF 23524	Alberti 1970a	=0,015009	Pragian	Cephalon
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	471	Large eyes	Middle shelf	Predator/Scavenger	42.13	CGMTA	Alberti 1969	=0,012935	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops bronni	472	Large eyes	Inner shelf	Predator/Scavenger	1.9	UA 6843	McKellar 2009	=0,014485	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	473	Large eyes	Inner shelf	Predator/Scavenger	2.1	UA 6848	McKellar 2009	=0,023115	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	474	Large eyes	Inner shelf	Predator/Scavenger	2.4	UA 6848	McKellar 2009	=0,023115	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	475	Large eyes	Inner shelf	Predator/Scavenger	2.9	UA 6861	McKellar 2009	=0,023115	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	476	Large eyes	Inner shelf	Predator/Scavenger	3.11	UA 6851	McKellar 2009	=0,017547	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	477	Large eyes	Inner shelf	Predator/Scavenger	3.21a	CGMTA	Alberti 1983	=0,026021	Pragian	Cranidium

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Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	478	Large eyes	Inner shelf	Predator/Scavenger	3.22	CGMTA	Alberti 1983	=0.026021	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	479	Large eyes	Inner shelf	Predator/Scavenger	3.23a	CGMTA	Alberti 1983	=0.031502	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	480	Large eyes	Inner shelf	Predator/Scavenger	3.24a	Coll. Lierl (Hamburg)	Alberti 1983	=0.031502	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	481	Large eyes	Inner shelf	Predator/Scavenger	3.25	SMF 32498	Alberti 1983	=0.029187	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	482	Large eyes	Inner shelf	Predator/Scavenger	3.26	SMF 36580	Alberti 1983	=0.034545	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes algericanus	483	Large eyes	Inner shelf	Predator/Scavenger	3.27a	SH	Alberti 1983	=0.026021	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes algericanus	484	Large eyes	Inner shelf	Predator/Scavenger	3.28a	SH	Alberti 1983	=0.028007	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops pembertoni	485	Large eyes	Inner shelf	Predator/Scavenger	4.10	UA 6862	McKellar 2009	=0.014815	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops struveianus	486	Large eyes	Inner shelf	Predator/Scavenger	4.29	SH	Alberti 1983	=0.028007	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops pembertoni	487	Large eyes	Inner shelf	Predator/Scavenger	5.4	UA 6863	McKellar 2009	=0.015113	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	488	Large eyes	Inner shelf	Predator/Scavenger	7.81a	SMF 36602	Alberti 1983	=0.028219	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes cephalotes	489	Large eyes	Inner shelf	Predator/Scavenger	14.1a	CGMTA 313	Alberti 1970a	=0.027185	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops bronni	490	Large eyes	Inner shelf	Predator/Scavenger	14.3a	CGMTA 312	Alberti 1970a	=0.014709	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops bronni	491	Large eyes	Inner shelf	Predator/Scavenger	14.4a	SMF 23513	Alberti 1970a	=0.019785	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops intermedius chlupaci	492	Large eyes	Inner shelf	Predator/Scavenger	14.5a	CGMTA 314	Alberti 1970a	=0.027185	Pragian	Cephalon
Phacopida	Phacopidae	Reedops	Reedops sternbergi	493	Large eyes	Inner shelf	Predator/Scavenger	14.6a	CGMTA 315	Alberti 1970a	=0.022044	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	494	Large eyes	Inner shelf	Predator/Scavenger	15.1a	CGMTA 319	Alberti 1970a	=0.028952	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	495	Large eyes	Inner shelf	Predator/Scavenger	15.2a	SMF 23516	Alberti 1970a	=0.011608	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	496	Large eyes	Inner shelf	Predator/Scavenger	15.3a	CGMTA 320	Alberti 1970a	=0.016014	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	497	Large eyes	Inner shelf	Predator/Scavenger	15.7	CGMTA 318	Alberti 1970a	=0.015067	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	498	Large eyes	Inner shelf	Predator/Scavenger	15.8a	SMF 23515	Alberti 1970a	=0.015067	Pragian	Cranidium
Phacopida	Phacopidae	Reedops	Reedops maurulus	499	Large eyes	Inner shelf	Predator/Scavenger	15.9a	CGMTA 317	Alberti 1970a	=0.026065	Pragian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	500	Large eyes	Middle shelf	Predator/Scavenger	3b	MU-G-SR. Tr.S7/Ph024	Crônier Abbache 2018	=0.047613	Eifelian	Cephalon
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	501	Large eyes	Middle shelf	Predator/Scavenger	3f	MU-G-SR.Tr.S7/Ph004	Crônier Abbache 2018	=0.085679	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	502	Large eyes	Middle shelf	Predator/Scavenger	3i	MU-G-SR. Tr.S4/Ph065	Crônier Abbache 2018	=0.031577	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	503	Large eyes	Middle shelf	Predator/Scavenger	3l	MU-G-SR. Tr.S4/Ph150	Crônier Abbache 2018	=0.074906	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	504	Large eyes	Middle shelf	Predator/Scavenger	6.64a	LGFS5A	Alberti 1981a	=0.084400	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	505	Large eyes	Middle shelf	Predator/Scavenger	13.1a	SMF 23561	Alberti 1970a	=0.011396	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	506	Large eyes	Middle shelf	Predator/Scavenger	13.2a	GCGMTA 331	Alberti 1970a	=0.020908	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	507	Large eyes	Middle shelf	Predator/Scavenger	13.3a	SMF 23562	Alberti 1970a	=0.019335	Eifelian	Cranidium
Phacopida	Phacopidae	Struveaspis	Struveaspis maroccanica	508	Large eyes	Middle shelf	Predator/Scavenger	13.4a	CGMTA 8	Alberti 1970a	=0.016382	Eifelian	Cranidium
Phacopida	Phacopidae	Trifoliops	Trifoliops nigrilus	509	Blind	Deep	Predator/Scavenger	3d	MUA/1094/008	Crônier 2013	=0.044636	Famennian	Cranidium
Phacopida	Phacopidae	Trifoliops	Trifoliops trifolius	510	Blind	Deep	Predator/Scavenger	5e	UM-IP 722	Feist 2016	=0.027387	Famennian	Blind
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus lelievrei	511	Blind	Deep	Predator/Scavenger	1.1b	UM2-Cct26	Crônier 1997	=0.017863	Famennian	Blind
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus lelievrei	512	Blind	Deep	Predator/Scavenger	1.6	UM2-Cct48	Crônier 1997	=0.007911	Famennian	Cranidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus caecus	513	Blind	Deep	Predator/Scavenger	3a	MUA/1094/007	Crônier 2013	=0.037878	Famennian	Cranidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus mahboubii	514	Blind	Deep	Predator/Scavenger	4a	UM-IP 718	Feist 2016	=0.052613	Famennian	Blind
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus mahboubii	515	Blind	Deep	Predator/Scavenger	4c	UM-IP 719	Feist 2016	=0.074023	Famennian	Blind

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Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus mahnoubii	516	Blind	Deep	Predator/Scavenger	4j	UM-IP 720	Feist 2016	=0,043437	Famennian	Blind
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus caecus	517	Blind	Deep	Predator/Scavenger	4i	UM-IP 721	Feist 2016	=0,016391	Famennian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops zizensis	518	Large eyes	Middle shelf	Predator/Scavenger	2.13	UM2 - RF 162	Feist 2000	=0,016246	Eifelian	Cephalon
Phacopida	Phacopidae	Chotecops	Chotecops zizensis	519	Large eyes	Middle shelf	Predator/Scavenger	2.14a	CGMTA	Alberti 1983	=0,024660	Eifelian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	520	Large eyes	Middle shelf	Predator/Scavenger	4d	MU-G-Sr.T r.A6/Ph008	Crônier Abbache 2018	=0,090867	Eifelian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	521	Large eyes	Middle shelf	Predator/Scavenger	4i	MU-G-Sr.T r.A6/Ph013	Crônier Abbache 2018	=0,076898	Eifelian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	522	Large eyes	Middle shelf	Predator/Scavenger	5e		Crônier Abbache 2018	=0,107075	Eifelian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	523	Large eyes	Middle shelf	Predator/Scavenger	5h		Crônier Abbache 2018	=0,041663	Eifelian	Cranidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	524	Large eyes	Middle shelf	Predator/Scavenger	5m		Crônier Abbache 2018	=0,066601	Eifelian	Cephalon
Proetida	Proetidae	Buchiproetus	Buchiproetus pribyli pribyli	525	Large eyes	Middle shelf	Predator/Scavenger	2.8a	CGMTA 41	Alberti 1981a	=0,033893	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus rudrichteri	526	Large eyes	Middle shelf	Predator/Scavenger	3.u	UM-IP 822	Feist 2018	=0,005376	Emsian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	527	Large eyes	Middle shelf	Predator/Scavenger	9.2a	SMF 23124	Alberti 1969	=0,013727	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	528	Large eyes	Middle shelf	Predator/Scavenger	9.3a	CGMTA 42	Alberti 1969	=0,013305	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	529	Large eyes	Middle shelf	Predator/Scavenger	9.4	SMF 23125	Alberti 1969	=0,017389	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	530	Large eyes	Middle shelf	Predator/Scavenger	9.5a	SMF 23126	Alberti 1969	=0,014012	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	531	Large eyes	Middle shelf	Predator/Scavenger	9.6a	CGMTA 43	Alberti 1969	=0,011731	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	532	Large eyes	Middle shelf	Predator/Scavenger	9.7a	SMF 23127	Alberti 1969	=0,015169	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	533	Large eyes	Middle shelf	Predator/Scavenger	9.8a	SMF 23128	Alberti 1969	=0,012032	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	534	Large eyes	Middle shelf	Predator/Scavenger	9.9a	SMF 23129	Alberti 1969	=0,012032	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus pribyli pribyli	535	Large eyes	Middle shelf	Predator/Scavenger	9.13a	CGMTA 40	Alberti 1969	=0,015503	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus pribyli pribyli	536	Large eyes	Middle shelf	Predator/Scavenger	9.14	SMF 23118	Alberti 1969	=0,008316	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus pribyli pribyli	537	Large eyes	Middle shelf	Predator/Scavenger	9.15a	SMF 23119	Alberti 1969	=0,008560	Pragian	Cranidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mauretanicus	538	Large eyes	Middle shelf	Predator/Scavenger	a.2	SMF 23124	Alberti 1967a	=0,014160	Pragian	Cranidium
Proetida	Proetidae	Coniproetus	Coniproetus finitimus tenuigranifer	539	Large eyes	Inner shelf	Predator/Scavenger	4.2a	CGMTA 187	Alberti 1969	=0,020711	Pragian	Cranidium
Proetida	Proetidae	Coniproetus	Coniproetus condensus mesembrinus	540	Large eyes	Inner shelf	Predator/Scavenger	4.3a	CGMTA 16	Alberti 1969	=0,012781	Pragian	Cranidium
Proetida	Proetidae	Coniproetus	Coniproetus eurysthene nomas	541	Large eyes	Inner shelf	Predator/Scavenger	4.5a	CGMT-TM 132	Alberti 1969	=0,014208	Pragian	Cranidium
Proetida	Proetidae	Coniproetus	Indet	542	Large eyes	Inner shelf	Predator/Scavenger	b.3	CGMTA 180	Alberti 1967b	=0,008507	Emsian	Cranidium
Proetida	Proetidae	PROETINAE	Indet	543	Large eyes	Inner shelf	Predator/Scavenger	4.1a	CGMTA 180	Alberti 1969	=0,013686	Emsian	Cranidium
Proetida	Proetidae	Coniproetus	Coniproetus foucauldi	544	Large eyes	Inner shelf	Predator/Scavenger	4.4a	ISCR	Alberti 1969	=0,008157	Lochkovian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus sp A	545	Large eyes	Middle shelf	Predator/Scavenger	1.4	No name	Alberti 1966c	=0,003343		Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus djemelensis	546	Large eyes	Middle shelf	Predator/Scavenger	1.5a	GPIH	Alberti 1981a	=0,025873	Emsian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus pusulosus	547	Large eyes	Middle shelf	Predator/Scavenger	3.w	UM-IP 820	Feist 2018	=0,009801	Emsian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus nssp A	548	Large eyes	Middle shelf	Predator/Scavenger	4.3	CGMTA 241	Alberti 1970a	=0,005166	Givetian	Cranidium

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Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus marrakechensis	549	Large eyes	Middle shelf	Predator/Scavenger	7.11	CGMTA 28	Alberti 1969	=0,009958	Eifelian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus marrakechensis	550	Large eyes	Middle shelf	Predator/Scavenger	7.12a	SMF 23093	Alberti 1969	=0,008831	Eifelian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus djemelensis	551	Large eyes	Middle shelf	Predator/Scavenger	7m	Di/UO/011	Khalidi 2016	=0,059507	Emsian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus djemelensis	552	Large eyes	Middle shelf	Predator/Scavenger	8f	Di/UO/037	Khalidi 2016	=0,073521	Emsian	Cephalon
Proetida	Proetidae	Cornuproetus	Cornuproetus walliseri	553	Large eyes	Middle shelf	Predator/Scavenger	9.1a	CGMTA 28	Alberti 1969	=0,005213		Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus rudrichteri	554	Large eyes	Middle shelf	Predator/Scavenger	9.11a	SMF 23122	Alberti 1969	=0,012058	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus taciturnus nssp A	555	Large eyes	Middle shelf	Predator/Scavenger	9.12a	SMF 23186	Alberti 1969	=0,016807	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus taciturnus	556	Large eyes	Middle shelf	Predator/Scavenger	10.1a	SMF 23132	Alberti 1969	=0,017012	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus taciturnus	557	Large eyes	Middle shelf	Predator/Scavenger	10.2a	SMF 23133	Alberti 1969	=0,017012	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus taciturnus	558	Large eyes	Middle shelf	Predator/Scavenger	10.3a	SMF 23134	Alberti 1969	=0,014847	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus taciturnus	559	Large eyes	Middle shelf	Predator/Scavenger	10.4	CGMTA 45	Alberti 1969	=0,019028	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus pernix pernix	560	Large eyes	Middle shelf	Predator/Scavenger	10.5a	SMF 23111	Alberti 1969	=0,021412	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus pernix pernix	561	Large eyes	Middle shelf	Predator/Scavenger	10.6a	SMF 23112	Alberti 1969	=0,011384	Pragian	Cranidium
Proetida	Proetidae	Cornuproetus	Cornuproetus rudrichteri	562	Large eyes	Middle shelf	Predator/Scavenger	a.4	SMF 23122	Alberti 1967a	=0,012563	Pragian	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus fauremureta	563	Large eyes	Middle shelf	Predator/Scavenger	Doubleton_	SMF 23115	Alberti 1969	=0,010668		Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus fauremureta	564	Large eyes	Middle shelf	Predator/Scavenger	Doubleton_	CGMTA 38	Alberti 1969	=0,009894		Cranidium
Proetida	Proetidae	Cornuproetus	Indet	565	Large eyes	Middle shelf	Predator/Scavenger	Crônier_2	PIMUZ 35177	Crônier Oudot 2018	=0,008665	Emsian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	566	Large eyes	Middle shelf	Predator/Scavenger	1.2	UMC-IP 434	Lerosey-Aubril 2006	=0,001886	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	567	Large eyes	Middle shelf	Predator/Scavenger	1.3	UMC-IP 435	Lerosey-Aubril 2006	=0,002809	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	568	Large eyes	Middle shelf	Predator/Scavenger	1.4	UMC-IP 436	Lerosey-Aubril 2006	=0,002841	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	569	Large eyes	Middle shelf	Predator/Scavenger	1.5	UMC-IP 437	Lerosey-Aubril 2006	=0,003597	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	570	Large eyes	Middle shelf	Predator/Scavenger	1.6	UMC-IP 438	Lerosey-Aubril 2006	=0,004424	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	571	Large eyes	Middle shelf	Predator/Scavenger	1.7	UMC-IP 439	Lerosey-Aubril 2006	=0,004672	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	572	Large eyes	Middle shelf	Predator/Scavenger	1.8	UMC-IP 440	Lerosey-Aubril 2006	=0,004672	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	573	Large eyes	Middle shelf	Predator/Scavenger	1.9	UMC-IP 441	Lerosey-Aubril 2006	=0,005100	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	574	Large eyes	Middle shelf	Predator/Scavenger	1.10	UMC-IP 442	Lerosey-Aubril 2006	=0,005263	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	575	Large eyes	Middle shelf	Predator/Scavenger	1.11	UMC-IP 443	Lerosey-Aubril 2006	=0,004715	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole sp A	576	Large eyes	Middle shelf	Predator/Scavenger	2.32	UMC-IP 486	Lerosey-Aubril 2006	=0,004347	Famennian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	577	Large eyes	Middle shelf	Predator/Scavenger	5.9a	CGMTA 260	Alberti 1970a	=0,006258	Eifelian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	578	Large eyes	Middle shelf	Predator/Scavenger	5.10	SMF 23479	Alberti 1970a	=0,006359	Eifelian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	579	Large eyes	Middle shelf	Predator/Scavenger	5.11	CGMTA 261	Alberti 1970a	=0,005580	Eifelian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	580	Large eyes	Middle shelf	Predator/Scavenger	5.12	SMF 23480	Alberti 1970a	=0,005335	Eifelian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides termieri	581	Large eyes	Middle shelf	Predator/Scavenger	14.19a	CGMTA 58	Alberti 1969	=0,004664	Emsian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	582	Large eyes	Middle shelf	Predator/Scavenger	14.22	SMF 23163	Alberti 1969	=0,006545	Eifelian	Cranidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides termieri	583	Large eyes	Middle shelf	Predator/Scavenger	16.2	SMF 18189	Alberti 1964	=0,003282	Emsian	Cranidium
Proetida	Proetidae	Dalejoproetus	Dalejoproetus owensi	584	Large eyes	Inner shelf	Predator/Scavenger	4.13	NHM It 28949	Johnson 2012	=0,037207	Pragian	Cephalon
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	585	Large eyes	Deep	Predator/Scavenger	16.1a	CGMT-AT 159	Alberti 1969	=0,014471	Emsian	Cranidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	586	Large eyes	Deep	Predator/Scavenger	16.2	CGMTA 70	Alberti 1969	=0,011453	Emsian	Cranidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	587	Large eyes	Deep	Predator/Scavenger	16.3	SMF 23185	Alberti 1969	=0,011453	Emsian	Cranidium

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Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	588	Large eyes	Deep	Predator/Scavenger	16.4a	SMF 23184	Alberti 1969	=0,009663	Emsian	Cranidium
Proetida	Proetidae	Diademaproetus	Diademaproetus antatlasius	589	Large eyes	Deep	Predator/Scavenger	16.7a	CGMT-As 38	Alberti 1969	=0,014471	Eifelian	Cranidium
Proetida	Proetidae	Diademaproetus	Diademaproetus mohamedi	590	Large eyes	Deep	Predator/Scavenger	40.14	UA 13393	Chatterton 2006	=0,071908	Eifelian	Cranidium
Proetida	Proetidae	DREVERMAN NII NA E	Indet	591	Blind	Deep	Predator/Scavenger	28.16	SMF 23319	Alberti 1969	=0,004482	Emsian	Cranidium
Proetida	Proetidae	DREVERMAN NII NA E	Indet	592	Blind	Deep	Predator/Scavenger	28.18a	SMF 23320	Alberti 1969	=0,004581	Emsian	Cranidium
Proetida	Proetidae	DREVERMAN NII NA E	Indet	593	Blind	Deep	Predator/Scavenger	28.19	CGMTA 126	Alberti 1969	=0,005077	Emsian	Cranidium
Proetida	Proetidae	Eopalpebralia	Eopalpebralia hermanni	594	Blind	Middle shelf	Predator/Scavenger	3.21	SMF 36268	Alberti 1981a	=0,012245	Emsian	Cranidium
Proetida	Proetidae	Eopalpebralia	Eopalpebralia hermanni	595	Blind	Middle shelf	Predator/Scavenger	18;1	CGMT	Alberti 1969	=0,006228	Emsian	Cranidium
Proetida	Proetidae	Eopiriproetus	Eopiriproetus microphthalmus	596	Blind	Middle shelf	Predator/Scavenger	18.15a	CGMTA 84	Alberti 1969	=0,007315	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis		597	Large eyes	Middle shelf	Predator/Scavenger	6.69	SH	Alberti 1983	=0,011412	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis erbeni	598	Large eyes	Middle shelf	Predator/Scavenger	6.70	SH	Alberti 1983	=0,005533	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis cicatricosa	599	Large eyes	Middle shelf	Predator/Scavenger	6.71	CGMTA	Alberti 1983	=0,005866	Lochkovian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	600	Large eyes	Middle shelf	Predator/Scavenger	8.17a	CGMTA 358	Alberti 1970a	=0,004407	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis cicatricosa	601	Large eyes	Middle shelf	Predator/Scavenger	8.18a	CGMTA 304	Alberti 1970a	=0,006501	Lochkovian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	603	Large eyes	Middle shelf	Predator/Scavenger	28.7	SMF 23013	Alberti 1969	=0,004558	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	604	Large eyes	Middle shelf	Predator/Scavenger	28;8	SMF 23014	Alberti 1969	=0,004895	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	605	Large eyes	Middle shelf	Predator/Scavenger	28.9a	SMF 23015	Alberti 1969	=0,004066	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	606	Large eyes	Middle shelf	Predator/Scavenger	28.10	CGMTA 5	Alberti 1969	=0,004826	Pragian	Cranidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	607	Large eyes	Middle shelf	Predator/Scavenger	28;11	CGMTA 6	Alberti 1969	=0,004600	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus emerita	608	Large eyes	Middle shelf	Predator/Scavenger	3.j	UM-IP 817	Feist 2018	=0,010983	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	609	Large eyes	Middle shelf	Predator/Scavenger	3.s	UM-IP 819	Feist 2018	=0,011975	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi saharae	610	Large eyes	Middle shelf	Predator/Scavenger	6.67	SMF 36563	Alberti 1983	=0,015440	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australomaurus	611	Large eyes	Middle shelf	Predator/Scavenger	6.68	CGMTA	Alberti 1983	=0,018698	Eifelian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	612	Large eyes	Middle shelf	Predator/Scavenger	7.7	CGMTA 283	Alberti 1970a	=0,018651	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	613	Large eyes	Middle shelf	Predator/Scavenger	7.8a	SMF 23495	Alberti 1970a	=0,015383	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus ferentarius	614	Large eyes	Middle shelf	Predator/Scavenger	16.5	SMF 18185	Alberti 1964	=0,007160	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	615	Large eyes	Middle shelf	Predator/Scavenger	23.1a	SMF 23256	Alberti 1969	=0,014209	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	616	Large eyes	Middle shelf	Predator/Scavenger	23.2a	CGMTA 102	Alberti 1969	=0,016176	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	617	Large eyes	Middle shelf	Predator/Scavenger	23.3a	SMF 23257	Alberti 1969	=0,012008	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	618	Large eyes	Middle shelf	Predator/Scavenger	23.4a	CGMTA 193	Alberti 1969	=0,008688	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	619	Large eyes	Middle shelf	Predator/Scavenger	23.5a	SMF 23264	Alberti 1969	=0,014211	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	620	Large eyes	Middle shelf	Predator/Scavenger	23.6a	SMF 23265	Alberti 1969	=0,009691	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	621	Large eyes	Middle shelf	Predator/Scavenger	23.7	SMF 23266	Alberti 1969	=0,012157	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	622	Large eyes	Middle shelf	Predator/Scavenger	23.8a	CGMTA 106	Alberti 1969	=0,013226	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi saharae	623	Large eyes	Middle shelf	Predator/Scavenger	23.10a	CGMTA 181	Alberti 1969	=0,011096	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	624	Large eyes	Middle shelf	Predator/Scavenger	26.1a	SMF 23284	Alberti 1969	=0,016580	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	625	Large eyes	Middle shelf	Predator/Scavenger	262a	SMF 23285	Alberti 1969	=0,025959	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	626	Large eyes	Middle shelf	Predator/Scavenger	26.3a	SMF 23286	Alberti 1969	=0,019441	Pragian	Cranidium

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Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	627	Large eyes	Middle shelf	Predator/Scavenger	26.4a	CGMTA 112	Alberti 1969	=0,016580	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	628	Large eyes	Middle shelf	Predator/Scavenger	26.5a	CGMTA 113	Alberti 1969	=0,019273	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	629	Large eyes	Middle shelf	Predator/Scavenger	26.8a	SMF 23271	Alberti 1969	=0,024955		Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	630	Large eyes	Middle shelf	Predator/Scavenger	26.9	SMF 23272	Alberti 1969	=0,007369		Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	631	Large eyes	Middle shelf	Predator/Scavenger	26.10a	CGMTA 109	Alberti 1969	=0,004998		Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	632	Large eyes	Middle shelf	Predator/Scavenger	26.11	SMF 23273	Alberti 1969	=0,007111		Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	633	Large eyes	Middle shelf	Predator/Scavenger	26.12	SMF 23274	Alberti 1969	=0,008583		Cranidium
Proetida	Proetidae	Xiphogonium	Xiphogonium trautensteine nsis crassus	634	Large eyes	Inner shelf	Predator/Scavenger	27.5a	CGMTA 116	Alberti 1969	=0,006911	Emsian	Cranidium
Proetida	Proetidae	Xiphogonium	Xiphogonium trautensteine nsis crassus	635	Large eyes	Inner shelf	Predator/Scavenger	27.6a	SMF 23291	Alberti 1969	=0,004348	Emsian	Cranidium
Proetida	Proetidae	Xiphogonium	Xiphogonium trautensteine nsis crassus	636	Large eyes	Inner shelf	Predator/Scavenger	27.7	SMF 23292	Alberti 1969	=0,005976	Emsian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus munitus	638	Large eyes	Middle shelf	Predator/Scavenger	27.13a	CGMTA 123	Alberti 1969	=0,010548	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	639	Large eyes	Middle shelf	Predator/Scavenger	a.13	CGMTA 102	Alberti 1967a	=0,020001	Pragian	Cranidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi saharae	640	Large eyes	Middle shelf	Predator/Scavenger	b.14	CGMTA 181	Alberti 1967b	=0,014743	Emsian	Cranidium
Proetida	Proetidae	Gerastos	Gerastos akrechanus	641	Large eyes	Inner shelf	Predator/Scavenger	1.1a	ISCR	Alberti 1969	=0,014885	Emsian	Cranidium
Proetida	Proetidae	Gerastos	Gerastos akrechanus	642	Large eyes	Inner shelf	Predator/Scavenger	1.2	ISCR	Alberti 1969	=0,014239	Emsian	Cranidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	643	Large eyes	Inner shelf	Predator/Scavenger	1.3	UA 13278	Gibb 2010	=0,008811	Eifelien	Cranidium
Proetida	Proetidae	Gerastos	Gerastos akrechanus	644	Large eyes	Inner shelf	Predator/Scavenger	1.3a	ISCR	Alberti 1969	=0,014239	Emsian	Cranidium
Proetida	Proetidae	Gerastos	Gerastos prox umberianus	645	Large eyes	Inner shelf	Predator/Scavenger	1.4a	CGMTA 11	Alberti 1969	=0,011058		Cranidium
Proetida	Proetidae	Gerastos	Gerastos prox umberianus	646	Large eyes	Inner shelf	Predator/Scavenger	1.5a	SMF 23020	Alberti 1969	=0,012011		Cranidium
Proetida	Proetidae	Gerastos	Gerastos prox umberianus	647	Large eyes	Inner shelf	Predator/Scavenger	1.6a	SMF 23021	Alberti 1969	=0,008546		Cranidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	648	Large eyes	Inner shelf	Predator/Scavenger	2.8	UA 13465	Gibb 2010	=0,013213	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos rehamnanus	649	Large eyes	Inner shelf	Predator/Scavenger	3.6b	ISCR	Alberti 1969	=0,013067		Cranidium
Proetida	Proetidae	Gerastos	Gerastos hammii	650	Large eyes	Inner shelf	Predator/Scavenger	7.1	UA 13534	Gibb 2010	=0,008451	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	651	Large eyes	Inner shelf	Predator/Scavenger	8i	Di/UO/030	Khalidi 2016	=0,048535	Emsian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos discombobul atus	652	Large eyes	Inner shelf	Predator/Scavenger	11.12	UA 13469	Gibb 2010	=0,012255	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos cuvieri malisus	653	Large eyes	Inner shelf	Predator/Scavenger	13.3	UA 13551	Gibb 2010	=0,012902	Eifelien	Cephalon
Proetida	Proetidae	Gerastos	Gerastos raribus	654	Large eyes	Inner shelf	Predator/Scavenger	18.8	UA 13463	Gibb 2010	=0,006039	Givetian	Cranidium
Proetida	Proetidae	Gerastos	Gerastos izius	655	Large eyes	Inner shelf	Predator/Scavenger	24.6	UA 13570	Gibb 2010	=0,009669	Givetian	Cephalon
Proetida	Proetidae	Gerastos	Gerastos izius	656	Large eyes	Inner shelf	Predator/Scavenger	24.8	UA 13529	Gibb 2010	=0,009446	Givetian	Cephalon
Proetida	Proetidae	Interproetus	Interproetus walliseri	657	Large eyes	Middle shelf	Predator/Scavenger	2.16	SMF 23098	Alberti 1981a	=0,012028	Ludlow-Pridoli	Cranidium
Proetida	Proetidae	Kegeliella	Kegeliella listei bouregregus	658	Large eyes	Middle shelf	Predator/Scavenger	3.1b	CGMTA 15	Alberti 1969	=0,020975	Pragian	Cranidium
Proetida	Proetidae	Kegeliella	Kegeliella listei bouregregus	659	Large eyes	Middle shelf	Predator/Scavenger	3.3	SMF 23033	Alberti 1969	=0,019580	Pragian	Cranidium
Proetida	Proetidae	Kegeliella	Kegeliella listei prolistei	660	Large eyes	Middle shelf	Predator/Scavenger	3.4b	CGMTA 186	Alberti 1969	=0,019612	Pragian	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites moestus	661	Large eyes	Middle shelf	Predator/Scavenger	4m	MU-G-Sr.T r.A4 /Pr1 41	Crônier Abbache 2018	=0,033325	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	662	Large eyes	Middle shelf	Predator/Scavenger	6.11a	CGMTA 271	Alberti 1970a	=0,008166	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	663	Large eyes	Middle shelf	Predator/Scavenger	6.12a	SMF 23488	Alberti 1970a	=0,006081	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	664	Large eyes	Middle shelf	Predator/Scavenger	6.13a	SMF 23489	Alberti 1970a	=0,010058	Eifelien	Cranidium

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Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	665	Large eyes	Middle shelf	Predator/Scavenger	6.14	CGMTA 272	Alberti 1970a	=0,005079	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	666	Large eyes	Middle shelf	Predator/Scavenger	6.15	CGMTA 273	Alberti 1970a	=0,005131	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	667	Large eyes	Middle shelf	Predator/Scavenger	6.16	CGMTA 274	Alberti 1970a	=0,005878	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites baconi saharae	668	Large eyes	Middle shelf	Predator/Scavenger	20.2a	CGMTA 101	Alberti 1969	=0,006120	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites baconi saharae	669	Large eyes	Middle shelf	Predator/Scavenger	20.3	SMF 23253	Alberti 1969	=0,006537	Eifelien	Cranidium
Proetida	Proetidae	Koneprusites	Koneprusites baconi saharae	670	Large eyes	Middle shelf	Predator/Scavenger	20.4a	SMF 23254	Alberti 1969	=0,005704	Eifelien	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus solutus	671	Large eyes	Shallow	Predator/Scavenger	1.3	No name	Alberti 1966c	=0,006219		Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lahcei	672	Large eyes	Shallow	Predator/Scavenger	5.5	NHM It 28952	Johnson 2012	=0,031096	Pragian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	673	Large eyes	Shallow	Predator/Scavenger	6.6	NHM It 28955	Johnson 2012	=0,046560	Pragian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lorae	674	Large eyes	Shallow	Predator/Scavenger	15.9a	SMF 23176	Alberti 1969	=0,008917	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lorae	675	Large eyes	Shallow	Predator/Scavenger	15.10	CGMTA 66	Alberti 1969	=0,010668	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus praematurus	676	Large eyes	Shallow	Predator/Scavenger	15.12	CGMTA 61	Alberti 1969	=0,005404	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus praematurus	677	Large eyes	Shallow	Predator/Scavenger	15.13	CGMTA 62	Alberti 1969	=0,005975	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus praematurus	678	Large eyes	Shallow	Predator/Scavenger	15.14a	SMF 23168	Alberti 1969	=0,006065	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lepidus	679	Large eyes	Shallow	Predator/Scavenger	15.18a	SMF 23465	Alberti 1969	=0,005281	Lochkovian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus solutus	680	Large eyes	Shallow	Predator/Scavenger	15.19a	CGMTA 63	Alberti 1969	=0,007333		Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus praematurus	681	Large eyes	Shallow	Predator/Scavenger	17.1	SMF 18186	Alberti 1964	=0,005577	Pragian	Cranidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lorae	682	Large eyes	Shallow	Predator/Scavenger	a.8	SMF 23176	Alberti 1967a	=0,009317	Pragian	Cranidium
Proetida	Proetidae	Linguaproetus	Linguaproetus saharensis	683	Blind	Shallow	Predator/Scavenger	18.2a	CGMTA 184	Alberti 1969	=0,004314	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum junior	684	Large eyes	Middle shelf	Predator/Scavenger	2.15	CGMTA	Alberti 1981a	=0,015427	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	685	Large eyes	Middle shelf	Predator/Scavenger	5.1a	SMF 23465	Alberti 1970a	=0,005779	Emsian	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	686	Large eyes	Middle shelf	Predator/Scavenger	5.2a	CGMTA 247	Alberti 1970a	=0,006357	Emsian	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	687	Large eyes	Middle shelf	Predator/Scavenger	5.4	CGMTA 248	Alberti 1970a	=0,006186	Emsian	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	688	Large eyes	Middle shelf	Predator/Scavenger	5.48	SMF 36555	Alberti 1983	=0,006584	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	689	Large eyes	Middle shelf	Predator/Scavenger	5.58	SMF 36556	Alberti 1983	=0,005326	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	690	Large eyes	Middle shelf	Predator/Scavenger	14.1a	SMF 23145	Alberti 1969	=0,005622	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	691	Large eyes	Middle shelf	Predator/Scavenger	14.2a	SMF 23146	Alberti 1969	=0,004633	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	692	Large eyes	Middle shelf	Predator/Scavenger	14.3	SMF 23147	Alberti 1969	=0,005982	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	693	Large eyes	Middle shelf	Predator/Scavenger	14.4a	SMF 23148	Alberti 1969	=0,004633	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	694	Large eyes	Middle shelf	Predator/Scavenger	14.5	SMF 23149	Alberti 1969	=0,004322	Eifelien	Cranidium

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Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	695	Large eyes	Middle shelf	Predator/Scavenger	14.6	SMF 23150	Alberti 1969	=0,004472	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	696	Large eyes	Middle shelf	Predator/Scavenger	14.7	SMF 23151	Alberti 1969	=0,005511	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	697	Large eyes	Middle shelf	Predator/Scavenger	14.9	SMF 23153	Alberti 1969	=0,004952	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	698	Large eyes	Middle shelf	Predator/Scavenger	14.10a	SMF 23155	Alberti 1969	=0,004946	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	699	Large eyes	Middle shelf	Predator/Scavenger	14.12	CGMTA 51	Alberti 1969	=0,004238	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	700	Large eyes	Middle shelf	Predator/Scavenger	14.15	SMF 23433	Alberti 1969	=0,004633	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	701	Large eyes	Middle shelf	Predator/Scavenger	14.16	SMF 23434	Alberti 1969	=0,004941	Eifelien	Cranidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	702	Large eyes	Middle shelf	Predator/Scavenger	16.1	SMF 18188	Alberti 1964	=0,003938	Eifelien	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus midas amlanensis	703	Large eyes	Inner shelf	Predator/Scavenger	1.6	CGMTA 37	Alberti 1981a	=0,020741	Emsian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus midas amlanensis	704	Large eyes	Inner shelf	Predator/Scavenger	1.7	LGFSA	Alberti 1981a	=0,019600	Emsian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	705	Large eyes	Inner shelf	Predator/Scavenger	8.1a	SMF 23099	Alberti 1969	=0,014124	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	706	Large eyes	Inner shelf	Predator/Scavenger	8.2a	SMF 23100	Alberti 1969	=0,015039	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	707	Large eyes	Inner shelf	Predator/Scavenger	8.3	CGMTA 30	Alberti 1969	=0,013072	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	708	Large eyes	Inner shelf	Predator/Scavenger	8.4a	CGMTA 31	Alberti 1969	=0,011422	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	709	Large eyes	Inner shelf	Predator/Scavenger	8.5a	SMF 23101	Alberti 1969	=0,007096	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	710	Large eyes	Inner shelf	Predator/Scavenger	8.6a	SMF 23102	Alberti 1969	=0,008003	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	711	Large eyes	Inner shelf	Predator/Scavenger	8.8	CGMTA 320	Alberti 1969	=0,012097	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	712	Large eyes	Inner shelf	Predator/Scavenger	8.9	SMF 23104	Alberti 1969	=0,010974	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	713	Large eyes	Inner shelf	Predator/Scavenger	8.10a	SMF 23105	Alberti 1969	=0,006027	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	714	Large eyes	Inner shelf	Predator/Scavenger	8.11	GSTIH	Alberti 1969	=0,015455	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus tindoufanus	715	Large eyes	Inner shelf	Predator/Scavenger	8.13a	SMF 23106	Alberti 1969	=0,010801	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus tindoufanus	716	Large eyes	Inner shelf	Predator/Scavenger	8.14a	CGMTA 33	Alberti 1969	=0,008363	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus tindoufanus	717	Large eyes	Inner shelf	Predator/Scavenger	8.15a	SMF 23107	Alberti 1969	=0,008905	Pragian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus midas amlanensis	718	Large eyes	Inner shelf	Predator/Scavenger	10.10a	CGMTA 36	Alberti 1969	=0,012616	Emsian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus midas amlanensis	719	Large eyes	Inner shelf	Predator/Scavenger	10.11a	SMF 23114	Alberti 1969	=0,013049	Emsian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus pernix boutsharafenensis	720	Large eyes	Inner shelf	Predator/Scavenger	10.14a	CGMTA 35	Alberti 1969	=0,006897	Emsian	Cranidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	721	Large eyes	Inner shelf	Predator/Scavenger	a.1	SMF 23099	Alberti 1967a	=0,014959	Pragian	Cranidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	722	Large eyes	Middle shelf	Predator/Scavenger	3.L	UM-IP 818	Feist 2018	=0,007117	Emsian	Cranidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	723	Large eyes	Middle shelf	Predator/Scavenger	27.1a	CGMTA 119	Alberti 1969	=0,007318	Emsian	Cranidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	724	Large eyes	Middle shelf	Predator/Scavenger	27.2	SMF 23296	Alberti 1969	=0,007549	Emsian	Cranidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	725	Large eyes	Middle shelf	Predator/Scavenger	27.3	CGMTA 120	Alberti 1969	=0,009678	Emsian	Cranidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	726	Large eyes	Middle shelf	Predator/Scavenger	27.4a	SMF 23297	Alberti 1969	=0,009678	Emsian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus lecointrei	727	Large eyes	Middle shelf	Predator/Scavenger	1.13a	CGMTA 193	Alberti 1969	=0,015611	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	728	Large eyes	Middle shelf	Predator/Scavenger	2.3b	CGMTA 12	Alberti 1969	=0,017317	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	729	Large eyes	Middle shelf	Predator/Scavenger	2.4b	SMF 23024	Alberti 1969	=0,019969	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus ovalis	730	Large eyes	Middle shelf	Predator/Scavenger	2.6a	CGMTA 13	Alberti 1969	=0,017317	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus ovalis	731	Large eyes	Middle shelf	Predator/Scavenger	2.7a	SMF 23027	Alberti 1969	=0,012819	Pragian	Cranidium

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Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	732	Large eyes	Middle shelf	Predator/Scavenger	46.5	CGMTA 211	Alberti 1969	=0,015551	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	733	Large eyes	Middle shelf	Predator/Scavenger	b.1	CGMTA 12	Alberti 1967b	=0,021188	Pragian	Cranidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	734	Large eyes	Middle shelf	Predator/Scavenger	6	SMF 23024	Alberti 1982	=0,014796	Pragian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	735	Large eyes	Middle shelf	Predator/Scavenger	2.19	Gö 693-192	H. Alberti 1975a	=0,036994	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	736	Large eyes	Middle shelf	Predator/Scavenger	2.21	CGMT-HA 26	H. Alberti 1975a	=0,036994	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	737	Large eyes	Middle shelf	Predator/Scavenger	2.22	Gö 693-197	H. Alberti 1975a	=0,036994	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	738	Large eyes	Middle shelf	Predator/Scavenger	2.b	UMC-IP 424	Lerosey-Aubril Feist 2008	=0,004098	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	739	Large eyes	Middle shelf	Predator/Scavenger	2.c1	UMC-IP 425	Lerosey-Aubril Feist 2008	=0,004545	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	740	Large eyes	Middle shelf	Predator/Scavenger	2.d1	UMC-IP 426	Lerosey-Aubril Feist 2008	=0,004806	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	741	Large eyes	Middle shelf	Predator/Scavenger	3.g	UMC-IP 367	Lerosey-Aubril Feist 2008	=0,001582	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	742	Large eyes	Middle shelf	Predator/Scavenger	3.i	UMC-IP 369	Lerosey-Aubril Feist 2008	=0,002551	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	743	Large eyes	Middle shelf	Predator/Scavenger	3.j	UMC-IP 370	Lerosey-Aubril Feist 2008	=0,002747	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	744	Large eyes	Middle shelf	Predator/Scavenger	3.k	UMC-IP 371	Lerosey-Aubril Feist 2008	=0,003205	Famennian	Cranidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	745	Large eyes	Middle shelf	Predator/Scavenger	3.m	UMC-IP 313	Lerosey-Aubril Feist 2008	=0,003448	Famennian	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus wragei	746	Large eyes	Middle shelf	Predator/Scavenger	2.11	SMF 36235	Alberti 1981a	=0,015504	Eifelien	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus wragei	747	Large eyes	Middle shelf	Predator/Scavenger	2.13	CGMTA	Alberti 1981a	=0,013985	Eifelien	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus haentzscheli	748	Large eyes	Middle shelf	Predator/Scavenger	7.1a	CGMTA 64	Alberti 1969	=0,006906	Pragian	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus haentzscheli	749	Large eyes	Middle shelf	Predator/Scavenger	7.2a	SMF 23174	Alberti 1969	=0,005335	Pragian	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus haentzscheli	750	Large eyes	Middle shelf	Predator/Scavenger	7.3	SMF 23175	Alberti 1969	=0,005681	Pragian	Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus chouberti	751	Large eyes	Middle shelf	Predator/Scavenger	7.4	CGMTA 39	Alberti 1969	=0,009656		Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus chouberti	752	Large eyes	Middle shelf	Predator/Scavenger	7.5a	SMF 23116	Alberti 1969	=0,007848		Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus fauremuretae	753	Large eyes	Middle shelf	Predator/Scavenger	16.3	SMF 18184	Alberti 1964	=0,006741		Cranidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus chouberti	754	Large eyes	Middle shelf	Predator/Scavenger	17.6	SMF 18183	Alberti 1964	=0,007844		Cranidium
Proetida	Tropidocoryphidae	Phaetonellus	Phaetonellus planicauda africanus	755	Large eyes	Middle shelf	Predator/Scavenger	3.27	SMF 36259	Alberti 1981a	=0,029274	Emsian	Cranidium
Proetida	Tropidocoryphidae	Phaetonellus	Phaetonellus planicauda africanus	756	Large eyes	Middle shelf	Predator/Scavenger	3.31	CGMTA	Alberti 1981a	=0,031667	Emsian	Cranidium
Proetida	Tropidocoryphidae	Phaetonellus	Phaetonellus maurusius	757	Large eyes	Middle shelf	Predator/Scavenger	7.17a	CGMTA 287	Alberti 1970a	=0,005519	Emsian	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus ornatissimus maurus	758	Blind	Deep	Predator/Scavenger	16.4	SMF 18187	Alberti 1964	=0,003469	Emsian	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus ornatissimus maurus	759	Blind	Deep	Predator/Scavenger	18.3a	SMF 23219	Alberti 1969	=0,004611	Emsian	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	760	Blind	Deep	Predator/Scavenger	19.1a	SMF 23222	Alberti 1969	=0,006449	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	761	Blind	Deep	Predator/Scavenger	19.2a	CGMTA 89	Alberti 1969	=0,006622	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	762	Blind	Deep	Predator/Scavenger	19.3a	SMF 23223	Alberti 1969	=0,004932	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	763	Blind	Deep	Predator/Scavenger	19.4	SMF 23224	Alberti 1969	=0,005298	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	764	Blind	Deep	Predator/Scavenger	19.5	SMF 23226	Alberti 1969	=0,005624	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	765	Blind	Deep	Predator/Scavenger	19.7	SMF 23227	Alberti 1969	=0,007439	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	766	Blind	Deep	Predator/Scavenger	19.8	SMF 23228	Alberti 1969	=0,004336	Eifelien	Cranidium

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Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	767	Blind	Deep	Predator/Scavenger	19.9a	SMF 23229	Alberti 1969	=0,006449	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	768	Blind	Deep	Predator/Scavenger	19.10	CGMTA 92	Alberti 1969	=0,005202	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	769	Blind	Deep	Predator/Scavenger	19.11a	SMF 23230	Alberti 1969	=0,006900	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	770	Blind	Deep	Predator/Scavenger	19.12	SMF 23231	Alberti 1969	=0,004046	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	771	Blind	Deep	Predator/Scavenger	19.13	SMF 23232	Alberti 1969	=0,004519	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops patruelis	772	Blind	Deep	Predator/Scavenger	19.16	CGMTA 95?	Alberti 1969	=0,005048	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops patruelis	773	Blind	Deep	Predator/Scavenger	19.17	CGMTA 95	Alberti 1969	=0,005202	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops patruelis	774	Blind	Deep	Predator/Scavenger	19.18	CGMTA 96	Alberti 1969	=0,005375	Eifelien	Cranidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops patruelis	775	Blind	Deep	Predator/Scavenger	19.19	SMF 23234	Alberti 1969	=0,004599	Eifelien	Cranidium
Proetida	Proetidae	Podoliproetus	Podoliproetus rabatanus	776	Large eyes	Inner shelf	Predator/Scavenger	2.1	SMF 23028	Alberti 1969	=0,018035	Pragian	Cranidium
Proetida	Proetidae	Podoliproetus	Podoliproetus rabatanus	777	Large eyes	Inner shelf	Predator/Scavenger	2.2a	CGMTA 14	Alberti 1969	=0,014006	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus medius	778	Large eyes	Inner shelf	Predator/Scavenger	4.7a	CGMTA 19	Alberti 1969	=0,006616	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus gibbosus	779	Large eyes	Inner shelf	Predator/Scavenger	4.10a	CGMTA 20	Alberti 1969	=0,012450	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus gibbosus	780	Large eyes	Inner shelf	Predator/Scavenger	4.11a	SMF 23044	Alberti 1969	=0,013543	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	781	Large eyes	Inner shelf	Predator/Scavenger	5.1a	SMF 23046	Alberti 1969	=0,007969	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	782	Large eyes	Inner shelf	Predator/Scavenger	5.2a	SMF 23047	Alberti 1969	=0,007246	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	783	Large eyes	Inner shelf	Predator/Scavenger	5.3a	SMF 23048	Alberti 1969	=0,013922	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	784	Large eyes	Inner shelf	Predator/Scavenger	5.4	SMF 23049	Alberti 1969	=0,008404	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	785	Large eyes	Inner shelf	Predator/Scavenger	5.5a	SMF 23050	Alberti 1969	=0,007246	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	786	Large eyes	Inner shelf	Predator/Scavenger	5.6	SMF 23051	Alberti 1969	=0,012086	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	787	Large eyes	Inner shelf	Predator/Scavenger	5.7a	SMF 23052	Alberti 1969	=0,010304	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	788	Large eyes	Inner shelf	Predator/Scavenger	5.8a	CGMTA 211	Alberti 1969	=0,009280	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	789	Large eyes	Inner shelf	Predator/Scavenger	5.9a	SMF 23053	Alberti 1969	=0,010017	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	790	Large eyes	Inner shelf	Predator/Scavenger	5.10a	SMF 23054	Alberti 1969	=0,009603	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	791	Large eyes	Inner shelf	Predator/Scavenger	5.11a	CGMTA 22	Alberti 1969	=0,007222	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	792	Large eyes	Inner shelf	Predator/Scavenger	5.12a	CGMTA 23	Alberti 1969	=0,005940	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	793	Large eyes	Inner shelf	Predator/Scavenger	5.13a	CGMTA 24	Alberti 1969	=0,007444	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	794	Large eyes	Inner shelf	Predator/Scavenger	5.15	SMF 23055	Alberti 1969	=0,004918	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	795	Large eyes	Inner shelf	Predator/Scavenger	5.16	SMF 23056	Alberti 1969	=0,004739	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	796	Large eyes	Inner shelf	Predator/Scavenger	5.17	SMF 23057	Alberti 1969	=0,013318	Pragian	Cranidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	797	Large eyes	Inner shelf	Predator/Scavenger	17.3	SMF 18191	Alberti 1964	=0,005958	Pragian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia jaegeri jaegeri	798	Blind	Middle shelf	Predator/Scavenger	6.61	SMF 36561	Alberti 1983	=0,006425	Pragian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia jaegeri jaegeri	799	Blind	Middle shelf	Predator/Scavenger	6.62	SH	Alberti 1983	=0,005866	Pragian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia jaegeri jaegeri	800	Blind	Middle shelf	Predator/Scavenger	6.63	SH	Alberti 1983	=0,005866	Pragian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia baghdadlii	801	Blind	Middle shelf	Predator/Scavenger	6.66	SH	Alberti 1983	=0,011412	Emsian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia rabatensis senior	802	Blind	Middle shelf	Predator/Scavenger	8.1a	CGMTA 257	Alberti 1970a	=0,006070	Lochkovian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia rabatensis senior	803	Blind	Middle shelf	Predator/Scavenger	8.2	CGMTA 258	Alberti 1970a	=0,006616	Lochkovian	Cranidium
Proetida	Proetidae	Prodevermannia	Prodevermannia rabatensis senior	804	Blind	Middle shelf	Predator/Scavenger	8.3	SMF 23477	Alberti 1970a	=0,005485	Lochkovian	Cranidium

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Proetida	Proetidae	Prodrevermannia	Prodrevermannia medioxima	805	Blind	Middle shelf	Predator/Scavenger	21.4a	SMF 23244	Alberti 1969	=0,008880	Pragian	Cranidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia medioxima	806	Blind	Middle shelf	Predator/Scavenger	21.5a	CGMTA 99	Alberti 1969	=0,008880	Pragian	Cranidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri zemmoura	807	Blind	Middle shelf	Predator/Scavenger	21.11a	SMF 23241	Alberti 1969	=0,007551	Pragian	Cranidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri zemmoura	808	Blind	Middle shelf	Predator/Scavenger	21.12a	CGMTA 97	Alberti 1969	=0,007436	Pragian	Cranidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri zemmoura	809	Blind	Middle shelf	Predator/Scavenger	21.13a	SMF 23242	Alberti 1969	=0,005482	Pragian	Cranidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri zemmoura	810	Blind	Middle shelf	Predator/Scavenger	21.15	CGMTA 204	Alberti 1969	=0,006265	Pragian	Cranidium
Proetida	Proetidae	PROETINAE	Indet	811	Large eyes	Middle shelf	Predator/Scavenger	1.12a	CGMT	Alberti 1969	=0,020104		Cranidium
Proetida	Proetidae	Ignoproetus	Ignoproetus waldschmidt	812	Large eyes	Middle shelf	Predator/Scavenger	6.1	SMF 23589	Alberti 1970a	=0,010147	Emsian	Cranidium
Proetida	Proetidae	Ignoproetus	Ignoproetus waldschmidt	813	Large eyes	Middle shelf	Predator/Scavenger	6.2a	SMF 23590	Alberti 1970a	=0,007831	Emsian	Cranidium
Proetida	Proetidae	Ignoproetus	Ignoproetus waldschmidt	814	Large eyes	Middle shelf	Predator/Scavenger	6.3	CGMTA 354	Alberti 1970a	=0,008874	Emsian	Cranidium
Proetida	Proetidae	Ignoproetus	Ignoproetus waldschmidt	815	Large eyes	Middle shelf	Predator/Scavenger	17.1a	SMF 23203	Alberti 1969	=0,009810	Eifelien	Cranidium
Proetida	Proetidae	Ignoproetus	Ignoproetus waldschmidt	816	Large eyes	Middle shelf	Predator/Scavenger	17.2a	CGMTA 79	Alberti 1969	=0,006894	Eifelien	Cranidium
Proetida	Proetidae	Proetopeltis	Proetopeltis neglectus hamlagdadicus	817	Large eyes	Middle shelf	Predator/Scavenger	17.10a	CGMTA 78	Alberti 1969	=0,007830	Eifelien	Cranidium
Proetida	Proetidae	Proetopeltis	Proetopeltis neglectus hamlagdadicus	818	Large eyes	Middle shelf	Predator/Scavenger	17.11a	SMF 23201	Alberti 1969	=0,008525	Eifelien	Cranidium
Proetida	Proetidae	Proetopeltis	Proetopeltis neglectus hamlagdadicus	819	Large eyes	Middle shelf	Predator/Scavenger	17.12	SMF 23202	Alberti 1969	=0,007324	Eifelien	Cranidium
Proetida	Proetidae	Proetus	Proetus orbitatus	820	Large eyes	Middle shelf	Predator/Scavenger	2.8a	CGMT	Alberti 1969	=0,016502		Cranidium
Proetida	Proetidae	Proetus	Proetus proetus sp A aff granulosus	821	Large eyes	Middle shelf	Predator/Scavenger	3.5a	CGMT-TM 21	Alberti 1970a	=0,016616	Emsian	Cephalon
Proetida	Proetidae	Proetus	Proetus proetus sp L	822	Large eyes	Middle shelf	Predator/Scavenger	3.6a	ISCR	Alberti 1970a	=0,015535	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus maghrebus	823	Large eyes	Middle shelf	Predator/Scavenger	4.5	CGMTA 242	Alberti 1970a	=0,005539	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus posterior	824	Large eyes	Middle shelf	Predator/Scavenger	4.7a	SMF 23461	Alberti 1970a	=0,006022	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus posterior	825	Large eyes	Middle shelf	Predator/Scavenger	4.8	CGMTA 244	Alberti 1970a	=0,006258	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus maghrebus	826	Large eyes	Middle shelf	Predator/Scavenger	5.46	SMF 36554	Alberti 1983	=0,007006	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	827	Large eyes	Middle shelf	Predator/Scavenger	13.1a	SMF 23138	Alberti 1969	=0,007688	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	828	Large eyes	Middle shelf	Predator/Scavenger	13.2a	CGMTA 46	Alberti 1969	=0,006921	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	829	Large eyes	Middle shelf	Predator/Scavenger	13.3a	SMF 23137	Alberti 1969	=0,007327	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	830	Large eyes	Middle shelf	Predator/Scavenger	13.4a	CGMT-AT 204/1	Alberti 1969	=0,007199	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	831	Large eyes	Middle shelf	Predator/Scavenger	13.5	CGMT-AT 204/1	Alberti 1969	=0,007659	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	832	Large eyes	Middle shelf	Predator/Scavenger	13.6a	CGMTA 48	Alberti 1969	=0,006085	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	833	Large eyes	Middle shelf	Predator/Scavenger	13.7a	SMF 23141	Alberti 1969	=0,005399	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	834	Large eyes	Middle shelf	Predator/Scavenger	13.8	SMF 23142	Alberti 1969	=0,004598	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	835	Large eyes	Middle shelf	Predator/Scavenger	13.9a	SMF 23143	Alberti 1969	=0,004398	Pragian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp A	836	Large eyes	Middle shelf	Predator/Scavenger	40.1	UA 13259	Chatterton 2006	=0,026225	Emsian	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus haasi	837	Large eyes	Middle shelf	Predator/Scavenger	40.8	UA 13265	Chatterton 2006	=0,023544	Eifelien	Cranidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp B	838	Large eyes	Middle shelf	Predator/Scavenger	40.11	UA 13260	Chatterton 2006	=0,034202	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	840	Large eyes	Middle shelf	Predator/Scavenger	6.7a	SMF 23472	Alberti 1970a	=0,005288	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	841	Large eyes	Middle shelf	Predator/Scavenger	12.1	SMF 23192	Alberti 1969	=0,006148	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	842	Large eyes	Middle shelf	Predator/Scavenger	12.2a	CGMTA 75	Alberti 1969	=0,009026	Eifelien	Cranidium

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Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	843	Large eyes	Middle shelf	Predator/Scavenger	12.3	CGMTA 76	Alberti 1969	=0,008473	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	844	Large eyes	Middle shelf	Predator/Scavenger	12.4a	SMF 23193	Alberti 1969	=0,008048	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	845	Large eyes	Middle shelf	Predator/Scavenger	12.5	SMF 23194	Alberti 1969	=0,006148	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	846	Large eyes	Middle shelf	Predator/Scavenger	12.6a	CGMTA 77	Alberti 1969	=0,007122	Eifelien	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis nitidus	847	Large eyes	Middle shelf	Predator/Scavenger	12.15a	CGMTA 192	Alberti 1969	=0,008673	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis maidericus	848	Large eyes	Middle shelf	Predator/Scavenger	12.16a	CGMTA 188	Alberti 1969	=0,004789	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	849	Large eyes	Middle shelf	Predator/Scavenger	12.7a	SMF 23001	Alberti 1969	=0,005132	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	850	Large eyes	Middle shelf	Predator/Scavenger	12.8	SMF 23002	Alberti 1969	=0,004494	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	851	Large eyes	Middle shelf	Predator/Scavenger	12.9	SMF 23428	Alberti 1969	=0,004448	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	852	Large eyes	Middle shelf	Predator/Scavenger	12.10a	SMF 23429	Alberti 1969	=0,005349	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	853	Large eyes	Middle shelf	Predator/Scavenger	12.11a	CGMTA 1	Alberti 1969	=0,006189	Emsian	Cranidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis creber creber	854	Large eyes	Middle shelf	Predator/Scavenger	12.12	SMF 23430	Alberti 1969	=0,005429	Emsian	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	855	Large eyes	Middle shelf	Predator/Scavenger	4.2	UA 13275	Gibb 2007	=0,007013	Eifelien	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	856	Large eyes	Middle shelf	Predator/Scavenger	6.3	UA 13282	Gibb 2007	=0,003799	Eifelien	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus dibbanus	857	Large eyes	Middle shelf	Predator/Scavenger	7.4	UA 13257	Gibb 2007	=0,007550	Emsian	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus elguerrouji	858	Large eyes	Middle shelf	Predator/Scavenger	8.5	UA 13262	Gibb 2007	=0,007366	Eifelien	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus elguerrouji	859	Large eyes	Middle shelf	Predator/Scavenger	9.2	UA 13261	Gibb 2007	=0,008787	Eifelien	Cranidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	860	Large eyes	Middle shelf	Predator/Scavenger	9.6	UA 13267	Gibb 2007	=0,007487	Eifelien	Cranidium
Proetida	Proetidae	Unguliproetus	Unguliproetus unguoides tener	861	Large eyes	Middle shelf	Predator/Scavenger	6.7	CGMTA 17	Alberti 1969	=0,007606	Emsian	Cranidium
Proetida	Proetidae	Unguliproetus	Unguliproetus unguoides tener	862	Large eyes	Middle shelf	Predator/Scavenger	17.2	SMF 18190	Alberti 1964	=0,005589	Emsian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus vicinus	863	Large eyes	Middle shelf	Predator/Scavenger	15.1a	SMF 23177	Alberti 1969	=0,011339	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus vicinus	864	Large eyes	Middle shelf	Predator/Scavenger	15.2	SMF 23178	Alberti 1969	=0,009166	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus vicinus	865	Large eyes	Middle shelf	Predator/Scavenger	15.3	CGMTA 67	Alberti 1969	=0,006712	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus vicinus	866	Large eyes	Middle shelf	Predator/Scavenger	15.4	SMF 23179	Alberti 1969	=0,005095	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus subtenuis	867	Large eyes	Middle shelf	Predator/Scavenger	15.6a	CGMTA 69	Alberti 1969	=0,009051	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus subtenuis	868	Large eyes	Middle shelf	Predator/Scavenger	15.7a	SMF 23180	Alberti 1969	=0,007111	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus vicinus subtenuis	869	Large eyes	Middle shelf	Predator/Scavenger	15.8	SMF 23181	Alberti 1969	=0,007111	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus boucoti	870	Large eyes	Middle shelf	Predator/Scavenger	27.15a	SMF 23302	Alberti 1969	=0,008428	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus boucoti	871	Large eyes	Middle shelf	Predator/Scavenger	27.16a	SMF 23303	Alberti 1969	=0,008556	Pragian	Cranidium
Proetida	Proetidae	Vicinoproetus	Vicinoproetus boucoti	872	Large eyes	Middle shelf	Predator/Scavenger	27.17	CGMTA 124	Alberti 1969	=0,007447	Pragian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	873	Large eyes	Inner shelf	Predator/Scavenger	32.1a	CGMTA 137	Alberti 1969	=0,007667	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	874	Large eyes	Inner shelf	Predator/Scavenger	32.2a	SMF 23351	Alberti 1969	=0,005801	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	875	Large eyes	Inner shelf	Predator/Scavenger	32.3a	SMF 23352	Alberti 1969	=0,006147	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	876	Large eyes	Inner shelf	Predator/Scavenger	32.4	CGMTA 138	Alberti 1969	=0,005801	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	877	Large eyes	Inner shelf	Predator/Scavenger	32.5	SMF 23353	Alberti 1969	=0,006654	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	878	Large eyes	Inner shelf	Predator/Scavenger	32.6a	SMF 23354	Alberti 1969	=0,006410	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	879	Large eyes	Inner shelf	Predator/Scavenger	32.7	CGMTA 139	Alberti 1969	=0,004853	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	880	Large eyes	Inner shelf	Predator/Scavenger	32.8	CGMT	Alberti 1969	=0,004853	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	881	Large eyes	Inner shelf	Predator/Scavenger	32.9	SMF 23355	Alberti 1969	=0,005821	Lochkovian	Cranidium

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Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	882	Large eyes	Inner shelf	Predator/Scavenger	32.10a	SMF 23356	Alberti 1969	=0,005896	Lochkovian	Cranidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	883	Large eyes	Inner shelf	Predator/Scavenger	32.11	SMF 23357	Alberti 1969	=0,004433	Lochkovian	Cranidium
Proetida	Proetidae	Haasproetus	Haasproetus wildungensis	884	Large eyes	Middle shelf	Predator/Scavenger	9.6	CGMT-HA 3	H. Alberti 1973	=0,008309	Famennian	Cranidium
Asaphida	Raphiophoridae	Raphiophorus	Raphiophorus rouaulti	885	Blind	Middle shelf	Predator/Scavenger	1.8	No name	Alberti 1966c	=0,005265	Ludlow-Pridoli	Cranidium
Asaphida	Raphiophoridae	Raphiophorus	Raphiophorus rouaulti	886	Blind	Middle shelf	Predator/Scavenger	1.9	No name	Alberti 1966c	=0,003980	Ludlow-Pridoli	Cranidium
Asaphida	Raphiophoridae	Raphiophorus	Raphiophorus rouaulti	887	Blind	Middle shelf	Predator/Scavenger	5.55	LGFSa	Alberti 1981a	=0,014017	Ludlow-Pridoli	Cranidium
Asaphida	Raphiophoridae	Raphiophorus	Raphiophorus rouaulti	888	Blind	Middle shelf	Predator/Scavenger	5.56	LGFSa	Alberti 1981a	=0,014017	Ludlow-Pridoli	Cranidium
Asaphida	Raphiophoridae	Raphiophorus	Raphiophorus rouaulti	889	Blind	Middle shelf	Predator/Scavenger	42.7	CGMTA 208	Alberti 1969	=0,005505	Ludlow-Pridoli	Cranidium
Corynexoch	Scutelluidae	Cavetia	Cavetia furcifera hamlaghadiana	891	Large eyes	Middle shelf	Predator/Scavenger	7	No name	Alberti 1981b	=0,016818	Emsian	Cranidium
Corynexoch	Scutelluidae	Heliopeltis	Heliopeltis ihmadii	894	Large eyes	Inner shelf	Predator/Scavenger	12a	UM-IP 705	Feist 2015	=0,021048		Cranidium
Corynexoch	Scutelluidae	Heliopeltis	Heliopeltis ihmadii	895	Large eyes	Inner shelf	Predator/Scavenger	13a	UM-IP 706	Feist 2015	=0,017241		Cranidium
Corynexoch	Scutelluidae	Heliopeltis	Heliopeltis ihmadii	896	Large eyes	Inner shelf	Predator/Scavenger	13e	UM-IP 707	Feist 2015	=0,015998		Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghadica	897	Large eyes	Inner shelf	Predator/Scavenger	1.8a	CGMTA 239	Alberti 1970a	=0,030878	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci hollardi	899	Large eyes	Inner shelf	Predator/Scavenger	4f	UA 14326	Feist 2015	=0,032255	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis bassei	900	Large eyes	Inner shelf	Predator/Scavenger	5b	UM-IP 654	Feist 2015	=0,023805	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghadica	901	Large eyes	Inner shelf	Predator/Scavenger	6a	UM-IP 658	Feist 2015	=0,030118	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghadica	902	Large eyes	Inner shelf	Predator/Scavenger	6e	UA 14328	Feist 2015	=0,011234	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis maghrebica	903	Large eyes	Inner shelf	Predator/Scavenger	7a	UM-IP 666	Feist 2015	=0,025509	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis maghrebica	904	Large eyes	Inner shelf	Predator/Scavenger	7d	UM-IP 667	Feist 2015	=0,022522	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis tafalaltensis	905	Large eyes	Inner shelf	Predator/Scavenger	8a	UA 14329	Feist 2015	=0,007220	Pragian	Cranidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis tafalaltensis	906	Large eyes	Inner shelf	Predator/Scavenger	8d	UM-IP 679	Feist 2015	=0,012193	Pragian	Cranidium
Corynexoch	Scutelluidae	Platyscutellum	Platyscutellum massai	914	Large eyes	Middle shelf	Predator/Scavenger	4		Alberti 1981b	=0,032443	Pragian	Cranidium
Corynexoch	Scutelluidae	Platyscutellum	Platyscutellum massai	915	Large eyes	Middle shelf	Predator/Scavenger	5	SMF 36336	Alberti 1981b	=0,032443	Pragian	Cranidium

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Corynexoch	Scutellidae	Platyscutellum	Platyscutellum massai	916	Large eyes	Middle shelf	Predator/Scavenger	5		Alberti 1982	=0,065376	Pragian	Cranidium
Corynexoch	Scutellidae	Sagittapeltis	Sagittapeltis belkai	917	Large eyes	Inner shelf	Predator/Scavenger	9a	UM-IP 694	Feist 2015	=0,020614	Emsian	Cranidium
Corynexoch	Scutellidae	Sagittapeltis	Sagittapeltis belkai	918	Large eyes	Inner shelf	Predator/Scavenger	9g	UM-IP 695	Feist 2015	=0,024969	Emsian	Cranidium
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum frix	919	Large eyes	Middle shelf	Predator/Scavenger	2.1a	CGMTA 234	Alberti 1970a	=0,025916	Pragian	Cephalon
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum lahzeni	920	Large eyes	Middle shelf	Predator/Scavenger	47.2	UA 13410	Chatterton 2006	=0,057221	Emsian	Cranidium
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum hammadi	921	Large eyes	Middle shelf	Predator/Scavenger	48.3	UA 13411	Chatterton 2006	=0,097256	Emsian	Cephalon
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum hammadi	922	Large eyes	Middle shelf	Predator/Scavenger	48.6	UA 13412	Chatterton 2006	=0,099918	Emsian	Cephalon
Corynexoch	Scutellidae	Thysanopeltis	Thysanopeltis speciosa austromaura	923	Large eyes	Middle shelf	Predator/Scavenger	1.2	GPIH	Alberti 1981a	=0,009406	Eifelian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe cogneyi	924	Large eyes	Middle shelf	Predator/Scavenger	17.4	SMF 18193	Alberti 1964	=0,004936	Pragian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe cogneyi	925	Large eyes	Middle shelf	Predator/Scavenger	17.5	SMF 18192	Alberti 1964	=0,005724	Pragian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe stirps	926	Large eyes	Middle shelf	Predator/Scavenger	29.17	SMF 23197	Alberti 1969	=0,011674	Pragian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe rugosa	927	Large eyes	Middle shelf	Predator/Scavenger	30.15a	CGMTA 31	Alberti 1969	=0,006373	Pragian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe rugosa	928	Large eyes	Middle shelf	Predator/Scavenger	30.16a	SMF 23342	Alberti 1969	=0,010973	Pragian	Cranidium
Proetida	Tropidocoryphidae	Alberticoryphe	Alberticoryphe stirps	929	Large eyes	Middle shelf	Predator/Scavenger	4.33	SMF 36288	Alberti 1981a	=0,021374	Pragian	Cranidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus decorus maurulus	930	Large eyes	Middle shelf	Predator/Scavenger	29.14	CGMTA 197	Alberti 1969	=0,012815	Ludlow-Pridoli	Cranidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus decorus maurulus	931	Large eyes	Middle shelf	Predator/Scavenger	29.15	SMF 23341	Alberti 1969	=0,013187	Ludlow-Pridoli	Cranidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus concentricus meridianus	932	Large eyes	Middle shelf	Predator/Scavenger	31.17a	CGMTA 135	Alberti 1969	=0,008098	Pragian	Cranidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus concentricus meridianus	933	Large eyes	Middle shelf	Predator/Scavenger	31.18	SMF 23347	Alberti 1969	=0,007191	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia tafalaltensis	934	Large eyes	Middle shelf	Predator/Scavenger	6.73	SMF 36586	Alberti 1983	=0,006438	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia tafalaltensis	935	Large eyes	Middle shelf	Predator/Scavenger	31.1a	CGMTA 183	Alberti 1969	=0,005704	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	936	Large eyes	Middle shelf	Predator/Scavenger	31.2	SMF 23333	Alberti 1969	=0,006834	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	937	Large eyes	Middle shelf	Predator/Scavenger	31.3a	SMF 23334	Alberti 1969	=0,005089	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	938	Large eyes	Middle shelf	Predator/Scavenger	31.4	SMF 23335	Alberti 1969	=0,005089	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	939	Large eyes	Middle shelf	Predator/Scavenger	31.5	CGMTA 128	Alberti 1969	=0,005353	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	940	Large eyes	Middle shelf	Predator/Scavenger	31.6	SMF 23336	Alberti 1969	=0,005594	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	941	Large eyes	Middle shelf	Predator/Scavenger	31.7	SMF 23337	Alberti 1969	=0,005465	Pragian	Cranidium
Proetida	Tropidocoryphidae	Denemarkia	Denemarkia africana	942	Large eyes	Middle shelf	Predator/Scavenger	31.8	SMF 23338	Alberti 1969	=0,005353	Pragian	Cranidium
Proetida	Tropidocoryphidae	Galbertianus	Galbertianus hollardi	943	Large eyes	Middle shelf	Predator/Scavenger	16.7a	SMF 18199	Alberti 1964	=0,004967		Cranidium
Proetida	Tropidocoryphidae	Galbertianus	Galbertianus draae	944	Large eyes	Middle shelf	Predator/Scavenger	31.15a	CGMTA 132	Alberti 1969	=0,005704	Pragian	Cranidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe mediterranea	945	Large eyes	Middle shelf	Predator/Scavenger	3.v	UM-IP 815	Feist 2018	=0,005682	Emsian	
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe mauretania	946	Large eyes	Middle shelf	Predator/Scavenger	30.1	SMF 23331	Alberti 1969	=0,006062	Pragian	Cranidium

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Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe hamlaghdadica	947	Large eyes	Middle shelf	Predator/Scavenger	30.6	SMF 23329	Alberti 1969	=0,007041	Pragian	Cranidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe maroccanica	948	Large eyes	Middle shelf	Predator/Scavenger	a.18	SMF 23332	Alberti 1967a	=0,007899	Pragian	Cranidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	949	Large eyes	Shallow	Predator/Scavenger	3.2	80202	Bignon 2014	=0,048541	Pragian	Cephalon
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	950	Large eyes	Shallow	Predator/Scavenger	3.4	JC 101	Bignon 2014	=0,046727	Pragian	Cephalon
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	951	Large eyes	Shallow	Predator/Scavenger	4.2	JC 103	Bignon 2014	=0,055858	Pragian	Cephalon
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	952	Large eyes	Shallow	Predator/Scavenger	4.3	JC 102	Bignon 2014	=0,053763	Pragian	Cephalon
Proetida	Proetidae	Perliproetus	Perliproetus africanus	953	Large eyes	Middle shelf	Predator/Scavenger	10	MB.T 6223	FeistWeyer 2018	=0,030289	Famennian	Cranidium
Proetida	Proetidae	Perliproetus	Perliproetus africanus	954	Large eyes	Middle shelf	Predator/Scavenger	1Z	MB.T 6228	FeistWeyer 2018	=0,036936	Famennian	Cranidium
Proetida	Proetidae	Perliproetus	Perliproetus africanus	955	Large eyes	Middle shelf	Predator/Scavenger	1T	MB.T 6221	FeistWeyer 2018	=0,028560	Famennian	Cranidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	956	Small eyes	Middle shelf	Particle feeding	2.3	UA 14313	Chatterton 2019	=0,058823	Eifelian	Cranidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	957	Small eyes	Middle shelf	Particle feeding	3.1	UA 14315	Chatterton 2019	=0,049998	Eifelian	Cranidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	958	Small eyes	Middle shelf	Particle feeding	4.1	UA 14318	Chatterton 2019	=0,005780	Eifelian	Cranidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides pankowskiorum	959	Small eyes	Middle shelf	Particle feeding	5.2	UA 14316	Chatterton 2019	=0,058136	Eifelian	Cranidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides pankowskiorum	960	Small eyes	Middle shelf	Particle feeding	5.4	UA 14264	Chatterton 2019	=0,079355	Eifelian	Cephalon
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides nicoleae	961	Small eyes	Middle shelf	Particle feeding	5.5	UA 14317	Chatterton 2019	=0,084743	Eifelian	Cranidium
Proetida	Aulacopleuridae	Cyphaspis	Cyphaspis lata	962	Large eyes	Middle shelf	Particle feeding	34.6a	SMF 23368	Alberti 1969	=0,006541	Pragian	Cranidium
Phacopida	Phacopidae	Morocops	Morocops torkozensis	963	Large eyes	Inner shelf	Predator/Scavenger	10.6	PIMUZ 7287	Klug 2008	=0,037315	Emsian	Cephalon
Phacopida	Acastidae	Morzadecops	Morzadecops zguidensis	964	Large eyes	Inner shelf	Predator/Scavenger	11.6	PIMUZ 7296	Klug 2008	=0,065673	Emsian	Cephalon
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	965	Large eyes	Shallow	Predator/Scavenger	11.10	PIMUZ 7291	Klug 2008	=0,086926	Emsian	Cephalon
Lichida	Odontopleuridae	Gondwanaspis	Gondwanaspis mirtentis	966	Large eyes	Middle shelf	Predator/Scavenger	2a	UM2-RF 172	Feist 2002	=0,005959	Frasnian	Cephalon
Phacopida	Dalmanitidae	Morocconites	Morocconites malladoides	967	Large eyes	Inner shelf	Predator/Scavenger	2c	No name	Edgecombe 1991	=0,008003		Cephalon
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	968	Large eyes	Inner shelf	Predator/Scavenger	1.1	JC106	Corbacho 2014	=0,084224	Pragian	Cephalon
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	969	Large eyes	Inner shelf	Predator/Scavenger	1.2	MGSB80843	Corbacho 2014	=0,057371	Pragian	Cephalon
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	970	Large eyes	Inner shelf	Predator/Scavenger	2.2	JC107	Corbacho 2014	=0,083734	Pragian	Cephalon
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	971	Large eyes	Inner shelf	Predator/Scavenger	2.5	BPM1091	Corbacho 2014	=0,113406	Pragian	Cephalon
Proetida	Proetidae	Sculptoproetus	Sculptoproetus raki	972	Large eyes	Middle shelf	Predator/Scavenger	3d	IRSBNa13414	Van Viersen 2019	=0,022975	Emsian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus arenicolus	973	Large eyes	Shallow	Predator/Scavenger	3i	IRSBNa13434	Van Viersen 2019	=0,045408	Pragian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	974	Large eyes	Middle shelf	Predator/Scavenger	4a	IRSBNa13416	Van Viersen 2019	=0,027395	Eifelian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	975	Large eyes	Middle shelf	Predator/Scavenger	5a	IRSBNa13420	Van Viersen 2019	=0,033879	Eifelian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	976	Large eyes	Middle shelf	Predator/Scavenger	5g	IRSBNa13419	Van Viersen 2019	=0,036340	Emsian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	977	Large eyes	Middle shelf	Predator/Scavenger	5m	IRSBNa13421	Van Viersen 2019	=0,043468	Emsian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus sp. A	978	Large eyes	Middle shelf	Predator/Scavenger	6e	IRSBNa13422	Van Viersen 2019	=0,045443		Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus pulchistriatus	979	Large eyes	Middle shelf	Predator/Scavenger	6j	IRSBNa13424	Van Viersen 2019	=0,048766	Emsian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus gibbae	980	Large eyes	Middle shelf	Predator/Scavenger	7h	IRSBNa13423	Van Viersen 2019	=0,020829	Emsian	Cephalon
Proetida	Proetidae	Timsaloproetus	Timsaloproetus pulchistriatus repens	981	Large eyes	Middle shelf	Predator/Scavenger	8a	IRSBNa13425	Van Viersen 2019	=0,025972	Emsian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella curvirostris	982	Large eyes	Inner shelf	Predator/Scavenger	10c	IRSBNa13427	Van Viersen 2019	=0,051265	Pragian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella curvirostris	983	Large eyes	Inner shelf	Predator/Scavenger	10d	IRSBNa13426	Van Viersen 2019	=0,031235	Pragian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella curvirostris	984	Large eyes	Inner shelf	Predator/Scavenger	10i	IRSBNa13428	Van Viersen 2019	=0,035709	Pragian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella lebruni	985	Large eyes	Inner shelf	Predator/Scavenger	11d	IRSBNa13429	Van Viersen 2019	=0,019604	Emsian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella lebruni	986	Large eyes	Inner shelf	Predator/Scavenger	11g	IRSBNa13430	Van Viersen 2019	=0,024383	Emsian	Cephalon
Proetida	Proetidae	Hollandiella	Hollandiella sp. A	987	Large eyes	Inner shelf	Predator/Scavenger	12a	IRSBNa13431	Van Viersen 2019	=0,028569		Cephalon

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Proetida	Proetidae	Hollandiella	Hollandiella verecunda	988	Large eyes	Inner shelf	Predator/Scavenger	13a	IRSBNa13432	Van Viersen 2019	=0,031235	Pragian	Cephalon
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	989	Large eyes	Shallow	Predator/Scavenger	13h	IRSBNa13433	Van Viersen 2019	=0,047606	Pragian	Cephalon
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis rufa	990	Large eyes	Middle shelf	Predator/Scavenger	15a	IRSBNa13435	Van Viersen 2019	=0,035709	Eifelian	Cephalon
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis sPA	991	Large eyes	Middle shelf	Predator/Scavenger	15l	IRSBNa13436	Van Viersen 2019	=0,027017		Cephalon
Proetida	Proetidae	Palpebralia	Palpebralia brecciae	992	Blind	Deep	Predator/Scavenger	2c	UM2-RF179	Feist 2002	=0,017953	Frasnian	Cranidium
Proetida	Proetidae	Palpebralia	Palpebralia brecciae	993	Blind	Deep	Predator/Scavenger	2j	UM2-RF182	Feist 2002	=0,017057	Frasnian	Cranidium
Phacopida	Acastidae	Coltraneia	Coltraneia oufatenensis	0	Large eyes	Middle shelf	Predator/Scavenger	11.1a	No name	Morzadec 2001	=0,035829	Emsian	Pygidium
Phacopida	Acastidae	Coltraneia	Coltraneia oufatenensis	1	Large eyes	Middle shelf	Predator/Scavenger	11.3a	No name	Morzadec 2001	=0,021489	Emsian	Pygidium
Phacopida	Acastidae	Coltraneia	Coltraneia oufatenensis	2	Large eyes	Middle shelf	Predator/Scavenger	11.4	No name	Morzadec 2001	=0,021489	Emsian	Pygidium
Phacopida	Acastidae	Coltraneia	Coltraneia oufatenensis	3	Large eyes	Middle shelf	Predator/Scavenger	11.6	No name	Morzadec 2001	=0,041974	Emsian	Pygidium
Phacopida	Acastidae	Comura	Comura butyncki	4	Large eyes	Middle shelf	Predator/Scavenger	12.3c	No name	Morzadec 2001	=0,042611	Emsian	Pygidium
Phacopida	Acastidae	Comura	Comura butyncki	5	Large eyes	Middle shelf	Predator/Scavenger	12.4a	No name	Morzadec 2001	=0,033862	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	6	Large eyes	Middle shelf	Predator/Scavenger	3.1	No name	Morzadec 1997	=0,002491	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	7	Large eyes	Middle shelf	Predator/Scavenger	3.2	No name	Morzadec 1997	=0,002914	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	8	Large eyes	Middle shelf	Predator/Scavenger	3.3	No name	Morzadec 1997	=0,003469	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	9	Large eyes	Middle shelf	Predator/Scavenger	3.4	No name	Morzadec 1997	=0,004731	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	10	Large eyes	Middle shelf	Predator/Scavenger	3.7	No name	Morzadec 1997	=0,001867	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	11	Large eyes	Middle shelf	Predator/Scavenger	3.8a	No name	Morzadec 1997	=0,003275	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina ougartensis	12	Large eyes	Middle shelf	Predator/Scavenger	3.9	No name	Morzadec 1997	=0,004198	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina tafilaltensis	13	Large eyes	Middle shelf	Predator/Scavenger	6.6	No name	Morzadec 2001	=0,003495	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina tafilaltensis	14	Large eyes	Middle shelf	Predator/Scavenger	6.7	No name	Morzadec 2001	=0,003495	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina tafilaltensis	15	Large eyes	Middle shelf	Predator/Scavenger	7.6	No name	Morzadec 2001	=0,004140	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina tafilaltensis	16	Large eyes	Middle shelf	Predator/Scavenger	7.9	No name	Morzadec 2001	=0,003231	Emsian	Pygidium
Phacopida	Acastidae	Destombesina	Destombesina tafilaltensis	17	Large eyes	Middle shelf	Predator/Scavenger	7.10	No name	Morzadec 2001	=0,004140	Emsian	Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile erbeni	18	Large eyes	Deep	Predator/Scavenger	2.F	IGR 11943	Morzadec 1995	=0,010391	Emsian	Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	19	Large eyes	Deep	Predator/Scavenger	3.5	UA13645	Chatterton 2010	=0,059680		Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	20	Large eyes	Deep	Predator/Scavenger	4.12	UA13646	Chatterton 2010	=0,125876		Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile issoumourensis	21	Large eyes	Deep	Predator/Scavenger	4.13	UA13648	Chatterton 2010	=0,079381		Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile erbeni	22	Large eyes	Deep	Predator/Scavenger	7p	Di/UO/036	Khaldi 2016	=0,069418	Emsian	Pygidium
Phacopida	Acastidae	Erbenochile	Erbenochile erbeni	23	Large eyes	Deep	Predator/Scavenger	13.9	It27126	Chatterton 2006	=0,103597	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops lemaitreae	24	Large eyes	Middle shelf	Predator/Scavenger	5.2	IGR 11974	Morzadec 1997	=0,006032	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops lemaitreae	25	Large eyes	Middle shelf	Predator/Scavenger	5.5	IGR 11977	Morzadec 1997	=0,004176	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops lemaitreae	26	Large eyes	Middle shelf	Predator/Scavenger	5.6a	IGR 11978	Morzadec 1997	=0,007015	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops lemaitreae	27	Large eyes	Middle shelf	Predator/Scavenger	5.7a	IGR 11979	Morzadec 1997	=0,008497	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops burtandmimi	28	Large eyes	Middle shelf	Predator/Scavenger	6.4	UA13655	Chatterton 2010	=0,025069		Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	29	Large eyes	Middle shelf	Predator/Scavenger	6.5	IGR 11984	Morzadec 1997	=0,014217	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops burtandmimi	30	Large eyes	Middle shelf	Predator/Scavenger	6.9	UA13643	Chatterton 2010	=0,046688		Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	31	Large eyes	Middle shelf	Predator/Scavenger	6n	Di/UO/010	Khaldi 2016	=0,053188	Emsian	Pygidium

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Phacopida	Acastidae	Hollandops	Hollandops mesocristata	32	Large eyes	Middle shelf	Predator/Scavenger	7.2c	IGR 11988	Morzadec 1997	=0,014178	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	33	Large eyes	Middle shelf	Predator/Scavenger	7.4b	IGR 11990	Morzadec 1997	=0,021326	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	34	Large eyes	Middle shelf	Predator/Scavenger	7.5	IGR 11991	Morzadec 1997	=0,021326	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	35	Large eyes	Middle shelf	Predator/Scavenger	7.6a	IGR 11992	Morzadec 1997	=0,042542	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops boudibensis	36	Large eyes	Middle shelf	Predator/Scavenger	8.1c	CPM	Morzadec 2001	=0,012912	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops boudibensis	37	Large eyes	Middle shelf	Predator/Scavenger	8.4	CPM	Morzadec 2001	=0,010999	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops boudibensis	38	Large eyes	Middle shelf	Predator/Scavenger	8.5a	CPM	Morzadec 2001	=0,010999	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	39	Large eyes	Middle shelf	Predator/Scavenger	8.6	IGR 11995	Morzadec 1997	=0,005275	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	40	Large eyes	Middle shelf	Predator/Scavenger	8.6a	CPM	Morzadec 2001	=0,028055	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops boudibensis	41	Large eyes	Middle shelf	Predator/Scavenger	8.7	CPM	Morzadec 2001	=0,010999	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	42	Large eyes	Middle shelf	Predator/Scavenger	8.8	IGR 11996	Morzadec 1997	=0,008581	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	43	Large eyes	Middle shelf	Predator/Scavenger	8.9	CPM	Morzadec 2001	=0,004290	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops boudibensis	44	Large eyes	Middle shelf	Predator/Scavenger	8.10	CPM	Morzadec 2001	=0,019599	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	45	Large eyes	Middle shelf	Predator/Scavenger	9.1a	CPM	Morzadec 2001	=0,020935	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	46	Large eyes	Middle shelf	Predator/Scavenger	9.2a	CPM	Morzadec 2001	=0,010590	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	47	Large eyes	Middle shelf	Predator/Scavenger	9.3	CPM	Morzadec 2001	=0,010590	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	48	Large eyes	Middle shelf	Predator/Scavenger	9.4a	CPM	Morzadec 2001	=0,010590	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops burtandmimi ae	49	Large eyes	Middle shelf	Predator/Scavenger	9.5b	CPM	Morzadec 2001	=0,020935	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops burtandmimi ae	50	Large eyes	Middle shelf	Predator/Scavenger	9.6a	CPM	Morzadec 2001	=0,013945	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops burtandmimi ae	51	Large eyes	Middle shelf	Predator/Scavenger	9.7	CPM	Morzadec 2001	=0,008462	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	52	Large eyes	Middle shelf	Predator/Scavenger	13.2a	SMF 53769	Schraut 2000c	=0,081760	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	53	Large eyes	Middle shelf	Predator/Scavenger	13.4a	SMF 53735	Schraut 2000c	=0,140378	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	54	Large eyes	Middle shelf	Predator/Scavenger	13.5	SMF 53742	Schraut 2000c	=0,087222	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	55	Large eyes	Middle shelf	Predator/Scavenger	14.1a	SMF 53644	Schraut 2000c	=0,097024	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops mesocristata	56	Large eyes	Middle shelf	Predator/Scavenger	14.2a	SMF 53764	Schraut 2000c	=0,121010	Emsian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops aithassainor um	57	Large eyes	Middle shelf	Predator/Scavenger	17.1	UA 13440	Chatterton 2006	=0,117647	Eifelian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops aithassainor um	58	Large eyes	Middle shelf	Predator/Scavenger	18.7	UA 13442	Chatterton 2006	=0,081231	Eifelian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops aithassainor um	59	Large eyes	Middle shelf	Predator/Scavenger	18.8	UA 13441	Chatterton 2006	=0,065404	Eifelian	Pygidium
Phacopida	Acastidae	Hollandops	Hollandops aithassainor um	60	Large eyes	Middle shelf	Predator/Scavenger	18.9	UA 13444	Chatterton 2006	=0,065404	Eifelian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops megaspina	61	Large eyes	Shallow	Predator/Scavenger	4.5b	CPC	Morzadec 2001	=0,042596	Emsian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops marocanensis	62	Large eyes	Shallow	Predator/Scavenger	5.2b	CPM	Morzadec 2001	=0,028844	Emsian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops marocanensis	63	Large eyes	Shallow	Predator/Scavenger	5.3	CPM	Morzadec 2001	=0,010603	Emsian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops djazairensis	64	Large eyes	Shallow	Predator/Scavenger	8.4	IGR 12000	Morzadec 1997	=0,021195	Emsian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops tamnrherta	65	Large eyes	Shallow	Predator/Scavenger	21.6	UA 13329	Chatterton 2006	=0,073683	Emsian	Pygidium
Phacopida	Acastidae	Kayserops	Kayserops tamnrherta	66	Large eyes	Shallow	Predator/Scavenger	21.9	UA 13356	Chatterton 2006	=0,067521	Emsian	Pygidium
Phacopida	Acastidae	Metacanthina	Metacanthina matutina	67	Large eyes	Shallow	Predator/Scavenger	2.6	IGR 11953	Morzadec 1997	=0,006952	Lochkovian	Pygidium
Phacopida	Acastidae	Metacanthina	Metacanthina matutina	68	Large eyes	Shallow	Predator/Scavenger	2.7a	IGR 11954	Morzadec 1997	=0,014217	Lochkovian	Pygidium
Phacopida	Acastidae	Metacanthina	Metacanthina issoumouren sis	69	Large eyes	Shallow	Predator/Scavenger	3.2a	CPC	Morzadec 2001	=0,027831	Pragian	Pygidium
Phacopida	Acastidae	Metacanthina	Metacanthina issoumouren sis	70	Large eyes	Shallow	Predator/Scavenger	3.3b	CPC	Morzadec 2001	=0,027831	Pragian	Pygidium

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Phacopida	Acastidae	Metacanthina	Metacanthina maderensis	71	Large eyes	Shallow	Predator/Scavenger	3.4c	CPC	Morzadec 2001	=0,020987	Pragian	Pygidium
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	72	Large eyes	Inner shelf	Predator/Scavenger	14.3	CPC	Morzadec 2001	=0,021012	Eifelian	Pygidium
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	73	Large eyes	Inner shelf	Predator/Scavenger	14.4	CPC	Morzadec 2001	=0,010616	Eifelian	Pygidium
Phacopida	Acastidae	Mrakibina	Mrakibina cattoi	74	Large eyes	Inner shelf	Predator/Scavenger	14.7	CPC	Morzadec 2001	=0,021012	Eifelian	Pygidium
Phacopida	Acastidae	Odontochile	Odontochile magrebianum	75	Large eyes	Middle shelf	Predator/Scavenger	15.9a	SMF 57066	Schraut 2000c	=0,147471	Pragian	Pygidium
Phacopida	Acastidae	Morzadecops	Morzadecops zguidensis	76	Large eyes	Inner shelf	Predator/Scavenger	4.1b	CPC	Morzadec 2001	=0,021189	Emsian	Pygidium
Phacopida	Acastidae	Morzadecops	Morzadecops zguidensis	77	Large eyes	Inner shelf	Predator/Scavenger	4.4	CPM	Morzadec 2001	=0,021189	Emsian	Pygidium
Phacopida	Acastidae	Protacanthina	Protacanthina robusticostata	78	Large eyes	Shallow	Predator/Scavenger	1.5a	IGR11921	Morzadec 1990	=0,008442	Lochkovian	Pygidium
Phacopida	Acastidae	Protacanthina	Protacanthina robusticostata	79	Large eyes	Shallow	Predator/Scavenger	2.1a	IGR 11924	Morzadec 1990	=0,008394	Lochkovian	Pygidium
Phacopida	Acastidae	Protacanthina	Protacanthina robusticostata	80	Large eyes	Shallow	Predator/Scavenger	2.4a	IGR 11926	Morzadec 1990	=0,006034	Lochkovian	Pygidium
Phacopida	Acastidae	Protacanthina	Protacanthina robusticostata	81	Large eyes	Shallow	Predator/Scavenger		IGR11921	Morzadec 1997	=0,008574	Lochkovian	Pygidium
								Doubleton					
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus minimus	82	Large eyes	Shallow	Predator/Scavenger	1.7a	CPM	Morzadec 2001	=0,006089	Pragian	Pygidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus minimus	83	Large eyes	Shallow	Predator/Scavenger	1.10	CPM	Morzadec 2001	=0,006089	Pragian	Pygidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus sarirus	84	Large eyes	Shallow	Predator/Scavenger	2.2b	CPC	Morzadec 2001	=0,014029	Pragian	Pygidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus quaterspinosus	85	Large eyes	Shallow	Predator/Scavenger	2.3b	CPC	Morzadec 2001	=0,014029	Pragian	Pygidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus quaterspinosus	86	Large eyes	Shallow	Predator/Scavenger	2.4a	CPM	Morzadec 2001	=0,003521	Pragian	Pygidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus sp 1	87	Large eyes	Shallow	Predator/Scavenger	2.5	CPM	Morzadec 2001	=0,008372	Emsian	Pygidium
Phacopida	Acastidae	Pseudocryphaeus	Pseudocryphaeus quaterspinosus	88	Large eyes	Shallow	Predator/Scavenger	2.6	CPM	Morzadec 2001	=0,002643	Pragian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge termierorum	89	Large eyes	Middle shelf	Predator/Scavenger	2.7a	IGR 10289	Morzadec 1988	=0,021298	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge termierorum	90	Large eyes	Middle shelf	Predator/Scavenger	13.1c	CPC	Morzadec 2001	=0,021066	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	91	Large eyes	Middle shelf	Predator/Scavenger	13.5a	CPC	Morzadec 2001	=0,042507	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge elegans	92	Large eyes	Middle shelf	Predator/Scavenger	15.1	SMF 53622	Schraut 2000c	=0,128705	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge elegans	93	Large eyes	Middle shelf	Predator/Scavenger	22.5	UA 13370	Chatterton 2006	=0,188533	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	94	Large eyes	Middle shelf	Predator/Scavenger	22.6	UA 13369	Chatterton 2006	=0,177508	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge praestans	95	Large eyes	Middle shelf	Predator/Scavenger	23.6	UA 13372	Chatterton 2006	=0,115084	Emsian	Pygidium
Phacopida	Acastidae	Psychopyge	Psychopyge hammerorum	96	Large eyes	Middle shelf	Predator/Scavenger	25.6	UA 13375	Chatterton 2006	=0,125687	Emsian	Pygidium
Phacopida	Acastidae	Quadrops	Quadrops flexuosa	97	Large eyes	Inner shelf	Predator/Scavenger	11.6b	CPC	Morzadec 2001	=0,042279	Emsian	Pygidium
Phacopida	Acastidae	Saharops	Saharops bensaidi	98	Large eyes	Shallow	Predator/Scavenger	14.1b	No name	Morzadec 2001	=0,042580	Emsian	Pygidium
Phacopida	Acastidae	Saharops	Saharops bensaidi	99	Large eyes	Shallow	Predator/Scavenger	14.2a	No name	Morzadec 2001	=0,042580	Emsian	Pygidium

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Phacopida	Acastidae	Coltraneia	Coltraneia saourensis	100	Large eyes	Middle shelf	Predator/Scavenger	2.1a	IGR 11948	Morzadec 1997	=0,010461	Emsian	Pygidium
Phacopida	Acastidae	Coltraneia	Coltraneia saourensis	101	Large eyes	Middle shelf	Predator/Scavenger	2.3a	IGR11950	Morzadec 1997	=0,010554	Emsian	Pygidium
Phacopida	Acastidae	Coltraneia	Coltraneia saourensis	102	Large eyes	Middle shelf	Predator/Scavenger	2.3b	IGR11950	Morzadec 1997	=0,014032	Emsian	Pygidium
Phacopida	Acastidae	Treveropyge	Treveropyge maura	103	Large eyes	Shallow	Predator/Scavenger	10.1b	CPC	Morzadec 2001	=0,042142	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	104	Large eyes	Middle shelf	Predator/Scavenger	15.1a	No name	Morzadec 2001	=0,029645	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	105	Large eyes	Middle shelf	Predator/Scavenger	15.3a	CPC	Morzadec 2001	=0,024057	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	106	Large eyes	Middle shelf	Predator/Scavenger	15.3b	CPC	Morzadec 2001	=0,024057	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	107	Large eyes	Middle shelf	Predator/Scavenger	15.4b	COW n°1.3.83	Morzadec 2001	=0,021216	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops hammii	108	Large eyes	Middle shelf	Predator/Scavenger	27.6	UA 13446	Chatterton 2006	=0,071182	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops hammii	109	Large eyes	Middle shelf	Predator/Scavenger	28.5	UA 13449	Chatterton 2006	=0,073179	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops hammii	110	Large eyes	Middle shelf	Predator/Scavenger	29.6	UA 13450	Chatterton 2006	=0,101524	Emsian	Pygidium
Phacopida	Acastidae	Walliserops	Walliserops trifurcatus	111	Large eyes	Middle shelf	Predator/Scavenger	31.5	UA 13447	Chatterton 2006	=0,125319	Emsian	Pygidium
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura ignorata	112	Large eyes	Middle shelf	Particle feeding	Alberti196	CGMTA 158	Alberti 1969	=0,017829	Eifelian	Pygidium
Proetida	Aulacopleuridae	Aulacopleura	Aulacopleura ignorata	113	Large eyes	Middle shelf	Particle feeding	Alberti196	SMF 23381	Alberti 1969	=0,020068	Eifelian	Pygidium
Proetida	Aulacopleuridae	Chamaeleosapis	Chamaeleosapis lkomalii	114	Large eyes	Middle shelf	Particle feeding	6a	UA11821	Lerosey-Aubril 2008	=0,015150	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Indet	115	Small eyes	Middle shelf	Particle feeding	46.20	CGMTA 225	Alberti 1969	=0,007879	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides walteri	116	Large eyes	Middle shelf	Particle feeding	1b	IRSNB a12875	Van Viersen 2014	=0,057033		Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides lerougei	117	Large eyes	Middle shelf	Particle feeding	11d	IRSNB a13014	Van Viersen 2016	=0,016611	Emsian	Pygidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	118	Large eyes	Middle shelf	Particle feeding	9.24	No name	Alberti 1970a	=0,004647	Ludlow-Pridoli	Pygidium
Proetida	Aulacopleuridae	Maurotarion	Maurotarion maurum	119	Large eyes	Middle shelf	Particle feeding	46.19	CGMTA 220	Alberti 1969	=0,004534	Ludlow-Pridoli	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya hamlagdadica	120	Large eyes	Middle shelf	Particle feeding	4.44	CGMTA	Alberti 1981a	=0,015257	Emsian	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya hamlagdadica	121	Large eyes	Middle shelf	Particle feeding	4.45	SMF 36271	Alberti 1981a	=0,015257	Emsian	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya hamlagdadica	122	Large eyes	Middle shelf	Particle feeding	4.46	SMF 36272	Alberti 1981a	=0,016424	Emsian	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya yolkiniana	123	Large eyes	Middle shelf	Particle feeding	6.74	CGMTA	Alberti 1983	=0,005227	Pragian	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya maura	124	Large eyes	Middle shelf	Particle feeding	9.3	CGMTA 298	Alberti 1970a	=0,004256	Emsian	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya meridiana	125	Large eyes	Middle shelf	Particle feeding	9.5	CGMTA 295	Alberti 1970a	=0,004334	Ludlow-Pridoli	Pygidium
Proetida	Aulacopleuridae	Scharya	Scharya tafilaltensis	126	Large eyes	Middle shelf	Particle feeding	9.6a	CGMTA 301	Alberti 1970a	=0,004159	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	127	Small eyes	Deep	Predator/Scavenger	8.12	UA 13337	Chatterton 2006	=0,017563	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	128	Small eyes	Deep	Predator/Scavenger	9.2	UA 13332	Chatterton 2006	=0,040075	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	129	Small eyes	Deep	Predator/Scavenger	9.12	UA 13343	Chatterton 2006	=0,026108	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides zguilmensis	130	Small eyes	Deep	Predator/Scavenger	9.13	UA 13340	Chatterton 2006	=0,061451	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	131	Small eyes	Deep	Predator/Scavenger	Alberti_19	SGMRA 10	Alberti 1966a	=0,013237	Emsian	Pygidium

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Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	132	Small eyes	Deep	Predator/Scavenger	Alberti_19	SMF 235	Alberti 1970a	=0,014553	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	133	Small eyes	Deep	Predator/Scavenger	Alberti_19	CGMTA 337	Alberti 1970a	=0,014074	Emsian	Pygidium
Phacopida	Calmoniidae	Acastoides	Acastoides hollardi	134	Small eyes	Deep	Predator/Scavenger	Alberti_19	CGMTA 338	Alberti 1970a	=0,013829	Emsian	Pygidium
Phacopida	Calymenidae	Gravicalymene	Gravicalymene hamlagdadia	135	Large eyes	Middle shelf	Predator/Scavenger	6.59	CGMTA	Alberti 1981a	=0,096483	Pragian	Pygidium
Phacopida	Calymenidae	Gravicalymene	Gravicalymene maura	136	Large eyes	Middle shelf	Predator/Scavenger	42.2	SMF 23135	Alberti 1969	=0,020592	Pragian	Pygidium
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus maurus	137	Large eyes	Middle shelf	Predator/Scavenger	5a	SMF 23016	Alberti 1966a	=0,015934	Pragian	Pygidium
Phacopida	Cheiruridae	Crotalocephalus	Crotalocephalus maurus	138	Large eyes	Middle shelf	Predator/Scavenger	38.9	SMF 23016	Alberti 1969	=0,018402	Pragian	Pygidium
Phacopida	Acastidae	Morocconites	Morocconites maurus	139	Large eyes	Inner shelf	Predator/Scavenger	Alberti_19	CGMTA 341	Alberti 1970a	=0,020970		Pygidium
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	140	Large eyes	Inner shelf	Predator/Scavenger	6.2a	SMF 53836	Schraut 2000c	=0,087822	Pragian	Pygidium
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	141	Large eyes	Inner shelf	Predator/Scavenger	6.3a	SMF 53837	Schraut 2000c	=0,100230	Pragian	Pygidium
Phacopida	Homalonotidae	Parahomalonotus	Parahomalonotus planus	142	Large eyes	Inner shelf	Predator/Scavenger	6.4a	SMF 53842	Schraut 2000c	=0,149784	Pragian	Pygidium
Phacopida	Homalonotidae	Indet		143			Predator/Scavenger	11.7a	CGMTA 364	Alberti 1970a	=0,021155	Ludlow-Pridoli	Pygidium
Phacopida	Homalonotidae	Wenddoria	Wenddoria calvus	144	Large eyes	Middle shelf	Predator/Scavenger	32.6	UA 13378	Chatterton 2006	=0,262733	Emsian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) bassei	145	Large eyes	Middle shelf	Predator/Scavenger	7.5	UA 13653	Chatterton 2010	=0,022202	Eifelian	Pygidium

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Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) bassei	146	Large eyes	Middle shelf	Predator/Scavenger	7.6	UA 16854	Chatterton 2010	=0,021012	Eifelian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	147	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MGSB79489	Corbacho Kier 2013	=0,014005	Pragian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	148	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MGSB79489	Corbacho Kier 2013	=0,007153	Pragian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	149	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MGSB79486	Corbacho Kier 2013	=0,019230	Pragian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) bassei	150	Large eyes	Middle shelf	Predator/Scavenger		Corbacho BPM1049	Corbacho Kier 2013	=0,010183	Eifelian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	151	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MMB101	Corbacho Kier 2013	=0,013440	Pragian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	152	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MMB106	Corbacho Kier 2013	=0,013190	Pragian	Pygidium
Lichida	Lichidae	Acanthopyge	Acanthopyge (Belenopyge) estevei	153	Large eyes	Middle shelf	Predator/Scavenger		Corbacho MMB108	Corbacho Kier 2013	=0,013812	Pragian	Pygidium
Lichida	Lichidae	Akantharges	Akantharges mbareki	154	Large eyes	Middle shelf	Predator/Scavenger	3.2	JC95	Corbacho Lopez- Soriano 2013	=0,044246	Eifelian	Pygidium
Lichida	Lichidae	Akantharges	Akantharges mbareki	155	Large eyes	Middle shelf	Predator/Scavenger	3.5	MGSB79879	Corbacho Lopez- Soriano 2013	=0,053188	Eifelian	Pygidium
Lichida	Lichidae	Akantharges	Akantharges mbareki	156	Large eyes	Middle shelf	Predator/Scavenger	3.6	JC96	Corbacho Lopez- Soriano 2013	=0,048541	Eifelian	Pygidium

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Lichida	Lichidae	Besseiarges	Basseiarges mellishae	157	Large eyes	Middle shelf	Predator/Scavenger	1.1	MMB104	Corbacho Lopez-Soriano 2013	=0,059520	Eifelian	Pygidium
Lichida	Lichidae	Besseiarges	Basseiarges mellishae	158	Large eyes	Middle shelf	Predator/Scavenger	1.2	MMB102	Corbacho Lopez-Soriano 2013	=0,056815	Eifelian	Pygidium
Lichida	Lichidae	Besseiarges	Basseiarges mellishae	159	Large eyes	Middle shelf	Predator/Scavenger	1.3	MMB103	Corbacho Lopez-Soriano 2013	=0,046727	Eifelian	Pygidium
Lichida	Lichidae	Besseiarges	Basseiarges mellishae	160	Large eyes	Middle shelf	Predator/Scavenger	1.4	MGSB79774	Corbacho Lopez-Soriano 2013	=0,061724	Eifelian	Pygidium
Lichida	Lichidae	Ceratarges	Ceratarges ziregensis	161	Large eyes	Inner shelf	Predator/Scavenger	1a	NHMM 2011 001	Van Viersen 2011	=0,035711	Eifelian	Pygidium
Lichida	Lichidae	Ceratarges	Ceratarges koumalii	162	Large eyes	Inner shelf	Predator/Scavenger	2d	NHMM 2011 002	Van Viersen 2011	=0,033321	Eifelian	Pygidium
Lichida	Lichidae	Ceratarges	Ceratarges aries	163	Large eyes	Inner shelf	Predator/Scavenger	3b	NHMM 2011 003	Van Viersen 2011	=0,038741	Eifelian	Pygidium
Lichida	Lichidae	Perunaspis	Perunaspis longispinus	164	Large eyes	Middle shelf	Predator/Scavenger	20.21	No name	Alberti 1970a	=0,005224	Eifelian	Pygidium
Lichida	Lichidae	Perunaspis	Perunaspis longispinus	165	Large eyes	Middle shelf	Predator/Scavenger	20.22	CGMTA 375	Alberti 1970a	=0,008187	Eifelian	Pygidium
Lichida	Odontopleuridae	Ceratocephala	Ceratocephala hoernesii	166	Large eyes	Middle shelf	Predator/Scavenger	3f	MGSB79774	Feist 2018	=0,007690	Emsian	Pygidium
Lichida	Odontopleuridae	Ceratocephala	Ceratocephala hoernesii	167	Large eyes	Middle shelf	Predator/Scavenger	19.11	CGMTA 345	Alberti 1970a	=0,017006	Emsian	Pygidium
Lichida	Odontopleuridae	Isoprusia	Isoprusia laportei	168	Large eyes	Middle shelf	Predator/Scavenger	3.q	UM-IP 810	Feist 2018	=0,007662	Emsian	Pygidium
Lichida	Odontopleuridae	Kettneraspis	Kettneraspis pigra	169	Large eyes	Deep	Predator/Scavenger	2.7	UM2-RF 169	Feist 2000	=0,007394	Eifelian	Pygidium
Lichida	Odontopleuridae	Kettneraspis	Kettneraspis pigra	170	Large eyes	Deep	Predator/Scavenger	19.9	CGMTA 369	Alberti 1970a	=0,012961	Eifelian	Pygidium
Lichida	Odontopleuridae	Kettneraspis	Kettneraspis pigra	171	Large eyes	Deep	Predator/Scavenger	41.5	SMF 23451	Alberti 1969	=0,021288	Eifelian	Pygidium
Lichida	Odontopleuridae	Koneprusia	Koneprusia subtermata	172	Large eyes	Middle shelf	Predator/Scavenger	19.14	CGMTA 348	Alberti 1970a	=0,007701	Emsian	Pygidium
Lichida	Odontopleuridae	Koneprusia	Koneprusia maura	173	Large eyes	Middle shelf	Predator/Scavenger	19.15a	CGMTA 349	Alberti 1970a	=0,007999	Pragian	Pygidium
Lichida	Odontopleuridae	Koneprusia	Koneprusia maura	174	Large eyes	Middle shelf	Predator/Scavenger	19.15b	CGMTA 349	Alberti 1970a	=0,007999	Pragian	Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi issoumourensis	175	Large eyes	Middle shelf	Predator/Scavenger	19.8	CGMTA 343	Alberti 1970a	=0,006330	Emsian	Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	176	Large eyes	Middle shelf	Predator/Scavenger	40.6	CGMTA 166	Alberti 1969	=0,012072	Pragian	Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	177	Large eyes	Middle shelf	Predator/Scavenger	40.8	SMF 23412	Alberti 1969	=0,014277	Pragian	Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi maura	178	Large eyes	Middle shelf	Predator/Scavenger	40.11	SMF 23406	Alberti 1969	=0,011581		Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi haddanei	179	Large eyes	Middle shelf	Predator/Scavenger	50.10	UA 13417	Chatterton 2006	=0,037586	Eifelian	Pygidium
Lichida	Odontopleuridae	Leonaspi	Leonaspi hastata	180	Large eyes	Middle shelf	Predator/Scavenger	b.31	CGMTA 166	Alberti 1967b	=0,014854	Pragian	Pygidium
Phacopida	Phacopidae	Acuticryphops	Acuticryphops acuticeps	181	Small eyes	Middle shelf	Predator/Scavenger	3f	UM2-RF 222	Feist 2002	=0,007416	Frasnian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops chattertoni	182	Large eyes	Inner shelf	Predator/Scavenger	4e	Di/UO/002	Khalidi 2016	=0,040649	Emsian	Pygidium
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	183	Large eyes	Middle shelf	Predator/Scavenger	4p	Di/UO/004	Khalidi 2016	=0,096136	Emsian	Pygidium
Phacopida	Phacopidae	Adrisiops	Adrisiops boudjemaai	184	Large eyes	Middle shelf	Predator/Scavenger	5r	Di/UO/005	Khalidi 2016	=0,116248	Emsian	Pygidium
Phacopida	Phacopidae	Adrisiops	Adrisiops weugi	185	Large eyes	Middle shelf	Predator/Scavenger	7d	NHMM 2016 007	Van Viersen 2017	=0,006711	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	186	Large eyes	Middle shelf	Predator/Scavenger	4.1	UA 13306	Chatterton 2006	=0,063851	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	187	Large eyes	Middle shelf	Predator/Scavenger	4.3	UA 13306	Chatterton 2006	=0,063851	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	188	Large eyes	Middle shelf	Predator/Scavenger	4.6	UA 13308	Chatterton 2006	=0,058471	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	189	Large eyes	Middle shelf	Predator/Scavenger	4.7	UA 13309	Chatterton 2006	=0,098781	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	190	Large eyes	Middle shelf	Predator/Scavenger	4.9	UA 13306	Chatterton 2006	=0,063851	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	191	Large eyes	Middle shelf	Predator/Scavenger	5.5	UA 13307	Chatterton 2006	=0,059370	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	192	Large eyes	Middle shelf	Predator/Scavenger	5.7	UA 13308	Chatterton 2006	=0,054830	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	193	Large eyes	Middle shelf	Predator/Scavenger	5.8	UA 13314	Chatterton 2006	=0,065539	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	194	Large eyes	Middle shelf	Predator/Scavenger	5.9	UA 13312	Chatterton 2006	=0,050383	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops speculator speculator	195	Large eyes	Middle shelf	Predator/Scavenger	6.c	Di/UO/013	Khalidi 2016	=0,057467	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops menchikoffi	196	Large eyes	Middle shelf	Predator/Scavenger	6.g	Di/UO/026	Khalidi 2016	=0,044246	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	Austerops speculator punctatus	197	Large eyes	Middle shelf	Predator/Scavenger	7.4	UA 13538	McKellar 2009	=0,010215	Eifelian	Pygidium

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Phacopida	Phacopidae	Austerops	<i>Austerops speculator punctatus</i>	198	Large eyes	Middle shelf	Predator/Scavenger	7.6	UA 13535	McKellar 2009	=0,012682	Eifelien	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	199	Large eyes	Middle shelf	Predator/Scavenger	7.10	UA 13328	Chatterton 2006	=0,055801	Eifelien	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops menchikoffi</i>	200	Large eyes	Middle shelf	Predator/Scavenger	7.12	UA 13327	Chatterton 2006	=0,066837	Eifelien	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops legrandi</i>	201	Large eyes	Middle shelf	Predator/Scavenger	7g	Di/UO/009	Khaldi 2016	=0,048068	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops legrandi</i>	202	Large eyes	Middle shelf	Predator/Scavenger	7i	Di/UO/025	Khaldi 2016	=0,046288	Emsian	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops kermiti</i>	203	Large eyes	Middle shelf	Predator/Scavenger	8.8	UA 13548	McKellar 2009	=0,008684	Eifelien	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops salamandar</i>	204	Large eyes	Middle shelf	Predator/Scavenger	10.2	UA 13549	McKellar 2009	=0,010177	Eifelien	Pygidium
Phacopida	Phacopidae	Austerops	<i>Austerops speculator speculator</i>	205	Large eyes	Middle shelf	Predator/Scavenger	Alberti197	ISCR	Alberti 1970a	=0,015217	Emsian	Pygidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops sp C</i>	206	Large eyes	Middle shelf	Predator/Scavenger	5m	Di/UO/015	Khaldi 2016	=0,029938	Emsian	Pygidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops stelcki</i>	207	Large eyes	Middle shelf	Predator/Scavenger	11.9	UA 13469	McKellar 2009	=0,013171	Emsian	Pygidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops slimanensis</i>	208	Large eyes	Middle shelf	Predator/Scavenger	16.12a	SMF 23519	Alberti 1970a	=0,017513	Lochkovian	Pygidium
Phacopida	Phacopidae	Boeckops	<i>Boeckops slimanensis</i>	209	Large eyes	Middle shelf	Predator/Scavenger	16.13	CGMTA 325	Alberti 1970a	=0,018614	Lochkovian	Pygidium
Phacopida	Phacopidae	Chlupacops	<i>Chlupacops laticeps</i>	210	Large eyes	Deep	Predator/Scavenger	3f	UM-IP 713	Feist 2016	=0,049984	Frasnian	Pygidium
Phacopida	Phacopidae	Chlupacops	<i>Chlupacops cryphoides</i>	211	Large eyes	Deep	Predator/Scavenger	3i	UM-IP 714	Feist 2016	=0,051265	Frasnian	Pygidium
Phacopida	Phacopidae	Denckmanites	<i>Denckmannites miser</i>	212	Small eyes	Deep	Predator/Scavenger	16.2	CGMTA 367	Alberti 1970a	=0,009884	Lochkovian	Pygidium
Phacopida	Phacopidae	Denckmanites	<i>Denckmannites miser</i>	213	Small eyes	Deep	Predator/Scavenger	16.3	No name	Alberti 1970a	=0,010933	Lochkovian	Pygidium
Phacopida	Phacopidae	Dianops	<i>Dianops algeriensis</i>	214	Blind	Deep	Predator/Scavenger	5i	UM-IP 726	Feist 2016	=0,042544	Famennian	Pygidium
Phacopida	Phacopidae	Dianops	Indet	215	Blind	Deep	Predator/Scavenger	6i	MUA/1094/004	Crônier 2013	=0,039995	Famennian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops megalomaniacus</i>	216	Large eyes	Shallow	Predator/Scavenger	1.1b	SMF 49341	Struve 1995	=0,058707	Givetian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops megalomaniacus</i>	217	Large eyes	Shallow	Predator/Scavenger	1.2b	SMF 49357	Struve 1995	=0,065033	Givetian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops megalomaniacus</i>	218	Large eyes	Shallow	Predator/Scavenger	2.4b	SMF 49354	Struve 1995	=0,057167	Givetian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops megalomaniacus</i>	219	Large eyes	Shallow	Predator/Scavenger	2.5	MB.T 1948	Struve 1995	=0,057827	Givetian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops armatus</i>	220	Large eyes	Shallow	Predator/Scavenger	5.12c	No name	Struve 1995	=0,089152	Givetian	Pygidium
Phacopida	Phacopidae	Drotops	<i>Drotops armatus</i>	221	Large eyes	Shallow	Predator/Scavenger	6.15a	No name	Struve 1995	=0,065485	Givetian	Pygidium
Phacopida	Phacopidae	Enigmatyge	<i>Enigmatyge marhoumensis</i>	222	Blind	Deep	Predator/Scavenger	5a	UM-IP 727	Feist 2016	=0,039186	Famennian	Pygidium
Phacopida	Phacopidae	Enigmatyge	<i>Enigmatyge marhoumensis</i>	223	Blind	Deep	Predator/Scavenger	5c	UM-IP 727	Feist 2016	=0,058798	Famennian	Pygidium
Phacopida	Phacopidae	Eocryphops	<i>Eocryphops termieri</i>	224	Small eyes	Middle shelf	Predator/Scavenger	Richter_2.	Nr 40	Richter 1943	=0,023208	Emsian	Pygidium
Phacopida	Phacopidae	Eophacops	<i>Eophacops bulliceps</i>	225	Large eyes	Middle shelf	Predator/Scavenger	11.6	CGMTA 374	Alberti 1970a	=0,010952	Ludlow-Pridoli	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	226	Large eyes	Middle shelf	Predator/Scavenger	8.24c	SMF 49368	Struve 1995	=0,058661	Givetian	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	227	Large eyes	Middle shelf	Predator/Scavenger	8.23h	SMF 49402	Struve 1995	=0,059221	Givetian	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	228	Large eyes	Middle shelf	Predator/Scavenger	8.25	SMF 49372	Struve 1995	=0,058095	Givetian	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	229	Large eyes	Middle shelf	Predator/Scavenger	9.26	SMF 49611A	Struve 1995	=0,058976	Givetian	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	230	Large eyes	Middle shelf	Predator/Scavenger	9.27	SMF 49374	Struve 1995	=0,056245	Givetian	Pygidium
Phacopida	Phacopidae	Hypsipariops	<i>Hypsipariops vagabundus</i>	231	Large eyes	Middle shelf	Predator/Scavenger	9.30b	SMF 49373	Struve 1995	=0,059301	Givetian	Pygidium

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Phacopida	Phacopidae	Hypsipariops	Hypsipariops africanus	232	Large eyes	Middle shelf	Predator/Scavenger	48.2	In 56877	Burton 1974	=0,211154	Eifelien	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	233	Large eyes	Inner shelf	Predator/Scavenger	1.5	UA 13295	Chatterton 2006	=0,057838	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	234	Large eyes	Inner shelf	Predator/Scavenger	1.8	UA 13294	Chatterton 2006	=0,075606	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	235	Large eyes	Inner shelf	Predator/Scavenger	1.10	UA 13298	Chatterton 2006	=0,077125	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	236	Large eyes	Inner shelf	Predator/Scavenger	2.10	UA 13302	Chatterton 2006	=0,136848	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	237	Large eyes	Inner shelf	Predator/Scavenger	2.12	UA 13302	Chatterton 2006	=0,097288	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops lebesus	238	Large eyes	Inner shelf	Predator/Scavenger	3.4	UA 13304	Chatterton 2006	=0,047408	Eifelien	Pygidium
Phacopida	Phacopidae	Morocops	Morocops torkozensis	239	Large eyes	Inner shelf	Predator/Scavenger	3.5	SMF 53624	Schraut 2000c	=0,076035	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops torkozensis	240	Large eyes	Inner shelf	Predator/Scavenger	3.6a	SMF 53719	Schraut 2000c	=0,092503	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	241	Large eyes	Inner shelf	Predator/Scavenger	3k	Di/UO/034	Khalidi 2016	=0,098020	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops chattertoni	242	Large eyes	Inner shelf	Predator/Scavenger	4c	Di/UO/001	Khalidi 2016	=0,051544	Emsian	Pygidium
Phacopida	Phacopidae	Adrisiops	Adrisiops fabrei	243	Large eyes	Middle shelf	Predator/Scavenger	4j	Di/UO/016	Khalidi 2016	=0,040649	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops spinifer	244	Large eyes	Inner shelf	Predator/Scavenger	6d	NHMM 2016 004	Van Viersen 2017	=0,042373	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops ovatus	245	Large eyes	Inner shelf	Predator/Scavenger	13.3	UA 6909	McKellar 2009	=0,029862	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops ovatus	246	Large eyes	Inner shelf	Predator/Scavenger	13.6	UA 6913	McKellar 2009	=0,012969	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops forteyi	247	Large eyes	Inner shelf	Predator/Scavenger	15.6	UA 6921	McKellar 2009	=0,020262	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops granulops	248	Large eyes	Inner shelf	Predator/Scavenger		Cronier_2 PIMUZ 35146	Crônier Oudot 2018	=0,013121	Emsian	Pygidium
Phacopida	Phacopidae	Morocops	Morocops davidbrutoni	249	Large eyes	Inner shelf	Predator/Scavenger		Cronier_2 PIMUZ 35159	Crônier Oudot 2018	=0,008576	Emsian	Pygidium
Phacopida	Phacopidae	Phacops sl	Phacops tafiuppernsis	250	Large eyes	Deep	Predator/Scavenger	2f	UM2/CCp003	Crônier 2001	=0,013294	Famennian	Pygidium
Phacopida	Phacopidae	Phacops sl	Phacops tafiuppernsis	251	Large eyes	Deep	Predator/Scavenger	3g	UM2/CCp010	Crônier 2001	=0,011045	Famennian	Pygidium
Phacopida	Phacopidae	Phacops sl	Phacops tafiuppernsis	252	Large eyes	Deep	Predator/Scavenger	3h	UM2/CCp009	Crônier 2001	=0,011568	Famennian	Pygidium
Phacopida	Phacopidae	Phacops	Phacops sensu lato sp B	253	Large eyes	Middle shelf	Predator/Scavenger	5g	Di/UO/033	Khalidi 2016	=0,104144	Emsian	Pygidium
Phacopida	Phacopidae	Phacops sl	Phacops zeregensis	254	Large eyes	Deep	Predator/Scavenger	5u	MUA/1094/002	Crônier 2013	=0,032255	Famennian	Pygidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	255	Large eyes	Middle shelf	Predator/Scavenger	6f	MU-G-Sr.T r.S4/Ph064	Crônier Abbache 2018	=0,047613	Eifelien	Pygidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	256	Large eyes	Middle shelf	Predator/Scavenger	6j	MU-G-Sr.T r.S7/Ph001	Crônier Abbache 2018	=0,062486	Eifelien	Pygidium
Phacopida	Phacopidae	Phacops sl	Indet	257	Large eyes	Deep	Predator/Scavenger	6k	MUA/1094/004	Crônier 2013	=0,038755	Famennian	Pygidium
Phacopida	Phacopidae	Phacops sl	Indet	258	Large eyes	Deep	Predator/Scavenger	6m	MUA/1094/005	Crônier 2013	=0,050495	Famennian	Pygidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensis	259	Large eyes	Middle shelf	Predator/Scavenger	6n	MU-G-Sr.T r.S7/Ph036	Crônier Abbache 2018	=0,099944	Eifelien	Pygidium
Phacopida	Phacopidae	Phacops	Phacops ouarouroutensis ouarouroutensoides	260	Large eyes	Middle shelf	Predator/Scavenger	7u	MU-G-Sr.T r.A2/Ph163	Crônier Abbache 2018	=0,096724	Eifelien	Pygidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	261	Large eyes	Middle shelf	Predator/Scavenger	46.23	CGMTA 223	Alberti 1969	=0,020395	Pragian	Pygidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis benziregensis	262	Large eyes	Middle shelf	Predator/Scavenger	8.88c	SH	Alberti 1983	=0,009214	Pragian	Pygidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis ezzhiligensis	263	Large eyes	Middle shelf	Predator/Scavenger	16.16	CGMTA 223	Alberti 1970a	=0,034247	Pragian	Pygidium
Phacopida	Phacopidae	Prokops	Prokops benziregensis benziregensis	264	Large eyes	Middle shelf	Predator/Scavenger	4.42	SH	Alberti 1983	=0,010473	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops bronni	265	Large eyes	Inner shelf	Predator/Scavenger	1.8	UA 6844	McKellar 2009	=0,010059	Pragian	Pygidium

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Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	266	Large eyes	Inner shelf	Predator/Scavenger	2.10	UA 6861	McKellar 2009	=0,019746	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes hamlagdadianus	267	Large eyes	Inner shelf	Predator/Scavenger	3.8	UA 6853	McKellar 2009	=0,014556	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops pembertoni	268	Large eyes	Inner shelf	Predator/Scavenger	4.6	UA 6875	McKellar 2009	=0,012229	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops pembertoni	269	Large eyes	Inner shelf	Predator/Scavenger	4.9	UA 6871	McKellar 2009	=0,012229	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops intermedius chlupaci	270	Large eyes	Inner shelf	Predator/Scavenger	4.11a	SMF 57095	Schraut 2000c	=0,083464	Pragian	Pygidium
Phacopida	Phacopidae	Struveaspis	Struveaspis bignoni	271	Large eyes	Middle shelf	Predator/Scavenger	1.2	80534	Corbacho 2014	=0,025707	Eifelian	Pygidium
Phacopida	Phacopidae	Struveaspis	Struveaspis bignoni	272	Large eyes	Middle shelf	Predator/Scavenger	1.4	JC 104	Corbacho 2014	=0,037732	Eifelian	Pygidium
Phacopida	Phacopidae	Struveaspis	Struveaspis micromma	273	Large eyes	Middle shelf	Predator/Scavenger	1.7	JC 105	Corbacho 2014	=0,039365	Eifelian	Pygidium
Phacopida	Phacopidae	Struveaspis	Struveaspis micromma	274	Large eyes	Middle shelf	Predator/Scavenger	14.7	CGMTA 366	Alberti 1970a	=0,009784	Eifelian	Pygidium
Phacopida	Phacopidae	Trifoliops	Trifoliops trifolius	275	Blind	Deep	Predator/Scavenger	5f	Di/UO/033	Khaldi 2016	=0,102020	Famennian	Pygidium
Phacopida	Phacopidae	Trifoliops	Trifoliops croniera	276	Blind	Deep	Predator/Scavenger	5o	Di/UO/007	Khaldi 2016	=0,135086	Famennian	Pygidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus lelievrei	277	Blind	Deep	Predator/Scavenger	1.13	UM2-CC155	Crônier 1997	=0,010599	Famennian	Pygidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus lelievrei	278	Blind	Deep	Predator/Scavenger	1.15a	UM2-CC132	Crônier 1997	=0,003176	Famennian	Pygidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus caecus	279	Blind	Deep	Predator/Scavenger	3b	MUA/1094/007	Crônier 2013	=0,037874	Famennian	Pygidium
Phacopida	Phacopidae	Trimerocephalus	Trimerocephalus mahboubii	280	Blind	Deep	Predator/Scavenger	4f	UM-IP 718	Feist 2016	=0,036358	Famennian	Pygidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	281	Large eyes	Middle shelf	Predator/Scavenger	5o	MU-G-Sr.Tr.A4/Ph136	Crônier Abbache 2018	=0,015544	Eifelian	Pygidium
Phacopida	Phacopidae	Chotecops	Chotecops hoseri	282	Large eyes	Middle shelf	Predator/Scavenger	5u	MU-G-Sr.Tr.A4/Ph109	Crônier Abbache 2018	=0,093704	Eifelian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus sp A	283	Large eyes	Inner shelf	Predator/Scavenger	1.4	SMF 36233	Alberti 1981a	=0,059873	Pragian	Pygidium
Proetida	Proetidae	Buchiproetus	Buchiproetus mendax	284	Large eyes	Middle shelf	Predator/Scavenger	11.21	CGMTA 190	Alberti 1969	=0,013816	Pragian	Pygidium
Proetida	Proetidae	Coniproetus	Coniproetus affinis	285	Large eyes	Inner shelf	Predator/Scavenger	3.10	CGMTA 212a	Alberti 1970a	=0,013225	Lochkovian	Pygidium
Proetida	Proetidae	Cornuproetus	Cornuproetus oudrissensis	286	Large eyes	Middle shelf	Predator/Scavenger	1.12	UM2-RF 160	Feist 2000	=0,008824	Givetian	Pygidium
Proetida	Proetidae	Cornuproetus	Cornuproetus pusulosus	287	Large eyes	Middle shelf	Predator/Scavenger	3x	UM-IP 820a	Feist 2018	=0,007896	Emsian	Pygidium
Proetida	Proetidae	Cornuproetus	Cornuproetus cornutus marrakechensis	288	Large eyes	Middle shelf	Predator/Scavenger	4.4	SMF 23095	Alberti 1970a	=0,010529	Eifelian	Pygidium
Proetida	Proetidae	Cornuproetus	Indet	289	Large eyes	Middle shelf	Predator/Scavenger	46.11	CGMTA 216	Alberti 1969	=0,009167	Emsian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	290	Large eyes	Middle shelf	Predator/Scavenger	2.14	UMC-IP 469	Lerosey-Aubril 2006	=0,002857	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	291	Large eyes	Middle shelf	Predator/Scavenger	2.15	UMC-IP 470	Lerosey-Aubril 2006	=0,003267	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	292	Large eyes	Middle shelf	Predator/Scavenger	2.16	UMC-IP 471	Lerosey-Aubril 2006	=0,003649	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	293	Large eyes	Middle shelf	Predator/Scavenger	2.17	UMC-IP 472	Lerosey-Aubril 2006	=0,003906	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	294	Large eyes	Middle shelf	Predator/Scavenger	2.18	UMC-IP 473	Lerosey-Aubril 2006	=0,004504	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	295	Large eyes	Middle shelf	Predator/Scavenger	2.19	UMC-IP 474	Lerosey-Aubril 2006	=0,005680	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	296	Large eyes	Middle shelf	Predator/Scavenger	2.20	UMC-IP 475	Lerosey-Aubril 2006	=0,006577	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	297	Large eyes	Middle shelf	Predator/Scavenger	2.22	UMC-IP 477	Lerosey-Aubril 2006	=0,005554	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole rectifrons	298	Large eyes	Middle shelf	Predator/Scavenger	2.23	UMC-IP 478	Lerosey-Aubril 2006	=0,002673	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymbole	Cyrtosymbole sp A	299	Large eyes	Middle shelf	Predator/Scavenger	2.31	UMC-IP 486	Lerosey-Aubril 2006	=0,004545	Famennian	Pygidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	300	Large eyes	Middle shelf	Predator/Scavenger	5.14	CGMTA 266	Alberti 1970a	=0,005413	Eifelian	Pygidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	301	Large eyes	Middle shelf	Predator/Scavenger	5.15	CGMTA 259	Alberti 1970a	=0,005780	Eifelian	Pygidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	302	Large eyes	Middle shelf	Predator/Scavenger	5.16	SMF 23483a	Alberti 1970a	=0,006392	Eifelian	Pygidium
Proetida	Proetidae	Cyrtosymboloides	Cyrtosymboloides samum	303	Large eyes	Middle shelf	Predator/Scavenger	5.17	SMF 23484a	Alberti 1970a	=0,006530	Eifelian	Pygidium
Proetida	Proetidae	Dalejeproetus	Dalejeproetus owensi	304	Large eyes	Inner shelf	Predator/Scavenger	4.10	NHM It 28949	Johnson 2012	=0,036642	Pragian	Pygidium
Proetida	Proetidae	Dalejeproetus	Dalejeproetus owensi	305	Large eyes	Inner shelf	Predator/Scavenger	4.14	NHM It 28950	Johnson 2012	=0,045975	Pragian	Pygidium

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Proetida	Proetidae	Dalejeproetus	Dalejeproetus owensi	306	Large eyes	Inner shelf	Predator/Scavenger	5.3	NHM It 28951	Johnson 2012	=0,036559	Pragian	Pygidium
Proetida	Proetidae	Dechenella	Dechenella ziatensis	307	Large eyes	Inner shelf	Predator/Scavenger	2.2a	IMGP G6 Orig K 1122-37	Feist 2000	=0,006290	Givetian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	308	Large eyes	Deep	Predator/Scavenger	20.11	SMF 23124	Alberti 1969	=0,012361	Emsian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	309	Large eyes	Deep	Predator/Scavenger	20.12	CGMT-TD 32	Alberti 1969	=0,014380	Emsian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	310	Large eyes	Deep	Predator/Scavenger	35.7	UA 13383	Chatterton 2006	=0,076087	Emsian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	311	Large eyes	Deep	Predator/Scavenger	36.3	UA 13384	Chatterton 2006	=0,084187	Emsian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	312	Large eyes	Deep	Predator/Scavenger	36.7	UA 13384	Chatterton 2006	=0,043840	Emsian	Pygidium
Proetida	Proetidae	Diademaproetus	Diademaproetus praecursor	313	Large eyes	Deep	Predator/Scavenger	37.9	UA 13444	Chatterton 2006	=0,086669	Emsian	Pygidium
Proetida	Proetidae	DREVERMAN NIINAE	314	Blind	Deep	Predator/Scavenger	28.20	SMF 23321	Alberti 1969	=0,004364	Emsian	Pygidium	
Proetida	Proetidae	DREVERMAN NIINAE	315	Blind	Deep	Predator/Scavenger	28.21	SMF 23322	Alberti 1969	=0,003273	Emsian	Pygidium	
Proetida	Proetidae	Eodrevermannia	Eodrevermannia rara africana	316	Blind	Middle shelf	Predator/Scavenger	8.10	CGMTA 292	Alberti 1970a	=0,004457	Emsian	Pygidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	317	Large eyes	Middle shelf	Predator/Scavenger	3	SMF 23012	Alberti 1966a	=0,004083	Pragian	Pygidium
Proetida	Proetidae	Erbenaspis	Erbenaspis erbeni	318	Large eyes	Middle shelf	Predator/Scavenger	8.14	CGMTA 293	Alberti 1970a	=0,004199	Lochkovian	Pygidium
Proetida	Proetidae	Erbenaspis	Erbenaspis erbeni	319	Large eyes	Middle shelf	Predator/Scavenger	8.15	SMF 23586	Alberti 1970a	=0,004348	Lochkovian	Pygidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	320	Large eyes	Middle shelf	Predator/Scavenger	8.16	CGMTA 357	Alberti 1970a	=0,004795	Pragian	Pygidium
Proetida	Proetidae	Erbenaspis	Erbenaspis arabica	321	Large eyes	Middle shelf	Predator/Scavenger	8.16	CGMTA 7	Alberti 1969	=0,004884	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	322	Large eyes	Middle shelf	Predator/Scavenger	1.2	No name	Alberti 1966c	=0,010381	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus subobscurus	323	Large eyes	Middle shelf	Predator/Scavenger	3.26	CGMTA	Alberti 1981a	=0,013224	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	324	Large eyes	Middle shelf	Predator/Scavenger	7.4	SMF 23495	Alberti 1970a	=0,018375	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	325	Large eyes	Middle shelf	Predator/Scavenger	7.9	CGMTA 284	Alberti 1970a	=0,018375	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	326	Large eyes	Middle shelf	Predator/Scavenger	7.10	SMF 23496	Alberti 1970a	=0,013076	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	327	Large eyes	Middle shelf	Predator/Scavenger	16.6	No name	Alberti 1964	=0,013338	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus meridianomaurus	328	Large eyes	Middle shelf	Predator/Scavenger	22.13a	CGMT-AT 204/1	Alberti 1969	=0,008136	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus meridianomaurus	329	Large eyes	Middle shelf	Predator/Scavenger	22.13b	CGMT-AT 204/1	Alberti 1969	=0,008136	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	330	Large eyes	Middle shelf	Predator/Scavenger	24.1	SMF 23258	Alberti 1969	=0,017552	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	331	Large eyes	Middle shelf	Predator/Scavenger	24.2	SMF 23259	Alberti 1969	=0,017189	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	332	Large eyes	Middle shelf	Predator/Scavenger	24.3	CGMTA 103	Alberti 1969	=0,011404	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	333	Large eyes	Middle shelf	Predator/Scavenger	24.4	SMF 23260	Alberti 1969	=0,017147	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	334	Large eyes	Middle shelf	Predator/Scavenger	24.5a	SMF 23261	Alberti 1969	=0,014640	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus tafilaltanus	335	Large eyes	Middle shelf	Predator/Scavenger	24.6	CGMTA 104	Alberti 1969	=0,012156	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti	336	Large eyes	Middle shelf	Predator/Scavenger	24.7	CGMTA 114	Alberti 1969	=0,010162	Pragian	Pygidium

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Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti helmuti	337	Large eyes	Middle shelf	Predator/Scavenger	24.8	SMF 23287	Alberti 1969	=0,011404	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti junior	338	Large eyes	Middle shelf	Predator/Scavenger	24.9	CGMTA 115	Alberti 1969	=0,011539	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti junior	339	Large eyes	Middle shelf	Predator/Scavenger	24.10	SMF 23289	Alberti 1969	=0,011404	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti junior	340	Large eyes	Middle shelf	Predator/Scavenger	24.11	SMF 23288	Alberti 1969	=0,010162	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	341	Large eyes	Middle shelf	Predator/Scavenger	24.12a	SMF 23282	Alberti 1969	=0,010744	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus notabilis	342	Large eyes	Middle shelf	Predator/Scavenger	24.13	SMF 23283	Alberti 1969	=0,017526	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	343	Large eyes	Middle shelf	Predator/Scavenger	24.16	SMF 23276	Alberti 1969	=0,017526	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	344	Large eyes	Middle shelf	Predator/Scavenger	24.17	SMF 23275	Alberti 1969	=0,007076	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	345	Large eyes	Middle shelf	Predator/Scavenger	24.18	CGMTA 111	Alberti 1969	=0,015109	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	346	Large eyes	Middle shelf	Predator/Scavenger	24.19	SMF 23278	Alberti 1969	=0,007260	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	347	Large eyes	Middle shelf	Predator/Scavenger	24.20	SMF 23277	Alberti 1969	=0,005916	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus maurulus	348	Large eyes	Middle shelf	Predator/Scavenger	25.1	CGMTA 194	Alberti 1969	=0,008243	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus papilio exornatus	349	Large eyes	Middle shelf	Predator/Scavenger	25.4	SMF 23301	Alberti 1969	=0,015090	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus papilio exornatus	350	Large eyes	Middle shelf	Predator/Scavenger	25.5	CGMTA 122	Alberti 1969	=0,013004	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus papilio exornatus	351	Large eyes	Middle shelf	Predator/Scavenger	25.6	CGMTA 73	Alberti 1969	=0,015956	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	352	Large eyes	Middle shelf	Predator/Scavenger	25.8	CGMTA 105	Alberti 1969	=0,013028	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	353	Large eyes	Middle shelf	Predator/Scavenger	25.9	SMF 23267	Alberti 1969	=0,011544	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	354	Large eyes	Middle shelf	Predator/Scavenger	25.10	CGMTA 107	Alberti 1969	=0,013455	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	355	Large eyes	Middle shelf	Predator/Scavenger	25.11	SMF 23268	Alberti 1969	=0,012140	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus dufresnoyi australis	356	Large eyes	Middle shelf	Predator/Scavenger	25.12	SMF 23269	Alberti 1969	=0,013455	Emsian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus cacuminatus	357	Large eyes	Middle shelf	Predator/Scavenger	46.17	CGMTA	Alberti 1969	=0,019125	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus berberus	358	Large eyes	Middle shelf	Predator/Scavenger	a.14	SMF 23298	Alberti 1967a	=0,013211	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus helmuti helmuti	359	Large eyes	Middle shelf	Predator/Scavenger	b.15	CGMTA 114	Alberti 1967b	=0,012962	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus meridianom aurus	360	Large eyes	Middle shelf	Predator/Scavenger	b.17	CGMTA 182	Alberti 1967b	=0,008266	Pragian	Pygidium
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus meridianom aurus	361	Large eyes	Middle shelf	Predator/Scavenger	CGMTA 182	Alberti 1969	=0,006687	Pragian	Pygidium	
Proetida	Tropidocoryphidae	Eremiproetus	Eremiproetus berberus	362	Large eyes	Middle shelf	Predator/Scavenger	SMF 23298	Alberti 1969	=0,012136	Pragian	Pygidium	

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Proetida	Proetidae	Gerastos	Gerastos prox umerbianus	363	Large eyes	Inner shelf	Predator/Scavenger	1.2	IMGP G6 Orig K 1122-5	Feist 2000	=0.003913	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos sp C	364	Large eyes	Inner shelf	Predator/Scavenger	Crónier_2	PIMUZ 35183	Crónier Oudot 2018	=0.010570	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	365	Large eyes	Inner shelf	Predator/Scavenger	1.7	UA 13527	Gibb 2010	=0.008365	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	366	Large eyes	Inner shelf	Predator/Scavenger	2.2	UA 13464	Gibb 2010	=0.011817	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos granulatus sensu	367	Large eyes	Inner shelf	Predator/Scavenger	2.6	UM2-RF 130	Feist 2000	=0.007625	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	368	Large eyes	Inner shelf	Predator/Scavenger	2.8	UA 13465	Gibb 2010	=0.013304	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	369	Large eyes	Inner shelf	Predator/Scavenger	2.13	UA 13466	Gibb 2010	=0.010499	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	370	Large eyes	Inner shelf	Predator/Scavenger	3.2	UA 13280	Gibb 2010	=0.003871	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	371	Large eyes	Inner shelf	Predator/Scavenger	4.5	UA 13530	Gibb 2010	=0.008880	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	372	Large eyes	Inner shelf	Predator/Scavenger	4.10	UA 13531	Gibb 2010	=0.007036	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	373	Large eyes	Inner shelf	Predator/Scavenger	4.11	UA 13531	Gibb 2010	=0.005463	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos aintawilus	374	Large eyes	Inner shelf	Predator/Scavenger	6.4	UA 13454	Gibb 2010	=0.003478	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	375	Large eyes	Inner shelf	Predator/Scavenger	5.6	UA 13533	Gibb 2010	=0.004153	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	376	Large eyes	Inner shelf	Predator/Scavenger	5.8	UA 13533	Gibb 2010	=0.006851	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos aintawilus	377	Large eyes	Inner shelf	Predator/Scavenger	6.5	UA 13455	Gibb 2010	=0.002762	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	378	Large eyes	Inner shelf	Predator/Scavenger	6.10	UA13651	Chatterton 2010	=0.036752	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos hammii	379	Large eyes	Inner shelf	Predator/Scavenger	7.7	UA 13537	Gibb 2010	=0.006961	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos hammii	380	Large eyes	Inner shelf	Predator/Scavenger	7.8	UA 13536	Gibb 2010	=0.006520	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos hammii	381	Large eyes	Inner shelf	Predator/Scavenger	7.10	UA 13538	Gibb 2010	=0.009337	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos lisanrasus	382	Large eyes	Inner shelf	Predator/Scavenger	8.7	UA 13548	Gibb 2010	=0.005817	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	383	Large eyes	Inner shelf	Predator/Scavenger	8k	Di/UO/031	Khaldi 2016	=0.038460	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	384	Large eyes	Inner shelf	Predator/Scavenger	8n	Di/UO/029	Khaldi 2016	=0.041317	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos ainrasifus	385	Large eyes	Inner shelf	Predator/Scavenger	9.8	UA 13460	Gibb 2010	=0.014195	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos ainrasifus	386	Large eyes	Inner shelf	Predator/Scavenger	9.11	UA 13459	Gibb 2010	=0.013969	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos ainrasifus	387	Large eyes	Inner shelf	Predator/Scavenger	10.5	UA 13549	Gibb 2010	=0.006638	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos discombobulatus	388	Large eyes	Inner shelf	Predator/Scavenger	11.7	UA 13469	Gibb 2010	=0.008608	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos discombobulatus	389	Large eyes	Inner shelf	Predator/Scavenger	11.11	UA 13467	Gibb 2010	=0.006632	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos discombobulatus	390	Large eyes	Inner shelf	Predator/Scavenger	11.12	UA 13469	Gibb 2010	=0.012448	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos cuvieri malisus	391	Large eyes	Inner shelf	Predator/Scavenger	12.9	UA 13458	Gibb 2010	=0.011682	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos sp C	392	Large eyes	Inner shelf	Predator/Scavenger	Crónier_2	Di/UO/029	Crónier Oudot 2018	=0.007704	Emsian	Pygidium

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Proetida	Proetidae	Gerastos	Gerastos cuvieri malisus	393	Large eyes	Inner shelf	Predator/Scavenger	13.13	UA 13553	Gibb 2010	=0,012081	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos cuvieri malisus	394	Large eyes	Inner shelf	Predator/Scavenger	14.6	UA 13457	Gibb 2010	=0,005350	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos taqus	395	Large eyes	Inner shelf	Predator/Scavenger	15.1	UA 13554	Gibb 2010	=0,004519	Eifelian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	396	Large eyes	Inner shelf	Predator/Scavenger	18.3	UA 13558	Gibb 2010	=0,008501	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos raribus	397	Large eyes	Inner shelf	Predator/Scavenger	18.7	UA 13463	Gibb 2010	=0,005228	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos raribus	398	Large eyes	Inner shelf	Predator/Scavenger	18.8	UA 13463	Gibb 2010	=0,006018	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	399	Large eyes	Inner shelf	Predator/Scavenger	21.4	UA 13561	Gibb 2010	=0,009256	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	400	Large eyes	Inner shelf	Predator/Scavenger	21.5	UA 13472	Gibb 2010	=0,006170	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	401	Large eyes	Inner shelf	Predator/Scavenger	22.5	UA 13560	Gibb 2010	=0,004590	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	402	Large eyes	Inner shelf	Predator/Scavenger	22.6	UA 13562	Gibb 2010	=0,005849	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	403	Large eyes	Inner shelf	Predator/Scavenger	23.9	UA 13569	Gibb 2010	=0,003408	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos emmetus	404	Large eyes	Inner shelf	Predator/Scavenger	23.10	UA 13568	Gibb 2010	=0,004169	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos izius	405	Large eyes	Inner shelf	Predator/Scavenger	24.10	UA 13570	Gibb 2010	=0,006702	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos izius	406	Large eyes	Inner shelf	Predator/Scavenger	24.11	UA 13529	Gibb 2010	=0,009798	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos izius	407	Large eyes	Inner shelf	Predator/Scavenger	25.7	UA 13473	Gibb 2010	=0,009050	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos izius	408	Large eyes	Inner shelf	Predator/Scavenger	25.9	UA 13473	Gibb 2010	=0,008047	Givetian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	409	Large eyes	Inner shelf	Predator/Scavenger	37.7	UA 13276	Chatterton 2006	=0,054866	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	410	Large eyes	Inner shelf	Predator/Scavenger	39.9	UA 13277	Chatterton 2006	=0,063487	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	411	Large eyes	Inner shelf	Predator/Scavenger	39.11	UA 13278	Chatterton 2006	=0,043132	Emsian	Pygidium
Proetida	Proetidae	Gerastos	Gerastos prox umberbianus	412	Large eyes	Inner shelf	Predator/Scavenger	46.6a	CGMTA 212b	Alberti 1969	=0,011593		Pygidium
Proetida	Proetidae	Gerastos	Gerastos tuberculatus marocensis	413	Large eyes	Inner shelf	Predator/Scavenger	54.7	UA 13438	Chatterton 2006	=0,021757	Emsian	Pygidium
Proetida	Proetidae	Helmutia	Helmutia rissanensis	414	Large eyes	Deep	Predator/Scavenger	1.6b	IMGP G6 Orig K 112 2-25	Feist 2000	=0,006480		Pygidium
Proetida	Proetidae	Helmutia	Helmutia rissanensis	415	Large eyes	Deep	Predator/Scavenger	1.7	UM2-RF 150	Feist 2000	=0,006825		Pygidium
Proetida	Proetidae	Helmutia	Helmutia rissanensis	416	Large eyes	Deep	Predator/Scavenger	1.9a	UM2-RF 151	Feist 2000	=0,005683		Pygidium
Proetida	Proetidae	Koneprusites	Indet	417	Large eyes	Middle shelf	Predator/Scavenger	2.11	IMGP G6 Orig K 1122-48	Feist 2000	=0,005980	Givetian	Pygidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	418	Large eyes	Middle shelf	Predator/Scavenger	6.18a	CGMTA 281	Alberti 1970a	=0,007665	Eifelian	Pygidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	419	Large eyes	Middle shelf	Predator/Scavenger	6.19	SMF 23491	Alberti 1970a	=0,005577	Eifelian	Pygidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	420	Large eyes	Middle shelf	Predator/Scavenger	6.20	CGMTA 282	Alberti 1970a	=0,006873	Eifelian	Pygidium
Proetida	Proetidae	Koneprusites	Koneprusites insons africanus	421	Large eyes	Middle shelf	Predator/Scavenger	6.21	SMF 23492	Alberti 1970a	=0,007918	Eifelian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus solutus	422	Large eyes	Shallow	Predator/Scavenger	1.6	No name	Alberti 1966c	=0,004703	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lahcei	423	Large eyes	Shallow	Predator/Scavenger	5.7	NHM It 28952	Johnson 2012	=0,030310	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus lahcei	424	Large eyes	Shallow	Predator/Scavenger	5.13	NHM It 28953	Johnson 2012	=0,018320	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	425	Large eyes	Shallow	Predator/Scavenger	6.1	NHM It 28954	Johnson 2012	=0,039976	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	426	Large eyes	Shallow	Predator/Scavenger	6.8	NHM It 28955	Johnson 2012	=0,045789	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus spendens	427	Large eyes	Shallow	Predator/Scavenger	6.13	NHM It 28956	Johnson 2012	=0,028182	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus spendens	428	Large eyes	Shallow	Predator/Scavenger	11.10	SMF 23169	Alberti 1969	=0,006215	Pragian	Pygidium
Proetida	Proetidae	Linguaproetus	Linguaproetus saharensis	429	Blind	Shallow	Predator/Scavenger	28.22	SMF 23439	Alberti 1969	=0,004873	Eifelian	Pygidium
Proetida	Proetidae	Linguaproetus	Linguaproetus saharensis	430	Blind	Shallow	Predator/Scavenger	28.23	SMF 23440	Alberti 1969	=0,004749	Eifelian	Pygidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	431	Large eyes	Middle shelf	Predator/Scavenger	5.6	CGMTA 250	Alberti 1970a	=0,006093	Emsian	Pygidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	432	Large eyes	Middle shelf	Predator/Scavenger	5.7a	CGMTA 251	Alberti 1970a	=0,005876	Emsian	Pygidium

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Proetida	Proetidae	Macrolepharum	Macrolepharum africanum ribatelfatanum	433	Large eyes	Middle shelf	Predator/Scavenger	5.8	SMF 23468	Alberti 1970a	=0,005228	Emsian	Pygidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	434	Large eyes	Middle shelf	Predator/Scavenger	11.12	CGMTA 203	Alberti 1969	=0,005557	Eifelian	Pygidium
Proetida	Proetidae	Macrolepharum	Macrolepharum africanum africanum	435	Large eyes	Middle shelf	Predator/Scavenger	46.15	CGMTA 219	Alberti 1969	=0,005732	Eifelian	Pygidium
Proetida	Proetidae	Montanproetus	Montanproetus tindoufanus	436	Large eyes	Inner shelf	Predator/Scavenger	11.6	SMF 23109	Alberti 1969	=0,010133	Pragian	Pygidium
Proetida	Proetidae	Montanproetus	Montanproetus chlupaci	437	Large eyes	Inner shelf	Predator/Scavenger	11.7	SMF 23187?	Alberti 1969	=0,011096	Pragian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	438	Large eyes	Middle shelf	Predator/Scavenger	25.17	CGMTA 117	Alberti 1969	=0,006742	Emsian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	439	Large eyes	Middle shelf	Predator/Scavenger	25.18	CGMTA 118	Alberti 1969	=0,008587	Emsian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	440	Large eyes	Middle shelf	Predator/Scavenger	25.19	CGMTA 119	Alberti 1969	=0,008749	Emsian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	441	Large eyes	Middle shelf	Predator/Scavenger	25.20	SMF 23294	Alberti 1969	=0,008398	Emsian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	442	Large eyes	Middle shelf	Predator/Scavenger	25.21	SMF 23295	Alberti 1969	=0,007810	Emsian	Pygidium
Proetida	Tropidocoryphidae	Nagaproetus	Nagaproetus frequens	443	Large eyes	Middle shelf	Predator/Scavenger	b.16	CGMTA 120	Alberti 1967b	=0,011164	Emsian	Pygidium
Proetida	Proetidae	Oehlertaspis	Oehlertaspis subpinguis	444	Large eyes	Middle shelf	Predator/Scavenger	46.9a	CGMTA 214	Alberti 1969	=0,011589	Emsian	Pygidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	445	Large eyes	Middle shelf	Predator/Scavenger	46.1	CGMTA 210	Alberti 1969	=0,015661	Pragian	Pygidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	446	Large eyes	Middle shelf	Predator/Scavenger	46.2	SMF 23483b	Alberti 1969	=0,016670	Pragian	Pygidium
Proetida	Proetidae	Orbitoproetus	Orbitoproetus africanus	447	Large eyes	Middle shelf	Predator/Scavenger	46.3	SMF 23484b	Alberti 1969	=0,013846	Pragian	Pygidium
Proetida	Proetidae	Orbitoproetus	Indet	448	Large eyes	Middle shelf	Predator/Scavenger	Crónier_2	Di/UO/029	Crónier Oudot 2018	=0,008725	Emsian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	449	Large eyes	Middle shelf	Predator/Scavenger	2.20	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	450	Large eyes	Middle shelf	Predator/Scavenger	2.25	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	451	Large eyes	Middle shelf	Predator/Scavenger	2.27	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	452	Large eyes	Middle shelf	Predator/Scavenger	2.E2	UMC-IP427	Lerosey-Aubril 2005	=0,004460	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	453	Large eyes	Middle shelf	Predator/Scavenger	2.F1	UMC-IP428	Lerosey-Aubril 2005	=0,005746	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	454	Large eyes	Middle shelf	Predator/Scavenger	3.1	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	455	Large eyes	Middle shelf	Predator/Scavenger	3.2	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	456	Large eyes	Middle shelf	Predator/Scavenger	3.3	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	457	Large eyes	Middle shelf	Predator/Scavenger	3.4	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	458	Large eyes	Middle shelf	Predator/Scavenger	3.5	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	459	Large eyes	Middle shelf	Predator/Scavenger	3.6	No name	H. Alberti 1975a	=0,036994	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	460	Large eyes	Middle shelf	Predator/Scavenger	4q	UMC-IP400	Lerosey-Aubril 2005	=0,001623	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	461	Large eyes	Middle shelf	Predator/Scavenger	4r	UMC-IP401	Lerosey-Aubril 2005	=0,001742	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	462	Large eyes	Middle shelf	Predator/Scavenger	4s	UMC-IP402	Lerosey-Aubril 2005	=0,001930	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	463	Large eyes	Middle shelf	Predator/Scavenger	4t	UMC-IP403	Lerosey-Aubril 2005	=0,002128	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	464	Large eyes	Middle shelf	Predator/Scavenger	4u	UMC-IP404	Lerosey-Aubril 2005	=0,002686	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	465	Large eyes	Middle shelf	Predator/Scavenger	4v	UMC-IP405	Lerosey-Aubril 2005	=0,003496	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	466	Large eyes	Middle shelf	Predator/Scavenger	4w	UMC-IP406	Lerosey-Aubril 2005	=0,004310	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	467	Large eyes	Middle shelf	Predator/Scavenger	4x	UMC-IP407	Lerosey-Aubril 2005	=0,004306	Famennian	Pygidium
Proetida	Proetidae	Osmolskabole	Osmolskabole prima	468	Large eyes	Middle shelf	Predator/Scavenger	4y	UMC-IP408	Lerosey-Aubril 2005	=0,003937	Famennian	Pygidium
Proetida	Proetidae	Palpebralia	Palpebralia brecciae	469	Blind	Deep	Predator/Scavenger	2i	UM2-RF 181	Feist 2002	=0,015746	Frasnian	Pygidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus wragei	470	Large eyes	Middle shelf	Predator/Scavenger	2.14	SMF 36237	Alberti 1981a	=0,020358	Eifelian	Pygidium
Proetida	Proetidae	Paralepidoproetus	Paralepidoproetus chouberti	471	Large eyes	Middle shelf	Predator/Scavenger	11.5	SMF 23427	Alberti 1969	=0,009640		Pygidium
Proetida	Tropidocoryphidae	Phaetonellus	Phaetonellus planicauda africanus	472	Large eyes	Middle shelf	Predator/Scavenger	3.29	CGMTA	Alberti 1981a	=0,035772	Emsian	Pygidium

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Proetida	Tropidocoryphidae	Phaetonellus	Phaetonellus planicauda africanus	473	Large eyes	Middle shelf	Predator/Scavenger	3.30	SMF 36264	Alberti 1981a	=0.036200	Emsian	Pygidium
Proetida	Proetidae	Piriproetus	Indet	474	Blind	Deep	Predator/Scavenger	3.24	SMF 36257	Alberti 1981a	=0.020358	Emsian	Pygidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	475	Blind	Deep	Predator/Scavenger	3.32	SMF 36291	Alberti 1981a	=0.012760	Eifelian	Pygidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	476	Blind	Deep	Predator/Scavenger	19.14	SMF 23225	Alberti 1969	=0.005336	Eifelian	Pygidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops patruelis	477	Blind	Deep	Predator/Scavenger	46.13	CGMTA 217	Alberti 1969	=0.005031	Eifelian	Pygidium
Proetida	Proetidae	Piriproetus	Piriproetus amblyops austromaurus	478	Blind	Deep	Predator/Scavenger	CGMTA 218	Alberti 1969	=0.005745	Eifelian	Pygidium	
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	479	Large eyes	Inner shelf	Predator/Scavenger	7.4	NHM It 28957	Johnson 2012	=0.037283	Pragian	Pygidium
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	480	Large eyes	Inner shelf	Predator/Scavenger	7.7	NHM It 28958	Johnson 2012	=0.037283	Pragian	Pygidium
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	481	Large eyes	Inner shelf	Predator/Scavenger	7.11	NHM It 28959	Johnson 2012	=0.037283	Pragian	Pygidium
Proetida	Proetidae	Podoliproetus	Podoliproetus sinespina	482	Large eyes	Inner shelf	Predator/Scavenger	8.5	NHM It 28960	Johnson 2012	=0.037035	Pragian	Pygidium
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	483	Large eyes	Inner shelf	Predator/Scavenger	8.11	NHM It 28961	Johnson 2012	=0.023295	Pragian	Pygidium
Proetida	Proetidae	Podoliproetus	Podoliproetus mirdani	484	Large eyes	Inner shelf	Predator/Scavenger	8.12	NHM It 28961	Johnson 2012	=0.023295	Pragian	Pygidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	485	Large eyes	Inner shelf	Predator/Scavenger	6.16	SMF 23087	Alberti 1969	=0.009070	Pragian	Pygidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	486	Large eyes	Inner shelf	Predator/Scavenger	6.17	SMF 23088	Alberti 1969	=0.010015	Pragian	Pygidium
Proetida	Proetidae	Pragoproetus	Pragoproetus tafilaltensis	487	Large eyes	Inner shelf	Predator/Scavenger	6.18	CGMTA 26	Alberti 1969	=0.010015	Pragian	Pygidium
Proetida	Proetidae	Pragoproetus	Pragoproetus gibbosus	488	Large eyes	Inner shelf	Predator/Scavenger	6.22	SMF 23045	Alberti 1969	=0.012510	Pragian	Pygidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri zemmoura	489	Blind	Middle shelf	Predator/Scavenger	3.25	SMF 36258	Alberti 1981a	=0.014330	Pragian	Pygidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri jaegeri	490	Blind	Middle shelf	Predator/Scavenger	6.64	SMF 36562	Alberti 1983	=0.005866	Pragian	Pygidium
Proetida	Proetidae	Prodrevermannia	Prodrevermannia jaegeri jaegeri	491	Blind	Middle shelf	Predator/Scavenger	6.65	SH	Alberti 1983	=0.005462	Pragian	Pygidium
Proetida	Proetidae	Proetina	Proetina ihmadii	492	Large eyes	Inner shelf	Predator/Scavenger	9.5	NHM It 28962	Johnson 2012	=0.018080	Pragian	Pygidium
Proetida	Proetidae	Ignoproetus	Proetopeltis waldschmidtii	493	Large eyes	Middle shelf	Predator/Scavenger	6.4	CGMTA 355	Alberti 1970a	=0.008322	Emsian	Pygidium
Proetida	Proetidae	Ignoproetus	Proetopeltis waldschmidtii	494	Large eyes	Middle shelf	Predator/Scavenger	6.5	SMF 23591	Alberti 1970a	=0.006750	Emsian	Pygidium
Proetida	Proetidae	CORNUPROETINAE	Indet	495			Predator/Scavenger	17.13	SMF 23205	Alberti 1969	=0.010335	Emsian	Pygidium
Proetida	Proetidae	CORNUPROETINAE	Indet	496			Predator/Scavenger	17.14	SMF 23206	Alberti 1969	=0.010335	Emsian	Pygidium
Proetida	Proetidae	Proetus	Proetus proetus sp B aff granulosis	497	Large eyes	Middle shelf	Predator/Scavenger	3.2	CGMT	Alberti 1970a	=0.014710	Eifelian	Pygidium
Proetida	Proetidae	Proetus	Proetus proetus sp A aff granulosis	498	Large eyes	Middle shelf	Predator/Scavenger	3.5d	CGMT-TM 21	Alberti 1970a	=0.013346	Emsian	Pygidium
Proetida	Proetidae	Proetus	Indet	499	Large eyes	Middle shelf	Predator/Scavenger	46.7	CGMTA 213	Alberti 1969	=0.010674	Emsian	Pygidium
Proetida	Proetidae	Proetus	Indet	500	Large eyes	Middle shelf	Predator/Scavenger	46.10	CGMTA 215	Alberti 1969	=0.004838	Emsian	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus maghrebus	501	Large eyes	Middle shelf	Predator/Scavenger	4.6	CGMTA 243	Alberti 1970a	=0.005260	Emsian	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sculptus antiquus	502	Large eyes	Middle shelf	Predator/Scavenger	11.8	SMF 23139	Alberti 1969	=0.005793	Pragian	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp A	503	Large eyes	Middle shelf	Predator/Scavenger	40.4	UA 13259	Chatterton 2006	=0.023965	Emsian	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp A	504	Large eyes	Middle shelf	Predator/Scavenger	40.5	UA 13258	Chatterton 2006	=0.026375	Emsian	Pygidium

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Proetida	Proetidae	Sculptoproetus	Sculptoproetus haasi	505	Large eyes	Middle shelf	Predator/Scavenger	40.9	UA 13266	Chatterton 2006	=0,030728	Eifelien	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus haasi	506	Large eyes	Middle shelf	Predator/Scavenger	40.10	UA 13269	Chatterton 2006	=0,050878	Eifelien	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus sp B	507	Large eyes	Middle shelf	Predator/Scavenger	40.13	UA 13262	Chatterton 2006	=0,040703	Eifelien	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	508	Large eyes	Middle shelf	Predator/Scavenger	4	SMF 23000	Alberti 1966a	=0,005627	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	509	Large eyes	Middle shelf	Predator/Scavenger	6.9	CGMTA 254	Alberti 1970a	=0,005651	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	510	Large eyes	Middle shelf	Predator/Scavenger	6.10	CGMTA 356	Alberti 1970a	=0,009132	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber tenuigranifer	511	Large eyes	Middle shelf	Predator/Scavenger	11.20	SMF 23195	Alberti 1969	=0,008644	Eifelien	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	512	Large eyes	Middle shelf	Predator/Scavenger		CGMTA 3	Alberti 1969	=0,004906	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	513	Large eyes	Middle shelf	Predator/Scavenger		CGMTA 4	Alberti 1969	=0,007054	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	514	Large eyes	Middle shelf	Predator/Scavenger		SMF 23003	Alberti 1969	=0,004899	Emsian	Pygidium
Proetida	Proetidae	Tafilaltaspis	Tafilaltaspis creber creber	515	Large eyes	Middle shelf	Predator/Scavenger		SMF 23000	Alberti 1969	=0,006388	Emsian	Pygidium

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Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	516	Large eyes	Middle shelf	Predator/Scavenger	4.6	UA13272	Gibb 2007	=0,005460	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	517	Large eyes	Middle shelf	Predator/Scavenger	4.7	UA13273	Gibb 2007	=0,004004	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	518	Large eyes	Middle shelf	Predator/Scavenger	5.1	UA13256	Gibb 2007	=0,011808	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	519	Large eyes	Middle shelf	Predator/Scavenger	5.10	UA13269	Gibb 2007	=0,015089	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	520	Large eyes	Middle shelf	Predator/Scavenger	6.14	UA13288	Gibb 2007	=0,004756	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus dibbanus	521	Large eyes	Middle shelf	Predator/Scavenger	7.5	UA13258	Gibb 2007	=0,007913	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus dibbanus	522	Large eyes	Middle shelf	Predator/Scavenger	7.8	UA13258	Gibb 2007	=0,008185	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus dibbanus	523	Large eyes	Middle shelf	Predator/Scavenger	7.9	UA13259	Gibb 2007	=0,007714	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus dibbanus	524	Large eyes	Middle shelf	Predator/Scavenger	7.10	UA13281	Gibb 2007	=0,003636	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus elguerrouji	525	Large eyes	Middle shelf	Predator/Scavenger	8.1	UA13262	Gibb 2007	=0,009831	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	526	Large eyes	Middle shelf	Predator/Scavenger	9.10	UA13268	Gibb 2007	=0,005522	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus elguerrouji	527	Large eyes	Middle shelf	Predator/Scavenger	9.12	UA13260	Gibb 2007	=0,011700	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	528	Large eyes	Middle shelf	Predator/Scavenger	9.13	UA13266	Gibb 2007	=0,009031	Eifelian	Pygidium
Proetida	Proetidae	Unguliproetus	Unguliproetus unguoides tener	529	Large eyes	Middle shelf	Predator/Scavenger	6.9	SMF 23039	Alberti 1969	=0,007372	Emsian	Pygidium
Proetida	Proetidae	Unguliproetus	Unguliproetus unguoides tener	530	Large eyes	Middle shelf	Predator/Scavenger	6.10	CGMTA 18	Alberti 1969	=0,007110	Emsian	Pygidium
Proetida	Proetidae	Unguliproetus	Unguliproetus unguoides tener	531	Large eyes	Middle shelf	Predator/Scavenger	6.11	SMF 23042	Alberti 1969	=0,007566	Emsian	Pygidium
Proetida	Proetidae	Voigtaspis	Voigtaspis voigti	532	Large eyes	Middle shelf	Predator/Scavenger	11.1	SMF 23208	Alberti 1969	=0,009630	Pragian	Pygidium
Proetida	Proetidae	Voigtaspis	Voigtaspis voigti	533	Large eyes	Middle shelf	Predator/Scavenger	11.2	CGMTA 83	Alberti 1969	=0,007340	Pragian	Pygidium
Proetida	Proetidae	Voigtaspis	Voigtaspis voigti	534	Large eyes	Middle shelf	Predator/Scavenger	11.3	SMF 23209	Alberti 1969	=0,008663	Pragian	Pygidium
Proetida	Proetidae	Voigtaspis	Voigtaspis voigti	535	Large eyes	Middle shelf	Predator/Scavenger	11.4a	CGMTA 82	Alberti 1969	=0,014387	Pragian	Pygidium
Proetida	Proetidae	Voigtaspis	Voigtaspis voigti	536	Large eyes	Middle shelf	Predator/Scavenger	b.8	CGMTA 82	Alberti 1967b	=0,018963	Pragian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	537	Large eyes	Inner shelf	Predator/Scavenger	33.4	CGMT	Alberti 1969	=0,007672	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	538	Large eyes	Inner shelf	Predator/Scavenger	33.5	No name	Alberti 1969	=0,008485	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	539	Large eyes	Inner shelf	Predator/Scavenger	33.6	SMF 23358	Alberti 1969	=0,006860	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	540	Large eyes	Inner shelf	Predator/Scavenger	33.7	CGMTA 145	Alberti 1969	=0,007588	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	541	Large eyes	Inner shelf	Predator/Scavenger	33.8	SMF 23359	Alberti 1969	=0,006744	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	542	Large eyes	Inner shelf	Predator/Scavenger	33.9	SMF 23360	Alberti 1969	=0,006308	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	543	Large eyes	Inner shelf	Predator/Scavenger	33.10	SMF 23361	Alberti 1969	=0,007012	Lochkovian	Pygidium
Proetida	Proetidae	Warbugella	Warbugella rugulosa maura	544	Large eyes	Inner shelf	Predator/Scavenger	33.11	CGMTA 205	Alberti 1969	=0,007012	Lochkovian	Pygidium
Proetida	Proetidae	Yuanjia	Yuanjia wildungensis	545	Large eyes	Middle shelf	Predator/Scavenger	9.2	G6 693-210	H. Alberti 1973	=0,009415	Famennian	Pygidium
Corynexoch	Scutelluidae	Cavetia	Cavetia furcifera hamlagdadiana	546	Large eyes	Middle shelf	Predator/Scavenger	3y	UA13266	Feist 2018	=0,024302	Emsian	Pygidium
Corynexoch	Scutelluidae	Cavetia	Cavetia furcifera hamlagdadiana	547	Large eyes	Middle shelf	Predator/Scavenger	8	No name	Alberti 1981b	=0,047222	Emsian	Pygidium
Corynexoch	Scutelluidae	Heliopeltis	Heliopeltis johnsoni	548	Large eyes	Inner shelf	Predator/Scavenger	12e	UM-IP 705	Feist 2015	=0,007352		Pygidium
Corynexoch	Scutelluidae	Heliopeltis	Heliopeltis johnsoni	549	Large eyes	Inner shelf	Predator/Scavenger	13h	UM-IP 710	Feist 2015	=0,008889		Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci hollardi	550	Large eyes	Inner shelf	Predator/Scavenger	2	No name	Alberti 1966b	=0,017114	Pragian	Pygidium

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Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis bassei	551	Large eyes	Inner shelf	Predator/Scavenger	3	Nr 1126	Alberti 1966b	=0.015531	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci hollardi	552	Large eyes	Inner shelf	Predator/Scavenger	4a	UA 14327	Feist 2015	=0.029065	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci hollardi	553	Large eyes	Inner shelf	Predator/Scavenger	4c	UM-IP 658	Feist 2015	=0.045043	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci hollardi	554	Large eyes	Inner shelf	Predator/Scavenger	4d	UA 14326	Feist 2015	=0.018796	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis bassei	555	Large eyes	Inner shelf	Predator/Scavenger	4h	UA 14325	Feist 2015	=0.023363	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis chlupaci rabatensis	556	Large eyes	Inner shelf	Predator/Scavenger	5	No name	Alberti 1966b	=0.017989	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis bassei	557	Large eyes	Inner shelf	Predator/Scavenger	5a	UM-IP 653	Feist 2015	=0.022726	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis bassei	558	Large eyes	Inner shelf	Predator/Scavenger	5e	UM-IP 655	Feist 2015	=0.017482	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis maghrebica	559	Large eyes	Inner shelf	Predator/Scavenger	6	No name	Alberti 1966b	=0.032786	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghdadica	560	Large eyes	Inner shelf	Predator/Scavenger	6i	UM-IP 663	Feist 2015	=0.021644	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghdadica	561	Large eyes	Inner shelf	Predator/Scavenger	6k	UM-IP 664	Feist 2015	=0.025124	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis hamlaghdadica	562	Large eyes	Inner shelf	Predator/Scavenger	6l	UM-IP 665	Feist 2015	=0.036488	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis maghrebica	563	Large eyes	Inner shelf	Predator/Scavenger	7i	SMF 36590	Feist 2015	=0.014083	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis tafilaltensis	564	Large eyes	Inner shelf	Predator/Scavenger	8e	UM-IP 682	Feist 2015	=0.019793	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis tafilaltensis	565	Large eyes	Inner shelf	Predator/Scavenger	8i	UM-IP 683	Feist 2015	=0.019417	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis tafilaltensis	566	Large eyes	Inner shelf	Predator/Scavenger	8k	UM-IP 678	Feist 2015	=0.019230	Pragian	Pygidium
Corynexoch	Scutelluidae	Kolihapeltis	Kolihapeltis maghrebica	567	Large eyes	Inner shelf	Predator/Scavenger	Doubleton_	No name	Alberti 1982	=0.038210	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus elayounensis	568	Large eyes	Inner shelf	Predator/Scavenger	1.2a	SMF 57073	Schraut 2000c	=0.086718	Pragian	Pygidium
Proetida	Proetidae	Buchiproetus	Buchiproetus pribyli pribyli	569	Large eyes	Middle shelf	Predator/Scavenger	2.9	SMF 36234	Alberti 1981a	=0.036146	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus hamlagdadicus	570	Large eyes	Inner shelf	Predator/Scavenger	1.10a	CGMTA	Alberti 1983	=0.035397	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus brongniarti menanensis	571	Large eyes	Inner shelf	Predator/Scavenger	4.3	SMF 76649	Schraut 2004	=0.053175	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus bohemicus	572	Large eyes	Inner shelf	Predator/Scavenger	4.10	SMF 76654	Schraut 2004	=0.045057	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus spatuliformis	573	Large eyes	Inner shelf	Predator/Scavenger	5.6	SMF 76658	Schraut 2004	=0.051371	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus spatuliformis	574	Large eyes	Inner shelf	Predator/Scavenger	5.8	SMF 76662	Schraut 2004	=0.051371	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus spatuliformis	575	Large eyes	Inner shelf	Predator/Scavenger	5.10	SMF 76663	Schraut 2004	=0.050497	Pragian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus rehamnanus	576	Large eyes	Inner shelf	Predator/Scavenger	6.7	UA13652	Chatterton 2010	=0.052633	Eifelian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus tenuistriatus	577	Large eyes	Inner shelf	Predator/Scavenger	7.7	SMF 76676	Schraut 2004	=0.047420	Emsian	Pygidium
Corynexoch	Scutelluidae	Paralejurus	Paralejurus rehamnanus	578	Large eyes	Inner shelf	Predator/Scavenger	7.9	SMF 76669	Schraut 2004	=0.029352	Emsian	Pygidium

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Corynexoch	Scutellidae	Paralejurus	Paralejurus tenuistriatus	579	Large eyes	Inner shelf	Predator/Scavenger	7.10	SMF 76676	Schraut 2004	=0,032031	Emsian	Pygidium
Corynexoch	Scutellidae	Platyscutellum	Platyscutellum megranense	580	Large eyes	Middle shelf	Predator/Scavenger	1.14a	CGMTA 231	Alberti 1970a	=0,020435	Pragian	Pygidium
Corynexoch	Scutellidae	Platyscutellum	Platyscutellum massai	581	Large eyes	Middle shelf	Predator/Scavenger	6	No name	Alberti 1981b	=0,033551	Pragian	Pygidium
Corynexoch	Scutellidae	Platyscutellum	Platyscutellum massai	582	Large eyes	Middle shelf	Predator/Scavenger	Alberti_19	No name	Alberti 1982	=0,065376	Pragian	Pygidium
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum frix	583	Large eyes	Middle shelf	Predator/Scavenger	2.2	CGMTA 235	Alberti 1970a	=0,017046	Pragian	Pygidium
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum hammadi	584	Large eyes	Middle shelf	Predator/Scavenger	48.6	UA 13412	Chatterton 2006	=0,101153	Emsian	Pygidium
Corynexoch	Scutellidae	Scabriscutellum	Scabriscutellum hammadi	585	Large eyes	Middle shelf	Predator/Scavenger	48.7	UA 13410	Chatterton 2006	=0,102334	Emsian	Pygidium
Corynexoch	Scutellidae	Thysanopeltis	Thysanopeltis speciosa	586	Large eyes	Middle shelf	Predator/Scavenger	8r	SMF 57113	Schraut 2000a	=0,030650	Eifelian	Pygidium
Proetida	Tropidocoryphidae	Chlupaciparia	Chlupaciparia zieglerei maroccania	587	Large eyes	Middle shelf	Predator/Scavenger	3p	UM2-RF 254	Feist 2002	=0,003445	Frasnian	Pygidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus decorus maurulus	588	Large eyes	Middle shelf	Predator/Scavenger	8.21	SMF 23501	Alberti 1970a	=0,007165	Ludlow-Pridoli	Pygidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus decorus maurulus	589	Large eyes	Middle shelf	Predator/Scavenger	29.16	SMF 23236	Alberti 1969	=0,011776	Ludlow-Pridoli	Pygidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus concentricus meridianus	590	Large eyes	Middle shelf	Predator/Scavenger	31.20	CGMTA 136	Alberti 1969	=0,006349	Pragian	Pygidium
Proetida	Tropidocoryphidae	Decoroproetus	Decoroproetus concentricus meridianus	591	Large eyes	Middle shelf	Predator/Scavenger	31.21	SMF 23349	Alberti 1969	=0,008060	Pragian	Pygidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe memnon nepos	592	Large eyes	Middle shelf	Predator/Scavenger	4.37	SMF 36269	Alberti 1981a	=0,041156	Emsian	Pygidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe hamlaghdadica	593	Large eyes	Middle shelf	Predator/Scavenger	30.7	SMF 23330	Alberti 1969	=0,009016	Pragian	Pygidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe hamlaghdadica	594	Large eyes	Middle shelf	Predator/Scavenger	30.8	CGMTA 127	Alberti 1969	=0,008140	Pragian	Pygidium
Proetida	Tropidocoryphidae	Tropidocoryphe	Tropidocoryphe amuri	595	Large eyes	Middle shelf	Predator/Scavenger	41.6	UA 13394	Chatterton 2006	=0,035555	Emsian	Pygidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	596	Large eyes	Shallow	Predator/Scavenger	3.3	80202	Bignon 2014	=0,042371	Pragian	Pygidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	597	Large eyes	Shallow	Predator/Scavenger	3.5	JC 101	Bignon 2014	=0,040981	Pragian	Pygidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	598	Large eyes	Shallow	Predator/Scavenger	4.5	JC 103	Bignon 2014	=0,042015	Pragian	Pygidium
Phacopida	Acastidae	Minicryphaeus	Minicryphaeus giganteus	599	Large eyes	Shallow	Predator/Scavenger	4.6	JC 102	Bignon 2014	=0,042011	Pragian	Pygidium
Proetida	Proetidae	Perliproetus	Perliproetus africanus	600	Large eyes	Middle shelf	Predator/Scavenger	1W	MB.T 6225	FeistWeyer 2018	=0,029399	Famennian	Pygidium
Proetida	Proetidae	Perliproetus	Perliproetus africanus	601	Large eyes	Middle shelf	Predator/Scavenger	1U	MB.T 6222	FeistWeyer 2018	=0,035692	Famennian	Pygidium
Phacopida	Phacopidae	Nephranops	Nephranops (Nephranops) incisus	602	Blind	Deep	Predator/Scavenger	4V	UM-IP 820b	Feist 2019	=0,011110	Famennian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	603	Small eyes	Middle shelf	Particle feeding	3.6	UA 14313	Chatterton 2019	=0,028900	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	604	Small eyes	Middle shelf	Particle feeding	4.3	UA 14320	Chatterton 2019	=0,007810	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides ammari	605	Small eyes	Middle shelf	Particle feeding	4.5	UA 14322	Chatterton 2019	=0,007873	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides pankowskiorum	606	Small eyes	Middle shelf	Particle feeding	5.2	UA 14316	Chatterton 2019	=0,058819	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides pankowskiorum	607	Small eyes	Middle shelf	Particle feeding	5.4	UA 14264	Chatterton 2019	=0,079363	Eifelian	Pygidium
Proetida	Aulacopleuridae	Cyphaspides	Cyphaspides nicoleae	608	Small eyes	Middle shelf	Particle feeding	5.5	UA 14317	Chatterton 2019	=0,085442	Eifelian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops bronni	609	Large eyes	Inner shelf	Predator/Scavenger	Frey8g_py	PIMUZ 30647	Frey 2014	=0,059938	Pragian	Pygidium
Phacopida	Phacopidae	Reedops	Reedops cephalotes	610	Large eyes	Inner shelf	Predator/Scavenger	Klug_11.2	PIMUZ 7289	Klug 2008	=0,064841	Emsian	Pygidium
Phacopida	Acastidae	Metacanthina	Metacanthina wallacei	611	Large eyes	Shallow	Predator/Scavenger	Klug_11.1	PIMUZ 7291	Klug 2008	=0,051938	Emsian	Pygidium

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Phacopida	Dalmanitidae	Morocconites	Morocconites malladoides	612	Large eyes	Inner shelf	Predator/Scavenger	Edgecomb	No name	Edgecombe 1991	=0,015954		Pygidium
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	613	Large eyes	Inner shelf	Predator/Scavenger	Corbacho	JC106	Corbacho 2014	=0,087062	Pragian	Pygidium
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	614	Large eyes	Inner shelf	Predator/Scavenger	Corbacho	KH200	Corbacho 2014	=0,144261	Pragian	Pygidium
Phacopida	Acastidae	Lanceaspis	Lanceaspis hammondi	615	Large eyes	Inner shelf	Predator/Scavenger	Corbacho	JC107	Corbacho 2014	=0,073056	Pragian	Pygidium
Proetida	Proetidae	Sculptoproetus	Sculptoproetus raki	616	Large eyes	Middle shelf	Predator/Scavenger	3h	IRSBNa13414	Van Viersen 2019	=0,012048	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	617	Large eyes	Middle shelf	Predator/Scavenger	4f	IRSBNa13416	Van Viersen 2019	=0,027387	Eifelian	Pygidium
Proetida	Proetidae	Koneprusites	Koneprusites oresibios	618	Large eyes	Middle shelf	Predator/Scavenger	4p	IRSBNa13415	Van Viersen 2019	=0,029847	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	619	Large eyes	Middle shelf	Predator/Scavenger	5a	IRSBNa13420	Van Viersen 2019	=0,033879	Eifelian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus haasi	620	Large eyes	Middle shelf	Predator/Scavenger	5r	IRSBNa13421	Van Viersen 2019	=0,016666	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus sp. A	621	Large eyes	Middle shelf	Predator/Scavenger	6d	IRSBNa13422	Van Viersen 2019	=0,045443		Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus gibbae	622	Large eyes	Middle shelf	Predator/Scavenger	7i	IRSBNa13423	Van Viersen 2019	=0,020198	Emsian	Pygidium
Proetida	Proetidae	Timsaloproetus	Timsaloproetus pulchrius repens	623	Large eyes	Middle shelf	Predator/Scavenger	8e	IRSBNa13425	Van Viersen 2019	=0,037709	Emsian	Pygidium
Proetida	Proetidae	Hollandiella	Hollandiella curvirostris	624	Large eyes	Inner shelf	Predator/Scavenger	10d	IRSBNa13426	Van Viersen 2019	=0,031235	Pragian	Pygidium
Proetida	Proetidae	Hollandiella	Hollandiella lebruni	625	Large eyes	Inner shelf	Predator/Scavenger	11d	IRSBNa13429	Van Viersen 2019	=0,019604	Emsian	Pygidium
Proetida	Proetidae	Hollandiella	Hollandiella lebruni	626	Large eyes	Inner shelf	Predator/Scavenger	11g	IRSBNa13430	Van Viersen 2019	=0,024383	Emsian	Pygidium
Proetida	Proetidae	Hollandiella	Hollandiella verecunda	627	Large eyes	Inner shelf	Predator/Scavenger	13a	IRSBNa13432	Van Viersen 2019	=0,031235	Pragian	Pygidium
Proetida	Proetidae	Lepidoproetus	Lepidoproetus maharchianus	628	Large eyes	Shallow	Predator/Scavenger	13j	IRSBNa13433	Van Viersen 2019	=0,023254	Pragian	Pygidium
Proetida	Tropidocoryphidae	Tafilaltaspis	Tafilaltaspis rufa	629	Large eyes	Middle shelf	Predator/Scavenger	15e	IRSBNa13435	Van Viersen 2019	=0,022221	Eifelian	Pygidium
Lichida	Odontopleuridae	Koneprusia	Koneprusia aboussalamae	630	Large eyes	Middle shelf	Predator/Scavenger	3n	MB.T. 4572	Feist McNamara 2007	=0,013329	Givetian	Pygidium

Article 6 :

reference	species	genus	family	order	section	basin	stage	substage	count	Formation
Corbacho Kier 2013 Bettaleria	Acanthopyge (Belenopyge) estevei	Acanthopyge	Lichidae	Lichida	El Achana	Maider	Pragian	Pragian	7	Ihandar
Cronier Oudot Klug DeBaets 2018 NJB Geol Pal	Indet	Acanthopyge	Lichidae	Lichida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Corbacho Kier 2013 Bettaleria	Acanthopyge (Belenopyge) estevei	Acanthopyge	Lichidae	Lichida	Jbel el Mrakib	Maider	Pragian	Pragian	3	Ihandar
Corbacho Kier 2013 Bettaleria	Acanthopyge (Belenopyge) bassei	Acanthopyge	Lichidae	Lichida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	1	El Otfal
Chatterton Gibbs 2010 Jpal	Acanthopyge (Belenopyge) bassei	Acanthopyge	Lichidae	Lichida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	2	El Otfal
Hollard 1963 Notes et Mémoires du SGM	Acastella jacquemonti levis	Acastella	Acastidae	Phacopida	Tanzida	Draa Valley	Lochkovian	lower Lochkovian	1	Lmhaïfid
Hollard 1963 Notes et Mémoires du SGM	Acastella jacquemonti tanzidensis	Acastella	Acastidae	Phacopida	Tanzida	Draa Valley	Lochkovian	lower Lochkovian	1	Lmhaïfid
Hollard 1963 Notes et Mémoires du SGM	Acastella patula	Acastella	Acastidae	Phacopida	Tanzida	Draa Valley	Lochkovian	lower Lochkovian	1	Lmhaïfid
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Acastoides haddadi	Acastoides	Calmoniidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Acastoides zguilmensis	Acastoides	Calmoniidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	19	Timrhamhart
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Adrisiops boudjemaai	Adrisiops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	4	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Adrisiops fabrei	Adrisiops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Adrisiops fabrei	Adrisiops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Adrisiops fabrei	Adrisiops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Burton Eldredge 1974 Palaeont	Adrisiops fabrei	Adrisiops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar
vanVierssen Holland Koppka 2017 Bull geo	Adrisiops weugi	Adrisiops	Phacopidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	El Otfal
Alberti 1983 Senck lethaea	Afrops larvifer	Afrops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	1	
Thomas Holloway 1988 Phil. TRSL	Akantharges mbarki	Akantharges	Lichidae	Lichida	Jdorf	Tafilalt	Eifelien		1	
Cobacho Lopez-Soriano 2013 Batalleria	Akantharges mbarki	Akantharges	Lichidae	Lichida	Tinejad	Tafilalt	Eifelien		4	
Alberti 1969 SenckNaturGesell	Alberticoryphe stirps	Alberticoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1981a Senck lethaea	Alberticoryphe stirps	Alberticoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Aulacopleura beyrichi africana	Aulacopleura	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1970a SenckNaturGesell	Aulacopleura beyrichi africana	Aulacopleura	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	2	Bou Tcharafine
Alberti 1981a Senck lethaea	Aulacopleura beyrichi africana	Aulacopleura	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	8	Bou Tcharafine
Alberti 1970a SenckNaturGesell	Aulacopleura beyrichi africana	Aulacopleura	Aulacopleuridae	Proetida	Jbel Amlane	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1981a Senck lethaea	Aulacopleura bohemia	Aulacopleura	Aulacopleuridae	Proetida	Jbel Bou Tscharafine	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Aulacopleura beyrichi africana	Aulacopleura	Aulacopleuridae	Proetida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Aulacopleura	Aulacopleuridae	Proetida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar	
Alberti 1981a Senck lethaea	Aulacopleurella mauretana	Aulacopleurella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops legrandi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	7	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops legrandi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	35	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	12	Chefar el Ahmar
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Eifelien	lower Eifelien	20	Chefar el Ahmar

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Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops speculator speculator	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	5	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops speculator speculator	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	4	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops speculator speculator	Austerops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
McKellar Chatterton 2009 Pal Canadiana	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Maider	Emsian	upper Emsian	10	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	11	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	13	Timrhamhart
Chatterton Gibbs 2010 Jpal	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	2	El Otfal
McKellar Chatterton 2009 Pal Canadiana	Austerops kermiti	Austerops	Phacopidae	Phacopida	Jbel Oufatene	Maider	Eifelien	lower Eifelien	8	El Otfal
McKellar Chatterton 2009 Pal Canadiana	Austerops salamandar	Austerops	Phacopidae	Phacopida	Jbel Oufatene	Maider	Eifelien	lower Eifelien	5	El Otfal
McKellar Chatterton 2009 Pal Canadiana	Austerops speculator punctatus	Austerops	Phacopidae	Phacopida	Jbel Oufatene	Maider	Eifelien	lower Eifelien	3	El Otfal
McKellar Chatterton 2009 Pal Canadiana	Austerops speculator punctatus	Austerops	Phacopidae	Phacopida	Jbel Oufatene	Maider	Eifelien	lower Eifelien	4	El Otfal
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Austerops menchikoffi	Austerops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Austerops salamandaroides	Austerops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	11	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Austerops sp B	Austerops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	3	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Austerops sp D	Austerops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	3	Chefar el Ahmar
Cobacho Lopez-Soriano 2013 Batalleria	Basseiarges mellishae	Basseiarges	Lichidae	Lichida	Jdorf	Tafilalt	Eifelien		4	
Alberti 1983 Senck lethaea	Boeckops algericus	Boeckops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	6	
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Boeckops sp C	Boeckops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Alberti 1983 Senck lethaea	Boeckops maidericus	Boeckops	Phacopidae	Phacopida	Timarzite	Maider	Pragian	Pragian	1	Ihandar
McKellar Chatterton 2009 Pal Canadiana	Boeckops stelcki	Boeckops	Phacopidae	Phacopida	Taharajat Oufatene	Maider	Emsian	upper Emsian	7	Tazoulait
Alberti 1969 SenckNaturGesell	Buchiproetus mauretanicus	Buchiproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1967a Senck leth	Buchiproetus mauretanicus	Buchiproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Buchiproetus mauretanicus	Buchiproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	6	lower Kess Kess
Feist Belka 2018 N.Jb Geol	Buchiproetus rudricherti	Buchiproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Feist Belka 2018 N.Jb Geol	Cavetia furcifera hamlagdadiana	Cavetia	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	12	upper Kess Kess
Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science	Cavetia furcifera hamlagdadiana	Cavetia	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian		upper Kess Kess
Alberti 1970a SenckNaturGesell	Cavetia furcifera hamlagdadiana	Cavetia	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Alberti 1981b Senck lethaea	Cavetia furcifera hamlagdadiana	Cavetia	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	2	upper Kess Kess
Alberti 1983 Senck lethaea	Cavetia furcifera hamlagdadiana	Cavetia	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	4	upper Kess Kess
vanViersen Prescher 2011 GeolBelgica	Ceratarges aries	Ceratarges	Lichidae	Lichida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	El Otfal
vanViersen Prescher 2011 GeolBelgica	Ceratarges koumalii	Ceratarges	Lichidae	Lichida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	El Otfal
vanViersen Prescher 2011 GeolBelgica	Ceratarges ziregensis	Ceratarges	Lichidae	Lichida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	El Otfal
Feist Belka 2018 N.Jb Geol	Ceratocephala hoernesi	Ceratocephala	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian		12	upper Kess Kess
Alberti 1970a SenckNaturGesell	Ceratocephala hoernesi	Ceratocephala	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Cronier Oudot Klug DeBaets 2018 N.Jb Geol Pal	Ceratocephala vesiculosa	Ceratocephala	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Lerosey-Aubril Feist Chatterton 2008 Geol Mag	Chamaeleospis lkomalii	Chamaeleospis	Aulacopleuridae	Proetida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	El Otfal
H.Alberti 1974 N.Jb Geol Pal	Chaunoproetus berberus	Chaunoproetus	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	7	Achguig
Feist Mahboubi Girard 2016 Bull geo	Chlupacops cryphoides	Chlupacops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Frasnian	middle Frasnian	4	Chefar el Ahmar
Feist Mahboubi Girard 2016 Bull geo	Chlupacops laticeps	Chlupacops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Frasnian	middle Frasnian	2	Chefar el Ahmar
Alberti 1983 Senck lethaea	Chotecops zizensis	Chotecops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine

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Stegemann 2006 Münstersche Forschungen Geol Pal	Chotecops sp1	Chotecops	Phacopidae	Phacopida	Hassi Nebech	Tafilalt	Givetian	upper Givetian	3	Achguig
Stegemann 2006 Münstersche Forschungen Geol Pal	Chotecops sp1	Chotecops	Phacopidae	Phacopida	Hassi Nebech	Tafilalt	Givetian	upper Givetian	1	Achguig
Feist Orth 2000 ProcSDS	Chotecops zizensis	Chotecops	Phacopidae	Phacopida	Jbel Mech Irdane	Tafilalt	Eifelian	upper Eifelian	3	Bou Tcharafine
Feist Orth 2000 ProcSDS	Chotecops zizensis	Chotecops	Phacopidae	Phacopida	Jbel Mech Irdane	Tafilalt	Givetian	lower Givetian	2	Bou Tcharafine
Feist Orth 2000 ProcSDS	Chotecops zizensis	Chotecops	Phacopidae	Phacopida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Chotecops hoseri	Chotecops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelian	lower Eifelian	4	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Chotecops hoseri	Chotecops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelian	lower Eifelian	47	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Chotecops hoseri	Chotecops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelian	lower Eifelian	5	Chefar el Ahmar
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Coltraneia effelesa	Coltraneia	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Morzadec 2001 PalaeontA	Coltraneia oufatensis	Coltraneia	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	2	El Otfal
Morzadec 1997 PalaeontA	Coltraneia saourensis	Coltraneia	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Morzadec 1997 PalaeontA	Coltraneia saourensis	Coltraneia	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Morzadec 1997 PalaeontA	Coltraneia saourensis	Coltraneia	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Cronier Oudot Klug DeBaets 2018 NJB Geol Pal	indet	Comura	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Morzadec 2001 PalaeontA	Comura bultyncki	Comura	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	2	Tazoulaït
Morzadec 2001 PalaeontA	Comura bultyncki	Comura	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	El Otfal
Alberti 1969 SenckNaturGesell	Coniproetus eurysthene nomas	Coniproetus	Proetidae	Proetida	El Atrous	Tafilalt	Pragian	Pragian	1	Seheb el Rhassel
Alberti 1969 SenckNaturGesell	Coniproetus condensus mesembrinus	Coniproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1981a Senck lethaea	Cornuproetus cornutus djemelensis	Cornuproetus	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Cornuproetus cornutus djemelensis	Cornuproetus	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Cornuproetus cornutus djemelensis	Cornuproetus	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Feist Belka 2018 N.Jb Geol	Cornuproetus pusulosus	Cornuproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Cronier Oudot Klug DeBaets 2018 NJB Geol Pal	indet	Cornuproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	4	Amerboh
Feist Orth 2000 ProcSDS	Cornuproetus oudrissensis	Cornuproetus	Proetidae	Proetida	Jbel Ou Driss	Maider	Givetian	lower Givetian	2	Taboumakhloûf
Alberti 1970a SenckNaturGesell	Cornuproetus cornutus sspA	Cornuproetus	Proetidae	Proetida	Jbel Ouhalane	Maider	Givetian		1	
Alberti 1983 Senck lethaea	Crotalocephalina gibbus benziregensis	Crotalocephalina	Cheiruridae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	20	
Alberti 1969 SenckNaturGesell	Crotalocephalina gibbus	Crotalocephalina	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Crotalocephalina gibbus	Crotalocephalina	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1983 Senck lethaea	Crotalocephalina gibbus auster	Crotalocephalina	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1983 Senck lethaea	Crotalocephalus meridianus	Crotalocephalus	Cheiruridae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	1	
Alberti 1983 Senck lethaea	Crotalocephalus pauper saharensis	Crotalocephalus	Cheiruridae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	4	
Alberti 1983 Senck lethaea	Crotalocephalus pauper saharensis	Crotalocephalus	Cheiruridae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	1	
Alberti 1983 Senck lethaea	Chrotalocephalus sternbergi	Crotalocephalus	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Alberti 1983 Senck lethaea	Crotalocephalus pauper hamlagdadicus	Crotalocephalus	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1981b Senck lethaea	Crotalocephalus pauper hamlagdadicus	Crotalocephalus	Cheiruridae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	3	lower Kess Kess
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Crotalocephalus	Cheiruridae	Phacopida	Jbel	Tafilalt	Pragian	Pragian	2	Seheb el	
Basse in Basse and Müller 2004 Wiebelsheim	Cyberella lemkei	Cyberella	Proetidae	Proetida	Taboumakhloûf	Maider	Eifelian	lower Eifelian	1	Taboumakhloûf
Chatterton Gibb McKellar 2019	Cyphaspides ammari	Cyphaspides	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelian		2	
Cronier Oudot Klug DeBaets 2018 NJB Geol Pal	Cyphaspides ammari	Cyphaspides	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	5	Amerboh

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Chatterton Gibb McKellar 2019	Cyphaspides nicoleae	Cyphaspides	Aulacopleuridae	Proetida	Jdorf	Tafilalt	Eifelien		1	Bou Tcharafine
Chatterton Gibb McKellar 2019	Cyphaspides pankowskiorum	Cyphaspides	Aulacopleuridae	Proetida	Jdorf	Tafilalt	Eifelien		2	Bou Tcharafine
Chatterton Gibb McKellar 2019	Cyphaspides ammari	Cyphaspides	Aulacopleuridae	Proetida	Talawarite	Tafilalt	Eifelien		8	Bou Tcharafine
vanViersen Holland 2016 GeolBelgica	Cyphaspis khraidensis	Cyphaspis	Aulacopleuridae	Proetida	Bou Dib	Maider	Emsian		1	
vanViersen Holland 2016 GeolBelgica	Cyphaspis kippingi	Cyphaspis	Aulacopleuridae	Proetida	Bou Dib	Maider	Emsian	upper Emsian	2	Tazoulaït
vanViersen Holland 2016 GeolBelgica	Cyphaspis smeengi	Cyphaspis	Aulacopleuridae	Proetida	Bou Dib	Maider	Eifelien	lower Eifelien	1	El Otfal
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Cyphaspis agayura	Cyphaspis	Aulacopleuridae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	5	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Cyphaspis agayura	Cyphaspis	Aulacopleuridae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Cyphaspis hamidi	Cyphaspis	Aulacopleuridae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Cyphaspis hamidi	Cyphaspis	Aulacopleuridae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
vanViersen Holland 2016 GeolBelgica	Cyphaspis eberhardiei	Cyphaspis	Aulacopleuridae	Proetida	Foum Zguid	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
vanViersen Holland 2016 GeolBelgica	Cyphaspis foumzguidensis	Cyphaspis	Aulacopleuridae	Proetida	Foum Zguid	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
Feist Belka 2018 N.Jb Geol	Cyphaspis akkae	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian		3	upper Kess Kess
Alberti 1981a Senck lethaea	Cyphaspis boutscharafinense	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1981a Senck lethaea	Cyphaspis hamlagdadicus	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1983 Senck lethaea	Cyphaspis lierli	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	3	lower Kess Kess
Cronier Oudot Klug DeBaets 2018 N.Jb Geol Pal	Cyphaspis sp Aprim	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Cronier Oudot Klug DeBaets 2018 N.Jb Geol Pal	Cyphaspis sp B boutscharafinense	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1969 SenckNaturGesell	indet	Cyphaspis	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien		1	lower Kess Kess
Alberti 1981a Senck lethaea	Cyphaspis boutscharafinense	Cyphaspis	Aulacopleuridae	Proetida	Jbel Bou Tscharafine	Tafilalt	Emsian	upper Emsian	3	Amerboh
Alberti 1969 SenckNaturGesell	Cyphaspis boutscharafinense	Cyphaspis	Aulacopleuridae	Proetida	Jbel Bou Tscharafine	Tafilalt	Emsian	upper Emsian	1	Amerboh
vanViersen Prescher 2014 GeolBelgica	Cyphaspis walteri	Cyphaspis	Aulacopleuridae	Proetida	Jbel el Mrakib	Maider				Bou Dib
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis agayura	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis eberhardiei	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	4	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis hamidi	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis hamidi	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	8	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis sp A	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Cyphaspis	Aulacopleuridae	Proetida	Jbel Gara el	Draa Valley	Emsian	upper Emsian	2	Timrhamh	
vanViersen Holland 2016 GeolBelgica	Cyphaspis lerougei	Cyphaspis	Aulacopleuridae	Proetida	Jbel Issoumour Unknown	Maider	Emsian		1	
vanViersen Holland 2016 GeolBelgica	Cyphaspis sp I	Cyphaspis	Aulacopleuridae	Proetida	Jbel Issoumour Unknown	Maider	Eifelien		1	
vanViersen Holland 2016 GeolBelgica	Cyphaspis eximia	Cyphaspis	Aulacopleuridae	Proetida	Jbel Oufatene	Maider	Eifelien		1	Taboumakhloûf
vanViersen Holland 2016 GeolBelgica	Cyphaspis bluhmi	Cyphaspis	Aulacopleuridae	Proetida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	Taboumakhloûf
vanViersen Holland 2016 GeolBelgica	Cyphaspis khraidensis	Cyphaspis	Aulacopleuridae	Proetida	Khraid	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
vanViersen Holland 2016 GeolBelgica	Cyphaspis maharchensis	Cyphaspis	Aulacopleuridae	Proetida	Maharch	Maider	Pragian	Pragian	1	Ihandar
vanViersen Holland 2016 GeolBelgica	Cyphaspis heisingi	Cyphaspis	Aulacopleuridae	Proetida	Mdâour el Kbir	Draa Valley	Pragian	Pragian	1	Assa
Crônier Abbache Khalidi Oudot Maillat Ouali-Mehadj 2018 Geol Mag	Cyphaspis sp A	Cyphaspis	Aulacopleuridae	Proetida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	2	Chefar el Ahmar
vanViersen Holland 2016 GeolBelgica	Cyphaspis ihmadii	Cyphaspis	Aulacopleuridae	Proetida	Taboumakhloûf	Maider	Givetian	lower Givetian	1	Bou Dib
vanViersen Holland 2016 GeolBelgica	Cyphaspis agayura	Cyphaspis	Aulacopleuridae	Proetida	Talawarite	Tafilalt	Emsian	upper Emsian	1	Amerboh
vanViersen Holland 2016 GeolBelgica	Cyphaspis juergenhollandi	Cyphaspis	Aulacopleuridae	Proetida	Talawarite	Tafilalt	Emsian	upper Emsian	1	Amerboh
Lerosey-Aubril Feist 2006 Pal	Cyrtosymbole rectifrons	Cyrtosymbole	Proetidae	Proetida	Korb el Atil	Tafilalt	Famennian	lower Famennian	85	Achguig
Lerosey-Aubril Feist 2006 Pal	Cyrtosymbole sp A	Cyrtosymbole	Proetidae	Proetida	Korb el Atil	Tafilalt	Famennian	lower Famennian	1	Achguig

Bases de données

H.Alberti 1976a Njb Geol Pal	Cyrtosymbolina varica	Cyrtosymbolina	Proetidae	Proetida	Bin Jbilel	Tafilalt	Famennian	lower Famennian	5	Achguig
H.Alberti 1976a Njb Geol Pal	Cyrtosymbolina varica	Cyrtosymbolina	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	lower Famennian	15	Achguig
H.Alberti 1976a Njb Geol Pal	Cyrtosymbolina varica	Cyrtosymbolina	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	lower Famennian	1	Achguig
Alberti 1970a SenckNaturGesell	Cyrtosymboloides samum	Cyrtosymboloides	Proetidae	Proetida	Gara Mdouard	Tafilalt	Eifelien	lower Eifelien	10	Amerboh
Johnson Fortey 2012 Jpal	Dalejeproetus owensi	Dalejeproetus	Proetidae	Proetida	Akka n'Talilite	Maider	Pragian	Pragian	3	Ihandar
Johnson Fortey 2012 Jpal	Dalejeproetus sagaouii	Dalejeproetus	Proetidae	Proetida	Jbel el Mrakib	Maider	Pragian	Pragian	3	Ihandar
Feist Orth 2000 ProcSDS	Dechenella gigouti	Dechenella	Proetidae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine
Feist Orth 2000 ProcSDS	Dechenella ziatensis	Dechenella	Proetidae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	8	Bou Tcharafine
Alberti 1983 Senck lethaea	Denckmannites morator	Denckmannites	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	1	
Alberti 1967b Senck leth	Denemarkia tafilaltensis	Denemarkia	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1983 Senck lethaea	Denemarkia tafilaltensis	Denemarkia	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering	Destombesina tafilaltensis	Destombesina	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Cronier Oudor Klug DeBaets 2018 Njb Geol Pal	Destombesina tafilaltensis	Destombesina	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Morzadec 2001 PalaeontA	Destombesina tafilaltensis	Destombesina	Acastidae	Phacopida	Jbel Bou Tscharafine	Tafilalt	Emsian	upper Emsian	8	Amerboh
Morzadec 1997 PalaeontA	Destombesina ougartensis	Destombesina	Acastidae	Phacopida	Zerhamra	Ougarta basin	Emsian	upper Emsian	11	Teferguenit
Alberti 1969 SenckNaturGesell	Diademaproetus praecursor	Diademaproetus	Proetidae	Proetida	Tissint	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Alberti 1969 SenckNaturGesell	Diademaproetus praecursor	Diademaproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	2	upper Kess Kess
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Diademaproetus mohamedi	Diademaproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Diademaproetus praecursor	Diademaproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Diademaproetus praecursor	Diademaproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	10	Timrhamhart
Alberti 1969 SenckNaturGesell	Diademaproetus praecursor	Diademaproetus	Proetidae	Proetida	Tizi Takereit	Maider	Emsian	upper Emsian	1	
Feist Mahboubi Girard 2016 Bull geo	Dianops algeriensis	Dianops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	upper Famennian	2	Argiles de Marhouma
Crônier Multi François Benyoucef Brice 2013 Geol Mag	Dianops algeriensis	Dianops	Phacopidae	Phacopida	Tamtert Zereg	Ougarta basin	Famennian	upper Famennian	1	Argiles de Marhouma
Crônier Multi François Benyoucef Brice 2013 Geol Mag	Dianops typhlops	Dianops	Phacopidae	Phacopida	Tamtert Zereg	Ougarta basin	Famennian	upper Famennian	1	Argiles de Marhouma
Crônier Multi François Benyoucef Brice 2013 Geol Mag	Dianops vicarius	Dianops	Phacopidae	Phacopida	Tamtert Zereg	Ougarta basin	Famennian	upper Famennian	3	Argiles de Marhouma
Crônier Multi François Benyoucef Brice 2013 Geol Mag	Dianops	Phacopidae	Phacopida	Tamtert	Ougarta basin	Famennian	upper Fa mennian	1	Argiles de	
Struve 1995 Senck lethaea	Drotops armatus	Drotops	Phacopidae	Phacopida	Jbel Issoumour Unknown	Maider	Givetian	lower Givetian	6	
Struve 1995 Senck lethaea	Drotops megalomanicus megalomanicus	Drotops	Phacopidae	Phacopida	Jbel Issoumour Unknown	Maider	Givetian	lower Givetian	26	
Struve 1995 Senck lethaea	Drotops megalomanicus subornatus	Drotops	Phacopidae	Phacopida	Jbel Issoumour Unknown	Maider	Givetian	lower Givetian	5	
McKellar Chatterton 2009 Pal Canadiana	Drotops armatus	Drotops	Phacopidae	Phacopida	Taboumakhlouf	Maider	Givetian	lower Givetian	1	Bou Dib
McKellar Chatterton 2009 Pal Canadiana	Drotops megalomanicus megalomanicus	Drotops	Phacopidae	Phacopida	Taboumakhlouf	Maider	Givetian	lower Givetian	1	Bou Dib
Feist Mahboubi Girard 2016 Bull geo	Enigmapyge marhoumensis	Enigmapyge	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	lower Famennian	1	Argiles de Marhouma
Holloway 2005 Pal Zeit	Eocryphops albertii	Eocryphops	Phacopidae	Phacopida	Jdorf	Maider	Eifelien	lower Eifelien	9	Bou Tcharafine
Alberti 1983 Senck lethaea	Erbenaspis erbeni	Erbenaspis	Proetidae	Proetida	Ben Zireg	Ougarta basin	Pragian	Pragian	2	
Morzadec 1995 Njb Geol Pal	Erbenochile erbeni	Erbenochile	Dalmanitidae	Phacopida	El Kseib	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Erbenochile erbeni	Erbenochile	Dalmanitidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Chatterton Gibbs 2010 Jpal	Erbenochile erbeni	Erbenochile	Dalmanitidae	Phacopida	Foum Zguid	Draa Valley	Emsian	upper Emsian	1	Timrhamhart

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Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Erbenochile erbeni	Erbenochile	Dalmanitidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Gibbs 2010 Jpal	Erbenochile issoumourensis	Erbenochile	Dalmanitidae	Phacopida	Jbel Issoumour SW	Maider			4	El Otfal
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Erbenochile erbeni	Erbenochile	Dalmanitidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Alberti 1969 SenckNaturGesell	Eremiproetus dufresnoyi australis	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	5	upper Kess Kess
Alberti 1970a SenckNaturGesell	Eremiproetus dufresnoyi australis	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	2	upper Kess Kess
Alberti 1983 Senck lethaea	Eremiproetus dufresnoyi australomaurus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Eifelian	lower Eifelian	5	Bou Tcharafine
Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Eremiproetus dufresnoyi saharae	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	6	Amerboh
Alberti 1967b Senck leth	Eremiproetus dufresnoyi saharae	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1969 SenckNaturGesell	Eremiproetus dufresnoyi saharae	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1983 Senck lethaea	Eremiproetus dufresnoyi saharae	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Feist Belka 2018 N.Jb Geol	Eremiproetus emerita	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Alberti 1969 SenckNaturGesell	Eremiproetus erfoudanus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1967b Senck leth	Eremiproetus helmuti helmuti	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Eremiproetus helmuti helmuti	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1969 SenckNaturGesell	Eremiproetus helmuti junior	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	3	lower Kess Kess
Alberti 1967b Senck leth	Eremiproetus meridianomaurus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Eremiproetus munitus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Feist Belka 2018 N.Jb Geol	Eremiproetus notabilis	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Alberti 1967a Senck leth	Eremiproetus tafilaltanus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Eremiproetus tafilaltanus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	7	lower Kess Kess
Alberti 1970a SenckNaturGesell	Eremiproetus tafilaltanus	Eremiproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
H.Alberti 1973 Njb Geol Pal	Franconicobole bordjensis maroccana	Franconicobole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	3	Achguig
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Gandlops tammrherthus	Gandlops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	8	Timrhamhart
Morzadec 1997 PalaeontA	Ganetops djemelensis	Ganetops	Acastidae	Phacopida	Dkhissa	Ougarta basin	Lochkovian	upper Lochkovian	4	Dkhissa
Morzadec 1997 PalaeontA	Ganetops djemelensis	Ganetops	Acastidae	Phacopida	El Kseib	Ougarta basin	Lochkovian	upper Lochkovian	2	Dkhissa
Morzadec 1997 PalaeontA	Ganetops djemelensis	Ganetops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Lochkovian	upper Lochkovian	3	Dkhissa
Morzadec 1997 PalaeontA	Ganetops djemelensis	Ganetops	Acastidae	Phacopida	Zerhamra	Ougarta basin	Lochkovian	upper Lochkovian	3	Dkhissa
Bignon Corbacho Lopez-Soriano 2014 Geobios	Minicryphaeus giganteus	Gen1	Acastidae	Phacopida	Jbel el Mrakib	Maider	Pragian	Pragian	4	Ihandar
Morzadec 2001 PalaeontA	Metacanthina issoumourensis	Gen1	Acastidae	Phacopida	Jbel Issoumour NW	Maider	Pragian	Pragian	3	Ihandar
Morzadec 2001 PalaeontA	Metacanthina maderensis	Gen1	Acastidae	Phacopida	Jbel Issoumour NW	Maider	Pragian	Pragian	1	Ihandar
Klug Kröger Korn Rücklin Schemm- Gregory DeBaets Mapes 2008 Pal Abt A	Metacanthina wallacei	Gen2	Acastidae	Phacopida	El Atrous	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Metacanthina wallacei	Gen2	Acastidae	Phacopida	Jbel Ouafilal-Filon 12	Tafilalt	Emsian	lower Emsian	3	Seheb el Rhassel
Klug Kröger Korn Rücklin Schemm- Gregory DeBaets Mapes 2008 Pal Abt A	Metacanthina wallacei	Gen2	Acastidae	Phacopida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	43	Seheb el Rhassel
Gibb Chatterton 2010 Pal Canadiana	Gerastos aintawilus	Gerastos	Proetidae	Proetida	Bou Dib	Maider	Eifelian	lower Eifelian	2	El Otfal
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Gerastos marocensis	Gerastos	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	6	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Gerastos marocensis	Gerastos	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	5	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadj 2016 Geol Mag	Gerastos marocensis	Gerastos	Proetidae	Proetida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	14	Chefar el Ahmar
Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Gerastos sp A vel Rhenocynproetus sp A	Gerastos	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	7	Amerboh

Bases de données

Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Gerastos sp B vel Rhenocynproetus sp B	Gerastos	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	16	Amerboh
Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Gerastos sp C	Gerastos	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Gibb Chatterton 2010 Pal Canadiana	Gerastos ainrasifus	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Eifelien	lower Eifelien	3	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos discombobulatus	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Eifelien	upper Eifelien	4	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos emmetus	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Givetian	lower Givetian	1	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos izius	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Givetian	lower Givetian	5	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos lisanrasus	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Eifelien	lower Eifelien	1	El Otfal
Gibb Chatterton 2010 Pal Canadiana	Gerastos taqus	Gerastos	Proetidae	Proetida	Jbel el Mrakib	Maider	Eifelien	lower Eifelien	2	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos aintawilus	Gerastos	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	7	Timrhamhart
Gibb Chatterton 2010 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	6	Timrhamhart
Chatterton Gibbs 2010 Jpal	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	2	El Otfal
Gibb Chatterton 2010 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	1	El Otfal
Gibb Chatterton 2010 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	El Otfal
Feist Orth 2000 ProcSDS	Gerastos granulosus sensu	Gerastos	Proetidae	Proetida	Jbel Ou Driss	Maider	Givetian	lower Givetian	3	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos cuvieri malisus	Gerastos	Proetidae	Proetida	Jbel Oufatene	Maider	Eifelien	upper Eifelien	3	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos cuvieri malisus	Gerastos	Proetidae	Proetida	Jbel Oufatene	Maider	Eifelien	upper Eifelien	3	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Jbel Oufatene	Maider	Emsian	upper Emsian	3	Tazoulaît
Feist Orth 2000 ProcSDS	Gerastos prox umerbianus	Gerastos	Proetidae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	3	Bou Tcharafine
Gibb Chatterton 2010 Pal Canadiana	Gerastos lisanrasus	Gerastos	Proetidae	Proetida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	El Otfal
Gibb Chatterton 2010 Pal Canadiana	Gerastos malisjildus	Gerastos	Proetidae	Proetida	Jbel Zireg	Maider	Eifelien	lower Eifelien	1	Taboumakhloûf
Gibb Chatterton 2010 Pal Canadiana	Gerastos hammii	Gerastos	Proetidae	Proetida	Saredrar	Maider	Eifelien	lower Eifelien	7	El Otfal
Gibb Chatterton 2010 Pal Canadiana	Gerastos emmetus	Gerastos	Proetidae	Proetida	Taboumakhloûf	Maider	Givetian	lower Givetian	1	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos emmetus	Gerastos	Proetidae	Proetida	Taboumakhloûf	Maider	Givetian	lower Givetian	6	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos emmetus	Gerastos	Proetidae	Proetida	Taboumakhloûf	Maider	Givetian	lower Givetian	2	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos emmetus	Gerastos	Proetidae	Proetida	Taboumakhloûf	Maider	Givetian	middle Givetian	1	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos raribus	Gerastos	Proetidae	Proetida	Taboumakhloûf	Maider	Givetian	lower Givetian	2	Bou Dib
Gibb Chatterton 2010 Pal Canadiana	Gerastos marocensis	Gerastos	Proetidae	Proetida	Talawarite	Tafilalt	Emsian	upper Emsian	3	Amerboh
Alberti 1981a Senck lethaea	Gravicalymene hamlagdadica	Gravicalymene	Calymenidae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	5	lower Kess Kess
Morzdec 1997 PalaeontA	Indet	Greenops	Acastidae	Phacopida	El Kseib	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
H.Alberti 1973 Njb Geol Pal	Haasproetus wildungensis	Haasproetus	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Famennian	4	Achguig
Alberti 1983 Senck lethaea	Indet	Harpes	Harpetidae	Harpetida	Ben Zireg	Ougarta basin	Pragian	Pragian	1	
Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Harpes hamarlaghdadensis	Harpes	Harpetidae	Harpetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	6	Amerboh
Zapalski Klug 2018 Njb Geol Pal	Harpes hamarlaghdadensis	Harpes	Harpetidae	Harpetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Feist Chatterton 2015 Palaeontology	Heliopeltis ihmadii	Heliopeltis	Scutelluidae	Corynexoch	Jbel Oufatene	Maider			3	Tazoulaît
Feist Chatterton 2015 Palaeontology	Heliopeltis johnsoni	Heliopeltis	Scutelluidae	Corynexoch	Jbel Oufatene	Maider			1	Tazoulaît
Feist Chatterton 2015 Palaeontology	Indet	Heliopeltis	Scutelluidae	Corynexoch	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Tazoulaît
Feist Orth 2000 ProcSDS	Helmutia rissanensis	Helmutia	Proetidae	Proetida	Jbel Mech Irdane	Tafilalt	Eifelien	upper Eifelien	7	Bou Tcharafine
Feist Orth 2000 ProcSDS	Helmutia rissanensis	Helmutia	Proetidae	Proetida	Jbel Mech Irdane	Tafilalt	Givetian	lower Givetian	7	Bou Tcharafine
Feist Orth 2000 ProcSDS	Helmutia sp A	Helmutia	Proetidae	Proetida	Jbel Mech Irdane	Tafilalt	Eifelien	upper Eifelien	1	Bou Tcharafine
Feist Orth 2000 ProcSDS	Helmutia tuberculatus	Helmutia	Proetidae	Proetida	Jbel Mech Irdane	Tafilalt	Eifelien	upper Eifelien	1	Bou Tcharafine
Feist Orth 2000 ProcSDS	Helmutia rissanensis	Helmutia	Proetidae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	9	Bou Tcharafine
vanViersen Lerouge 2019 Pal Zeit	Hollandiella curvirostris	Hollandiella	Proetidae	Proetida	El Achana	Maider	Pragian	Pragian	3	Ihandar
vanViersen Lerouge 2019 Pal Zeit	Hollandiella lebruni	Hollandiella	Proetidae	Proetida	Lansser	Draa Valley	Emsian	upper Emsian	2	Timrhamhart

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vanViersen Lerouge 2019 Pal Zeit	Hollandiella verecunda	Hollandiella	Proetidae	Proetida	Tafraoute	Maider	Pragian	Pragian	1	Ihandar
Morzadec 2001 PalaeontA	Hollandops boudibensis	Hollandops	Acastidae	Phacopida	Bou Dib	Maider	Emsian	upper Emsian	3	Er Remlia
Morzadec 1997 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	El Kseib	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Morzadec 1997 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjil 2016 Geol Mag	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	5	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjil 2016 Geol Mag	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Cronier Oudot Klug DeBaets 2018 N.Jb Geol Pal	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	2	Amerboh
Morzadec 2001 PalaeontA	Hollandops burtandmimiae	Hollandops	Acastidae	Phacopida	Jbel el Anhsar	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Morzadec 2001 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Jbel el Anhsar	Draa Valley	Emsian	upper Emsian	4	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Hollandops aithassainorum	Hollandops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	6	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Gibbs 2010 Jpal	Hollandops burtandmimiae	Hollandops	Acastidae	Phacopida	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	1	El Otfal
Chatterton Gibbs 2010 Jpal	Hollandops burtandmimiae	Hollandops	Acastidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	El Otfal
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Hollandops		Acastidae	Phacopida	Jbel	Tafilalt	Pragian	Pragian	1	Seheb el
Morzadec 2001 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Tazoulait
Morzadec 1997 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	11	Chefar el Ahmar
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Morzadec 1997 PalaeontA	Hollandops lemaitreae	Hollandops	Acastidae	Phacopida	Zerhamra	Ougarta basin	Emsian	upper Emsian	10	Teferguenit
Morzadec 1997 PalaeontA	Hollandops mesocristata	Hollandops	Acastidae	Phacopida	Zerhamra	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Hollandops aithassainorum	Hollandops	Acastidae	Phacopida	Zguilma	Draa Valley	Eifelien	lower Eifelien	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Hollandops aithassainorum	Hollandops	Acastidae	Phacopida	Zguilma	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
Crônier Malti François Benyoucef Brice 2013 Geol Mag	Houseops cryphoides	Houseops	Phacopidae	Phacopida	Gara Diba	Ougarta basin	Famennian	lower Famennian	1	Argiles de Marho uma
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Dar Kaoua	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Hassi Nebech	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Hassi Nebech	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Jbel Amlane	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Jbel Bou Tcharafine	Tafilalt	Givetian		1	
McKellar Chatterton 2009 Pal Canadiana	Hypsipariops vagabundus	Hypsipariops	Phacopidae	Phacopida	Jbel Issoumour SW	Maider	Givetian	lower Givetian	1	Bou Dib
Struve 1995 Senck lethaea	Hypsipariops vagabundus	Hypsipariops	Phacopidae	Phacopida	Jbel Issoumour Unknown	Maider	Givetian	lower Givetian	36	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Ouidane Chebbi	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Ras el Kebbar	Tafilalt	Givetian		1	
Stegemann 2006 Münstersche Forschungen Geol Pal	Hypsipariops torleyi	Hypsipariops	Phacopidae	Phacopida	Seheb el Rhassal 2	Tafilalt	Givetian		1	
Alberti 1981a Senck lethaea	Ignoproetus erfoudanus	Ignoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	11	Amerboh
Alberti 1970a SenckNaturGesell	Ignoproetus waldschmidti	Ignoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Alberti 1969 SenckNaturGesell	Ignoproetus waldschmidti	Ignoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	upper Eifelien	4	Bou Tcharafine
Feist Belka 2018 N.Jb Geol	Isoprusia laportei	Isoprusia	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Morzadec 2001 PalaeontA	Indet	Kayserops	Acastidae	Phacopida	Jbel Bou Tcharafine	Tafilalt	Emsian	lower Emsian	3	Seheb el Rhassel

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Morzadec 2001 PalaeontA	Kayserops marocanensis	Kayserops	Acastidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	Er Remlia
Morzadec 2001 PalaeontA	Kayserops marocanensis	Kayserops	Acastidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	Tazoulait
Morzadec 2001 PalaeontA	Kayserops marocanensis	Kayserops	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Tazoulait
Morzadec 1997 PalaeontA	Kayserops djazaïrensis	Kayserops	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Morzadec 1997 PalaeontA	Kayserops djazaïrensis	Kayserops	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Morzadec 1997 PalaeontA	Kayserops djazaïrensis	Kayserops	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Alberti 1969 SenckNaturGesell	Kegelella listei prolistei	Kegelella	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Ketneraspis pigra	Ketneraspis	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Eifelien	upper Eifelien	3	Bou Tcharafine
vanViersen Heising 2015 GeolBelgica	Ketneraspis prescheri	Ketneraspis	Odontopleuridae	Lichida	Jbel Issoumour Unknown	Maider	Pragian	Pragian	1	Ihandar
Feist Orth 2000 ProcSDS	Ketneraspis pigra	Ketneraspis	Odontopleuridae	Lichida	Jbel Mech Irdane	Tafilalt	Eifelien	upper Eifelien	1	Bou Tcharafine
Feist Chatterton 2015 Palaeontology	Kolihapeltis hamlaghdadica	Kolihapeltis	Scutelluidae	Corynexoch	Amsoy	Tafilalt	Pragian	Pragian	3	Seheb el Rhassel
Feist Chatterton 2015 Palaeontology	Kolihapeltis bassei	Kolihapeltis	Scutelluidae	Corynexoch	El Achana	Maider	Pragian	Pragian	4	Ihandar
Feist Chatterton 2015 Palaeontology	Kolihapeltis chlupaci hollardi	Kolihapeltis	Scutelluidae	Corynexoch	El Achana	Maider	Pragian	Pragian	3	Ihandar
Feist Chatterton 2015 Palaeontology	Kolihapeltis bassei	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1966b Pal Zeitschrift	Kolihapeltis bassei	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1966b Pal Zeitschrift	Kolihapeltis chlupaci hollardi	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Feist Chatterton 2015 Palaeontology	Kolihapeltis chlupaci hollardi	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	5	lower Kess Kess
Alberti 1970a SenckNaturGesell	Kolihapeltis hamlaghdadica	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Feist Chatterton 2015 Palaeontology	Kolihapeltis hamlaghdadica	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1966b Pal Zeitschrift	Kolihapeltis maghrebica	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1983 Senck Iethaea	Kolihapeltis maghrebica	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	4	lower Kess Kess
Feist Chatterton 2015 Palaeontology	Kolihapeltis maghrebica	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	4	lower Kess Kess
Feist Chatterton 2015 Palaeontology	Kolihapeltis tafilaltensis	Kolihapeltis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	8	lower Kess Kess
Alberti 1983 Senck Iethaea	Koneprusia brutoni	Koneprusia	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1970a SenckNaturGesell	Koneprusia subtermata	Koneprusia	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Alberti 1967b Senck Ieth	Koneprusia tafilaltana	Koneprusia	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Koneprusia dahmani	Koneprusia	Odontopleuridae	Lichida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	4	Timrhamhart
Feist McNamara 2007 Geol Mag	Koneprusia aboussalamae	Koneprusia	Odontopleuridae	Lichida	SW El Jorf	Maider	Givetian	upper Givetian	1	Bou Dîb
Alberti 1969 SenckNaturGesell	Koneprusites baconi saharae	Koneprusites	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	3	Bou Tcharafine
vanViersen Lerouge 2019 Pal Zeit	Koneprusites oresibios	Koneprusites	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Feist Orth 2000 ProcSDS	Indet	Koneprusites	Proetidae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Koneprusites moestus	Koneprusites	Proetidae	Proetida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar
Corbacho 2014a Bettleria	Lanceaspis hammondi	Lanceaspis	Acastidae	Phacopida	Oumjrane	Maider	Pragian	Pragian	25	Ihandar
Cronier Oudot Klug DeBaets 2018 Njb Geol Pal	Indet	Leonaspis	Odontopleuridae	Lichida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Leonaspis haddanei	Leonaspis	Odontopleuridae	Lichida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Leonaspis haddanei	Leonaspis	Odontopleuridae	Lichida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	5	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Leonaspis spinicurva	Leonaspis	Odontopleuridae	Lichida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	4	Timrhamhart
Alberti 1970a SenckNaturGesell	Leonaspis issoumourensis	Leonaspis	Odontopleuridae	Lichida	Jbel Issoumour SW	Maider	Emsian	lower Emsian	2	Bou Tiskouïne
Klug Kröger Korn Rücklin Schemm Gregory DeBaets Mapes 2008 Pal Abt A	Leonaspis issoumourensis	Leonaspis	Odontopleuridae	Lichida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Alberti 1969 SenckNaturGesell	Lepidoproetus praematurus	Lepidoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Johnson Fortey 2012 Jpal	Lepidoproetus maharchianus	Lepidoproetus	Proetidae	Proetida	Jbel el Mrakib	Maider	Pragian	Pragian	2	Ihandar
Johnson Fortey 2012 Jpal	Lepidoproetus lahceni	Lepidoproetus	Proetidae	Proetida	Jbel Oufatene	Maider	Pragian	Pragian	2	Ihandar

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Johnson Fortey 2012 Jpal	Lepidoproetus spendens	Lepidoproetus	Proetidae	Proetida	Jbel Oufatene	Maider	Pragian	Pragian	1	Ihandar
vanViersen Lerouge 2019 Pal Zeit	Lepidoproetus maharchianus	Lepidoproetus	Proetidae	Proetida	Jbel Zireg	Maider	Pragian	Pragian	1	Ihandar
vanViersen Lerouge 2019 Pal Zeit	Lepidoproetus arenicolus	Lepidoproetus	Proetidae	Proetida	Oum Jerane	Maider	Pragian	Pragian	1	Ihandar
Alberti 1969 SenckNaturGesell	Linguaproetus saharensis	Linguaproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Eifelien		2	
Alberti 1970a SenckNaturGesell	Linguaproetus saharensis	Linguaproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Eifelien		1	
Alberti 1967b Senck leth	Linguaproetus saharensis	Linguaproetus	Proetidae	Proetida	Jbel Ihrs	Tafilalt	Emsian	upper Emsian	1	Amerboh
Feist Belka 2018 N.Jb Geol	Lioharpes wendti	Lioharpes	Harpetidae	Harpetida	Hamar Laghdad	Tafilalt	Emsian		15	upper Kess Kess
Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A	Metacanthina	Acastidae	Phacopida	Ouidane	Tafilalt	Emsian	lower Emsian	4		Seheb el
Morzadec 2001 PalaeontA	Minicryphaeus quaterspinosus	Minicryphaeus	Acastidae	Phacopida	Jbel Issoumour NW	Maider	Pragian	Pragian	1	Ihandar
Morzadec 2001 PalaeontA	Minicryphaeus sarirus	Minicryphaeus	Acastidae	Phacopida	Jbel Issoumour NW	Maider	Pragian	Pragian	2	Ihandar
Morzadec 2001 PalaeontA	Minicryphaeus minimus	Minicryphaeus	Acastidae	Phacopida	Jbel Oufatene	Maider	Pragian	Pragian	10	Ihandar
Morzadec 2001 PalaeontA	Minicryphaeus quaterspinosus	Minicryphaeus	Acastidae	Phacopida	Jbel Oufatene	Maider	Pragian	Pragian	2	Ihandar
H. Alberti 1974 NJb Geol Pal	Mirabole kielanae	Mirabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Famennian	7	Achguig
Alberti 1981a Senck lethaea	Montanproetus midas amlanensis	Montanproetus	Proetidae	Proetida	Ben Zireg	Ougarta basin	Emsian	upper Emsian	1	
Alberti 1967a Senck leth	Montanproetus chlupaci	Montanproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Montanproetus chlupaci	Montanproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	30	lower Kess Kess
Alberti 1969 SenckNaturGesell	Montanproetus midas amlanensis	Montanproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	lower Emsian	4	Seheb el Rhassel
Alberti 1981a Senck lethaea	Montanproetus midas amlanensis	Montanproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Alberti 1969 SenckNaturGesell	Montanproetus midas amlanensis	Montanproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Alberti 1969 SenckNaturGesell	Montanproetus pernix boutsharafinensis	Montanproetus	Proetidae	Proetida	Jbel Bou Tscharafine	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Struve 1992 Senck lethaea	Morocconites expansus	Morocconites	Dalmanitidae	Phacopida	Alnif	Maider	Emsian	upper Emsian	1	Tazoulaït
Struve 1992 Senck lethaea	Morocconites lemkei	Morocconites	Dalmanitidae	Phacopida	Alnif	Maider	Emsian	upper Emsian	1	Tazoulaït
Struve in Boucot et al. 1989 Senck lethaea	Morocconites malladoïdes	Morocconites	Dalmanitidae	Phacopida	Alnif	Maider	Emsian	upper Emsian	1	Tazoulaït
McKellar Chatterton 2009 Pal Canadiana	Morocops fortayi	Morocops	Phacopidae	Phacopida	Bou Dib	Maider	Emsian	upper Emsian	6	Tazoulaït
vanViersen Holland Koppka 2017 Bull geo	Morocops fortayi	Morocops	Phacopidae	Phacopida	Bou Dib	Maider	Emsian	upper Emsian	1	Tazoulaït
McKellar Chatterton 2009 Pal Canadiana	Morocops lebesus	Morocops	Phacopidae	Phacopida	Bou Dib	Maider	Eifelien	lower Eifelien	2	El Otfal
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Morocops chattertoni	Morocops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Morocops chattertoni	Morocops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Morocops granulops	Morocops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	3	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Morocops granulops	Morocops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	27	Chefar el Ahmar
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Morocops granulops	Morocops	Phacopidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Schraut 2000a Senck Lethaea	Morocops sparsinodosus struvei	Morocops	Phacopidae	Phacopida	Foum Zguid	Draa Valley	Eifelien	lower Eifelien	5	Timrhamhart
Alberti 1983 Senck lethaea	Morocops tafilaltanus	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Cronier Oudot Klug DeBaets 2018 NJb Geol Pal	Morocops davidbrutoni	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	69	Amerboh
Cronier Oudot Klug DeBaets 2018 NJb Geol Pal	Morocops fortayi	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	5	Amerboh
Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering	Morocops granulops	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Cronier Oudot Klug DeBaets 2018 NJb Geol Pal	Morocops granulops	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	30	Amerboh
Klug Schulz DeBaets 2009 APP	Morocops granulops	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Zapalski Klug 2018 NJb Geol Pal	Morocops granulops	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Cronier Oudot Klug DeBaets 2018 NJb Geol Pal	Morocops sp A	Morocops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	2	Amerboh

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McKellar Chatterton 2009 Pal Canadiana	Morocops granulops	Morocops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Maider	Emsian	upper Emsian	7	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Morocops granulops	Morocops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Morocops granulops	Morocops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	8	Timrhamhart
McKellar Chatterton 2009 Pal Canadiana	Morocops lebesus	Morocops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Maider	Eifelian	lower Eifelian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Morocops lebesus	Morocops	Phacopidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Eifelian	lower Eifelian	3	Timrhamhart
McKellar Chatterton 2009 Pal Canadiana	Morocops fortayi	Morocops	Phacopidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	Tazoulaït
McKellar Chatterton 2009 Pal Canadiana	Morocops fortayi	Morocops	Phacopidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	Tazoulaït
Le Maître 1952 Mémoire de la Carte géologique de l'Algérie	Morocops granulops	Morocops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Emsian		2	
Crônier Abbache Khaldi Oudot Maillot Ouali-Mehadji 2018 Geol Mag	Morocops sp F	Morocops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelian	lower Eifelian	3	Chefar el Ahmar
Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A	Morocops torkozensis	Morocops	Phacopidae	Phacopida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	2	Seheb el Rhassel
McKellar Chatterton 2009 Pal Canadiana	Morocops ovatus	Morocops	Phacopidae	Phacopida	Taharajat Oufatene	Maider	Emsian	upper Emsian	1	Tazoulaït
McKellar Chatterton 2009 Pal Canadiana	Morocops ovatus	Morocops	Phacopidae	Phacopida	Taharajat Oufatene	Maider	Emsian	upper Emsian	6	Tazoulaït
McKellar Chatterton 2009 Pal Canadiana	Morocops fortayi	Morocops	Phacopidae	Phacopida	Talawarite	Tafilalt	Emsian	upper Emsian	9	Tazoulaït
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Morzadecops zguidensis	Morzadecops	Acastidae	Phacopida	Jbel Ouafilal-Filon 12	Tafilalt	Emsian	lower Emsian	60	Seheb el Rhassel
Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A	Morzadecops zguidensis	Morzadecops	Acastidae	Phacopida	Jbel Ouafilal-Filon 12	Tafilalt	Emsian	lower Emsian	4	Seheb el Rhassel
Morzadec 2001 PalaeontA	Morzadecops zguidensis	Morzadecops	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	lower Emsian	1	Bou Tiskaouïne
Morzadec 2001 PalaeontA	Morzadecops zguidensis	Morzadecops	Acastidae	Phacopida	Mdâour el Kbir	Draa Valley	Emsian	lower Emsian	3	Mdaouer el Kbir
Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A	Morzadecops zguidensis	Morzadecops	Acastidae	Phacopida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	12	Seheb el Rhassel
Morzadec 1997 PalaeontA	Morzadecops matutina	Morzadecops	Acastidae	Phacopida	Zerhamra	Ougarta basin	Lochkovian	upper Lochkovian	2	Dkhissa
Morzadec 1997 PalaeontA	Morzadecops matutina	Morzadecops	Acastidae	Phacopida	Zerhamra	Ougarta basin	Lochkovian	upper Lochkovian	4	Dkhissa
Morzadec 2001 PalaeontA	Mrakibina cattoi	Mrakibina	Acastidae	Phacopida	Jbel el Mrakib	Maider	Eifelian	lower Eifelian	3	El Otfal
Alberti 1981b Senck lethaea	Mulciberaspis georgei	Mulciberaspis	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Feist Belka 2018 N.Jb Geol	Nagaproetus frequens	Nagaproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Alberti 1967b Senck leth	Nagaproetus frequens	Nagaproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Alberti 1969 SenckNaturGesell	Nagaproetus frequens	Nagaproetus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	10	upper Kess Kess
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Odontochile hausmanni	Odontochile	Dalmanitidae	Phacopida	Jbel Ouafilal-Filon 12	Tafilalt	Pragian	Pragian	1	Seheb el Rhassel
Schraut 2000c Senck Lethaea	Odontochile magrebianum	Odontochile	Dalmanitidae	Phacopida	Fissint	Draa Valley	Pragian	Pragian	3	Assa
H.Alberti 1972 N.Jb Geol Pal	Omegops accipitrinus	Omegops	Phacopidae	Phacopida	Bordj Est	Tafilalt	Famennian	uppermost Famennian	9	Achguig
Alberti 1967b Senck leth	Orbitoproetus africanus	Orbitoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Orbitoproetus africanus	Orbitoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1969 SenckNaturGesell	Orbitoproetus ovalis	Orbitoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Cronier Oudot Klug DeBaets 2018 N.Jb Geol Pal	indet	Orbitoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Lerosey-Aubril Feist 2005 APP	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	5	Achguig
H.Alberti 1975a N.Jb Geol Pal	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	17	Achguig
Lerosey-Aubril Feist 2005 APP	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Famennian	middle Famennian	14	Achguig
Lerosey-Aubril Feist 2005 APP	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Jbel Bou Tscharafine	Tafilalt	Famennian	middle Famennian	12	Achguig
Lerosey-Aubril Feist 2005 APP	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Korb el Atil	Tafilalt	Famennian	middle Famennian	14	Achguig
Lerosey-Aubril Feist 2005 APP	Osmoskabole prima	Osmoskabole	Proetidae	Proetida	Ouidane Chebbi	Tafilalt	Famennian	middle Famennian	1	Achguig
Feist Orth 2000 ProcSDS	indet	Otarion	Aulacopleuridae	Proetida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine

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Alberti 1983 Senck lethaea	Otarionella bensaidi	Otarionella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1969 SenckNaturGesell	Otarionella magnifica	Otarionella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	25	lower Kess Kess
Alberti 1967b Senck leth	Otarionella magnifica	Otarionella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1967b Senck leth	Otarionella tafilaltense	Otarionella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	upper Kess Kess
Alberti 1969 SenckNaturGesell	Otarionella tafilaltense	Otarionella	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	2	upper Kess Kess
Alberti 1983 Senck lethaea	Paralejurus hamlagdadicus	Paralejurus	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1981a Senck lethaea	Paralejurus sp A	Paralejurus	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Chatterton Gibbs 2010 Jpal	Paralejurus rehamnanus	Paralejurus	Scutelluidae	Corynexoch	Jbel Issoumour SW	Maider	Eifelien	lower Eifelien	1	El Otfal
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Paralejurus campanifer	Paralejurus	Scutelluidae	Corynexoch	Jbel Ouafail-Filon 12	Tafilalt	Emsian	lower Emsian	2	Seheb el Rhassel
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Paralejurus elayounensis	Paralejurus	Scutelluidae	Corynexoch	Jbel Ouafail-Filon 12	Tafilalt	Pragian	Pragian	1	Seheb el Rhassel
Schraut Feist 2004 Jpal	Paralejurus rehamnanus	Paralejurus	Scutelluidae	Corynexoch	Jbel Oufatene	Maider	Emsian	upper Emsian	4	Tazoulaït
Schraut Feist 2004 Jpal	Paralejurus spatuliformis	Paralejurus	Scutelluidae	Corynexoch	Jbel Oufatene	Maider	Pragian	Pragian	7	Ihandar
Schraut Feist 2004 Jpal	Paralejurus tenuistriatus	Paralejurus	Scutelluidae	Corynexoch	Jbel Oufatene	Maider	Emsian	upper Emsian	2	Tazoulaït
Schraut Feist 2004 Jpal	Paralejurus bronngiarti menanensis	Paralejurus	Scutelluidae	Corynexoch	Mdâour el Kbir	Draa Valley	Pragian	Pragian	3	Assa
Schraut Feist 2004 Jpal	Paralejurus bohemicus	Paralejurus	Scutelluidae	Corynexoch	Tboumakhloûf	Maider	Pragian	Pragian	2	Ihandar
Alberti 1981a Senck lethaea	Paralepidoproetus wragei	Paralepidoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	3	Bou Tcharafine
Feist Weyer 2018 NJb Geol Pal	Periproetus africanus	Periproetus	Proetidae	Proetida	Bou Ifarheriou	Tafilalt	Famennian	upper Famennian	12	Achguig
Alberti 1970a SenckNaturGesell	Perunaspis longispinus	Perunaspis	Lichidae	Lichida	Gara Mduard	Tafilalt	Eifelien	lower Eifelien	1	Amerboh
Crônier Malti François Benyoucef Bricc 2013 Geol Mag	Phacops	Phacopidae	Phacopida	Idhir	Ougarta basin	Famennian	upper	1	Argiles de	
McKellar Chatterton 2009 Pal Canadiana	Phacops araw	Phacops	Phacopidae	Phacopida	Jbel Oufatene	Maider	Eifelien	lower Eifelien	4	El Otfal
Feist Orth 2000 ProcSDS	Indet	Phacops	Phacopidae	Phacopida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine
Crônier Clarkson 2001 TRSE	Phacops tafilaltensis	Phacops	Phacopidae	Phacopida	Korb el Atil	Tafilalt	Famennian	middle Famennian	40	Achguig
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Phacops sl spA	Phacops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Khalidi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Phacops sl spB	Phacops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	2	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Phacops ouarouroutensis	Phacops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	19	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Phacops ouarouroutensis	Phacops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	20	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Phacops ouarouroutensis	Phacops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	4	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Phacops ouarouroutensis	Phacops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	18	Chefar el Ahmar
Crônier Abbache Khalidi Oudot Maillet Ouali-Mehadjji 2018 Geol Mag	Phacops sp E	Phacops	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	4	Chefar el Ahmar
Crônier Malti François Benyoucef Bricc 2013 Geol Mag	Phacops tamtertensis	Phacops	Phacopidae	Phacopida	Tamtert Zereg	Ougarta basin	Famennian	middle Famennian	1	Argiles de Marhouma
Crônier Malti François Benyoucef Bricc 2013 Geol Mag	Phacops zeregensis	Phacops	Phacopidae	Phacopida	Tamtert Zereg	Ougarta basin	Famennian	middle Famennian	1	Argiles de Marhouma
Crônier Malti François Benyoucef Bricc 2013 Geol Mag	Phacops	Phacopidae	Phacopida	Tamtert	Ougarta basin	Famennian	upper Famennian	5	Argiles de	
Crônier Malti François Benyoucef Bricc 2013 Geol Mag	Phacops	Phacopidae	Phacopida	Tamtert	Ougarta basin	Famennian	upper Famennian	2	Argiles de	
Alberti 1981a Senck lethaea	Phaetonellus planicauda africanus	Phaetonellus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	12	Amerboh

Bases de données

Alberti 1970a SenckNaturGesell	Phaetonellus planicauda ulcifrons	Phaetonellus	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	2	Amerboh
Alberti 1981a Senck lethaea	Piriproetus amblyops austromaurus	Piriproetus	Proetidae	Proetida	Gara Mdouard	Tafilalt	Eifelien	lower Eifelien	1	Amerboh
Alberti 1970a SenckNaturGesell	Piriproetus ornatissimus maurus	Piriproetus	Proetidae	Proetida	Gara Mdouard	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1981a Senck lethaea	Piriproetus ornatissimus rissaniensis	Piriproetus	Proetidae	Proetida	Gara Mdouard	Tafilalt	Eifelien	lower Eifelien	2	Bou Tcharafine
Alberti 1967b Senck leth	Piriproetus amblyops patruelis	Piriproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1969 SenckNaturGesell	Piriproetus amblyops patruelis	Piriproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	5	Bou Tcharafine
Alberti 1969 SenckNaturGesell	Piriproetus amblyops austromaurus	Piriproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Eifelien	lower Eifelien	11	Bou Tcharafine
Alberti 1981a Senck lethaea	Indet	Piriproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1967b Senck leth	Piriproetus amblyops austromaurus	Piriproetus	Proetidae	Proetida	Jbel lhrs	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1983 Senck lethaea	Plagiolaria senex	Plagiolaria	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	3	
Alberti 1981b Senck lethaea	Platyscutellum massai	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1982 Natur und Museum	Platyscutellum massai	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1982 Natur und Museum	Platyscutellum massai	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1981b Senck lethaea	Platyscutellum massai	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1970a SenckNaturGesell	Platyscutellum tafilaltense	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Alberti 1981a Senck lethaea	Platyscutellum tafilaltense	Platyscutellum	Scutelluidae	Corynexoch	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Johnson Fortey 2012 Jpal	Podoliproetus mirdani	Podoliproetus	Proetidae	Proetida	Akka n'Talilite	Maider	Pragian	Pragian	1	Ihandar
Johnson Fortey 2012 Jpal	Podoliproetus sinespina	Podoliproetus	Proetidae	Proetida	Akka n'Talilite	Maider	Pragian	Pragian	1	Ihandar
Johnson Fortey 2012 Jpal	Podoliproetus mirdani	Podoliproetus	Proetidae	Proetida	Jbel el Mrakib	Maider	Pragian	Pragian	1	Ihandar
Johnson Fortey 2012 Jpal	Podoliproetus mirdani	Podoliproetus	Proetidae	Proetida	Jbel Oufatene	Maider	Pragian	Pragian	2	Ihandar
Alberti 1964 SenckNaturGesell	Pragoproetus tafilaltensis	Pragoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	40	lower Kess Kess
Alberti 1969 SenckNaturGesell	Pragoproetus tafilaltensis	Pragoproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	112	lower Kess Kess
Alberti 1983 Senck lethaea	Prodevermannia baghdadlii	Prodevermannia	Proetidae	Proetida	Ben Zireg	Ougarta basin	Emsian	lower Emsian	1	
Alberti 1983 Senck lethaea	Prodevermannia jaegeri jaegeri	Prodevermannia	Proetidae	Proetida	Ben Zireg	Ougarta basin	Pragian	Pragian	5	
Johnson Fortey 2012 Jpal	Proetina ihmadii	Proetina	Proetidae	Proetida	Jbel el Mrakib	Maider	Pragian	Pragian	1	Ihandar
Alberti 1969 SenckNaturGesell	Proetopeltis neglecta hamlagdadica	Proetopeltis	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	3	Bou Tcharafine
Alberti 1970a SenckNaturGesell	Proetus proetus sp B granulosus	Proetus	Proetidae	Proetida	Jbel el Mrakib	Maider	Eifelien	lower Eifelien	2	Timrhamhart
Alberti 1970a SenckNaturGesell	Proetus proetus sp A granulosus	Proetus	Proetidae	Proetida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Tazoulaït
Alberti 1983 Senck lethaea	Prokops benziregensis benziregensis	Prokops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	7	
Alberti 1983 Senck lethaea	Prokops chlpaci	Prokops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	15	
Morzadec 1990 Geobios	Protacanthina robusticostata	Protacanthina	Acastidae	Phacopida	Dkhissa	Ougarta basin	Lochkovian	upper Lochkovian	6	Dkhissa
Morzadec 1990 Geobios	Protacanthina robusticostata	Protacanthina	Acastidae	Phacopida	El Kseib	Ougarta basin	Lochkovian	upper Lochkovian	1	Dkhissa
Morzadec 1990 Geobios	Protacanthina robusticostata	Protacanthina	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Lochkovian	upper Lochkovian	2	Dkhissa
Morzadec 1990 Geobios	Protacanthina robusticostata	Protacanthina	Acastidae	Phacopida	Zerhamra	Ougarta basin	Lochkovian	upper Lochkovian	1	Dkhissa
Morzadec 2001 PalaeontA	Pseudocryphaeus sp 1	Pseudocryphaeus	Acastidae	Phacopida	Bou Dîb	Maider	Emsian	upper Emsian	1	Er Remlia
Morzadec 2001 PalaeontA	Pseudocryphaeus sp 2	Pseudocryphaeus	Acastidae	Phacopida	Jbel Bou Tcharafine	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
H. Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	5	Achguig
H. Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	2	Achguig
H. Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer gibber	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	3	Achguig

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H.Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer gibber	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	3	Achguig
H.Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer palmeus	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	3	Achguig
H.Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer palmeus	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	3	Achguig
H.Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer speculator	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	2	Achguig
H.Alberti 1975a NJb Geol Pal	Pseudowaribole (Pseudowaribole) conifer speculator	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	1	Achguig
H.Alberti 1975b NJb Geol Pal	Pseudowaribole (Pseudowaribole) familiaris	Pseudowaribole (Pseudowaribole)	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	4	Achguig
Morzadec 1988 PalaeontA	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Bou Dïb	Maider	Emsian	upper Emsian	2	Talus d'Issemour
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Bou Dïb	Maider	Emsian	upper Emsian	1	Tazoulaït
Morzadec 1988 PalaeontA	Psychopyge termierorum	Psychopyge	Acastidae	Phacopida	El Haidouriya	Draa Valley	Emsian	upper Emsian	1	Chefar el Ahmar
Cronier Oudot Klug DeBaets 2018 NJb Geol Pal	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Morzadec 1988 PalaeontA	Psychopyge termierorum	Psychopyge	Acastidae	Phacopida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	5	Amerboh
Morzadec 1988 PalaeontA	Psychopyge termierorum	Psychopyge	Acastidae	Phacopida	Jbel Bou Tcharafine	Tafilalt	Emsian	upper Emsian	8	Amerboh
Morzadec 1988 PalaeontA	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Psychopyge hammerorum	Psychopyge	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Morzadec 2001 PalaeontA	Psychopyge praestans	Psychopyge	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Psychopyge praestans	Psychopyge	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	5	Timrhamhart
Morzadec 2001 PalaeontA	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Jbel Issoumour Unknown	Maider	Emsian	upper Emsian	1	Tazoulaït
Morzadec 2001 PalaeontA	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	2	Tazoulaït
Morzadec 2001 PalaeontA	Psychopyge termierorum	Psychopyge	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Bou Tiskaouine
Morzadec 1997 PalaeontA	Psychopyge elegans	Psychopyge	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Teferguenit
Morzadec 1988 PalaeontA	Psychopyge termierorum	Psychopyge	Acastidae	Phacopida	Marhouma	Ougarta basin	Emsian	upper Emsian	1	Teferguenit
H.Alberti 1973 NJb Geol Pal	Pusillabole bordjensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	2	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole bordjensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	1	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole bordjensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	1	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole cognata	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	1	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole cornicula jebelensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	2	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole cornicula sobrina	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	8	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole cornicula tafilaltensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	2	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole erfoudensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	middle Famennian	3	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole erfoudensis zizensis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	upper Famennian	3	Achguig
H.Alberti 1973 NJb Geol Pal	Pusillabole radiata pusillaformis	Pusillabole	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	uppermost Fame nnian	5	Achguig
Morzadec 2001 PalaeontA	Quadrops flexosus	Quadrops	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	2	El Otfal
Feist Orth 2000 ProcSDS	indet	Radiaspis	Odontopleuridae	Lichida	Jbel Ziata	Tafilalt	Givetian	lower Givetian	1	Bou Tcharafine
Alberti 1983 Senck lethaea	Reedops cephalotes algericanus	Reedops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	2	
Alberti 1983 Senck lethaea	Reedops struveianus	Reedops	Phacopidae	Phacopida	Ben Zireg	Ougarta basin	Pragian	Pragian	6	
Alberti 1983 Senck lethaea	Reedops cephalotes hamlagdadianus	Reedops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	40	lower Kess Kess
McKellar Chatterton 2009 Pal Canadiana	Reedops cephalotes hamlagdadianus	Reedops	Phacopidae	Phacopida	Hamar Laghdad	Tafilalt	Pragian	Pragian	13	lower Kess Kess

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Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Reedops bronni	Reedops	Phacopidae	Phacopida	Jbel Ouafal-Filon 12	Tafilalt	Pragian	Pragian	1	Seheb el Rhassel
Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo	Reedops cephalotes hamlagdadianus	Reedops	Phacopidae	Phacopida	Jbel Ouafal-Filon 12	Tafilalt	Pragian	Pragian	7	Seheb el Rhassel
McKellar Chatterton 2009 Pal Canadiana	Reedops bronni	Reedops	Phacopidae	Phacopida	Jbel Oufatene Jbel Issoumour	Maider	Pragian	Pragian	2	Ihandar
McKellar Chatterton 2009 Pal Canadiana	Reedops bronni	Reedops	Phacopidae	Phacopida	Jbel Oufatene Jbel Issoumour	Maider	Pragian	Pragian	1	Ihandar
McKellar Chatterton 2009 Pal Canadiana	Reedops pembedoni	Reedops	Phacopidae	Phacopida	Jbel Oufatene Jbel Issoumour	Maider	Pragian	Pragian	14	Ihandar
McKellar Chatterton 2009 Pal Canadiana	Reedops pembedoni	Reedops	Phacopidae	Phacopida	Jbel Oufatene Jbel Issoumour	Maider	Pragian	Pragian	1	Ihandar
McKellar Chatterton 2009 Pal Canadiana	Reedops cephalotes hamlagdadianus	Reedops	Phacopidae	Phacopida	Mdâour el Kbir	Draa Valley	Pragian	Pragian	2	Assa
Klug Kröger Korn Rücklin Schemm- Gregory DeBaets Mapes 2008 Pal Abt A	Reedops cephalotes cephalotes	Reedops	Phacopidae	Phacopida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Rheiscutellum hammadi	Rheiscutellum	Scutellidae	Corynexoch	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Rheiscutellum lahzeni	Rheiscutellum	Scutellidae	Corynexoch	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Feist Chatterton 2015 Palaeontology	Sagittapeltis belkai	Sagittapeltis	Scutellidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	2	upper Kess Kess
Müller 2005 Geol et Pal	Scabrella aithssainei	Scabrella	Homalonotidae	Phacopida	Jbel Issoumour Unknown	Maider	Pragian	Pragian	1	Ihandar
Müller 2005 Geol et Pal	Scabrella propraodana	Scabrella	Homalonotidae	Phacopida	Jbel Issoumour Unknown	Maider	Pragian	Pragian	1	Ihandar
Cronier Oudot Klug DeBaets 2018 NJB Geol Pal	Indet	Scabriscutellum	Scutellidae	Corynexoch	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	4	Amerboh
Alberti 1981a Sencklethaea	Scharyia hamlagdadica	Scharyia	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	7	Amerboh
Alberti 1970a SenckNaturGesell	Scharyia tafilaltensis	Scharyia	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1983 Sencklethaea	Scharyia yokiniiana	Scharyia	Aulacopleuridae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1981a Sencklethaea	Sculptoporetus africanus africanus	Sculptoporetus	Proetidae	Proetida	Ben Zireg	Ougarta basin	Emsian		1	
Alberti 1967a Senckleth	Sculptoporetus maghrebus	Sculptoporetus	Proetidae	Proetida	El Atrous	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1969 SenckNaturGesell	Sculptoporetus maghrebus	Sculptoporetus	Proetidae	Proetida	El Atrous	Tafilalt	Emsian	lower Emsian	5	Seheb el Rhassel
Alberti 1983 Sencklethaea	Sculptoporetus africanus africanus	Sculptoporetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1981a Sencklethaea	Sculptoporetus africanus junior	Sculptoporetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	3	Bou Tcharafine
Alberti 1983 Sencklethaea	Sculptoporetus africanus ribatelfatanus	Sculptoporetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1970a SenckNaturGesell	Sculptoporetus sculptus posterior	Sculptoporetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	7	Amerboh
Alberti 1969 SenckNaturGesell	Sculptoporetus africanus africanus	Sculptoporetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Eifelien	lower Eifelien	40	Amerboh
Alberti 1964 SenckNaturGesell	Sculptoporetus africanus africanus	Sculptoporetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1983 Sencklethaea	Sculptoporetus spAA	Sculptoporetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Alberti 1983 Sencklethaea	Sculptoporetus maghrebus	Sculptoporetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Alberti 1970a SenckNaturGesell	Sculptoporetus maghrebus	Sculptoporetus	Proetidae	Proetida	Jbel Bou Tcharafine	Tafilalt	Emsian	lower Emsian	1	Seheb el Rhassel
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Sculptoporetus haasi	Sculptoporetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	3	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Sculptoporetus sp B	Sculptoporetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Sculptoporetus spA	Sculptoporetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	2	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Sculptoporetus spA	Sculptoporetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Alberti 1970a SenckNaturGesell	Sculptoporetus maghrebus	Sculptoporetus	Proetidae	Proetida	Jbel Issoumour SW	Maider	Emsian	lower Emsian	1	Bou Tiskouine
Alberti 1967b Senckleth	Sculptoporetus sculptus antiquus	Sculptoporetus	Proetidae	Proetida	Timarzite	Maider	Pragian	Pragian	1	Ihandar

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Alberti 1969 SenckNaturGesell	Sculptoproetus sculptus antiquus	Sculptoproetus	Proetidae	Proetida	Timarzite	Maider	Pragian	Pragian	3	Ihandar
Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A	Sculptoproetus maghrebus	Sculptoproetus	Proetidae	Proetida	Ouidane Chebbi	Tafilalt	Emsian	lower Emsian	2	Seheb el Rhassel
vanViersen Lerouge 2019 Pal Zeit	Sculptoproetus raki	Sculptoproetus	Proetidae	Proetida	Rissani South	Tafilalt	Emsian	upper Emsian	1	Amerboh
Schraut 2000b Senck Lethaea	Spiniscabrella struvei	Spiniscabrella	Homalonotidae	Phacopida	Jbel Issoumour N	Maider	Emsian	upper Emsian	2	Tazoulait
Alberti 1970a SenckNaturGesell	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Jbel Amlane	Tafilalt	Eifelien	upper Eifelien	3	Bou Tcharafine
Alberti 1981a Senck lethaea	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Jbel Amlane	Tafilalt	Eifelien	upper Eifelien	3	Bou Tcharafine
Alberti 1966a Senck leth	Struveaspis sp A	Struveaspis	Phacopidae	Phacopida	Jbel Amlane	Tafilalt	Eifelien	upper Eifelien	1	Bou Tcharafine
Alberti 1970a SenckNaturGesell	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Jbel Bou Tscharafine	Tafilalt	Eifelien	upper Eifelien	3	Bou Tcharafine
Alberti 1981a Senck lethaea	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Jbel Bou Tscharafine	Tafilalt	Eifelien	upper Eifelien	3	Bou Tcharafine
Corbacho 2014b Sc. Musci Geologici Seminarii Barcinonensis	Struveaspis bignoni	Struveaspis	Phacopidae	Phacopida	Jdorf	Tafilalt	Eifelien		2	
Corbacho 2014b Sc. Musci Geologici Seminarii Barcinonensis	Struveaspis micromma	Struveaspis	Phacopidae	Phacopida	Jdorf	Tafilalt	Eifelien		1	
Alberti 1981a Senck lethaea	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Marhouma	Ougarta basin	Eifelien	lower Eifelien	2	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	7	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	9	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Struveaspis maroccanica	Struveaspis	Phacopidae	Phacopida	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	4	Chefar el Ahmar
Alberti 1967b Senck leth	Tafilaltaspis creber tenuigranifer	Tafilaltaspis	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
Alberti 1969 SenckNaturGesell	Tafilaltaspis creber tenuigranifer	Tafilaltaspis	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	10	Bou Tcharafine
Alberti 1969 SenckNaturGesell	Tafilaltaspis nitidus	Tafilaltaspis	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	lower Emsian	1	upper Kess Kess
Alberti 1966a Senck leth	Tafilaltaspis creber creber	Tafilaltaspis	Tropidocoryphidae	Proetida	Jbel Amlane	Tafilalt	Emsian	upper Emsian	5	Amerboh
Alberti 1970a SenckNaturGesell	Tafilaltaspis creber creber	Tafilaltaspis	Tropidocoryphidae	Proetida	Jbel Amlane	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1969 SenckNaturGesell	Tafilaltaspis maidericus	Tafilaltaspis	Tropidocoryphidae	Proetida	Timarzite	Maider	Emsian	upper Emsian	1	
vanViersen Lerouge 2019 Pal Zeit	Tafilaltaspis rufa	Tafilaltaspis	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Eifelien	lower Eifelien	1	Bou Tcharafine
vanViersen Lerouge 2019 Pal Zeit	Tafilaltaspis spA	Tafilaltaspis	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt			1	
Schraut 2000a Senck Lethaea	Thysanopeltis speciosa	Thysanopeltis	Scutelluidae	Corynexoch	Foum Zguid	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
Alberti 1981a Senck lethaea	Thysanopeltis speciosa austromaura	Thysanopeltis	Scutelluidae	Corynexoch	Jbel Bou Tscharafine	Tafilalt	Eifelien	lower Eifelien	3	Bou Tcharafine
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Thysanopeltis speciosa	Thysanopeltis	Scutelluidae	Corynexoch	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	2	Timrhamhart
Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag	Thysanopeltis speciosa	Thysanopeltis	Scutelluidae	Corynexoch	Ouarourout	Ougarta basin	Eifelien	lower Eifelien	1	Chefar el Ahmar
Gibb Chatterton 2007 JPaleont	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Bou Dib	Maider	Eifelien	lower Eifelien	5	El Otfal
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Foum Zguid	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus pulchistriatus repens	Timsaloproetus	Proetidae	Proetida	Foum Zguid	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Gibb Chatterton 2007 JPaleont	Timsaloproetus dibbanus	Timsaloproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Gibb Chatterton 2007 JPaleont	Timsaloproetus elguerrouji	Timsaloproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	3	Timrhamhart
Gibb Chatterton 2007 JPaleont	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Eifelien	lower Eifelien	3	Timrhamhart
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Talawarite	Tafilalt	Emsian	upper Emsian	1	Amerboh
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus pulchistriatus pulchistriatus	Timsaloproetus	Proetidae	Proetida	Timarzite	Maider	Emsian	upper Emsian	1	Tazoulait
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Bou Dib	Maider	Eifelien	lower Eifelien	1	El Otfal
vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Bou Dib	Maider	Emsian	upper Emsian	1	Tazoulait
Gibb Chatterton 2007 JPaleont	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Zguilma	Draa Valley	Eifelien	lower Eifelien	1	Timrhamhart

Bases de données

vanViersen Lerouge 2019 Pal Zeit	Timsaloproetus haasi	Timsaloproetus	Proetidae	Proetida	Zguilma	Draa Valley	Eifelian	lower Eifelian	1	Timrhamhart
Morzadec 2001 PalaeontA	Treropyge maura	Treropyge	Acastidae	Phacopida	Jbel Oufatene	Maider	Emsian	upper Emsian	1	Tazoulait
Feist Mahboubi Girard 2016 Bull geo	Trifoliops croniera	Trifoliops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	lower Famennian	1	Argiles de Marhouma
Feist Mahboubi Girard 2016 Bull geo	Trifoliops septimanicus	Trifoliops	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	lower Famennian	2	Argiles de Marhouma
Crônier Malti François Benyoucef Bricé 2013 Geol Mag	Trimeroccephalus nigrilus	Trimeroccephalus	Phacopidae	Phacopida	Bécher	Ougarta basin	Famennian	upper Famennian	1	Argiles de Marhouma
Crônier Malti François Benyoucef Bricé 2013 Geol Mag	Trimeroccephalus caecus	Trimeroccephalus	Phacopidae	Phacopida	Cheffar-el-Ahmar	Ougarta basin	Famennian	middle Famennian	1	Argiles de Marhouma
Crônier Malti François Benyoucef Bricé 2013 Geol Mag	Trimeroccephalus nigrilus	Trimeroccephalus	Phacopidae	Phacopida	Gara Diba	Ougarta basin	Famennian	middle Famennian	1	Argiles de Marhouma
Crônier Feist 1997 Geobios	Trimeroccephalus lielievrei	Trimeroccephalus	Phacopidae	Phacopida	Korb el Atil	Tafilalt	Famennian	middle Famennian	213	Achguig
Feist Mahboubi Girard 2016 Bull geo	Trimeroccephalus caecus	Trimeroccephalus	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	middle Famennian	1	Argiles de Marhouma
Feist Mahboubi Girard 2016 Bull geo	Trimeroccephalus mahboubii	Trimeroccephalus	Phacopidae	Phacopida	Marhouma	Ougarta basin	Famennian	lower Famennian	3	Argiles de Marhouma
Alberti 1967a Senck leth	Tropidocoryphe hamlaghdadica	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	1	lower Kess Kess
Alberti 1969 SenckNaturGesell	Tropidocoryphe hamlaghdadica	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Pragian	Pragian	2	lower Kess Kess
Feist Belka 2018 N.Jb Geol	Tropidocoryphe mediterranea	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian		1	upper Kess Kess
Alberti 1981a Senck lethaea	Tropidocoryphe memnon nepos	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering	Tropidocoryphe memnon nepos	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	Amerboh
Alberti 1970a SenckNaturGesell	Tropidocoryphe memnon nepos	Tropidocoryphe	Tropidocoryphidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	3	Amerboh
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Tropidocoryphe amuri	Tropidocoryphe	Tropidocoryphidae	Proetida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Alberti 1969 SenckNaturGesell	Unguliproetus unguiloides unguiloides	Unguliproetus	Proetidae	Proetida	Hamar Laghdad	Tafilalt	Emsian	upper Emsian	1	upper Kess Kess
Alberti 1969 SenckNaturGesell	Unguliproetus unguiloides tener	Unguliproetus	Proetidae	Proetida	Jbel Amlane	Tafilalt	Emsian	upper Emsian	2	Amerboh
H.Alberti 1976b N.Jb Geol Pal	Vittaella vitta	Vittaella	Proetidae	Proetida	Bordj Est	Tafilalt	Famennian	lower Famennian	1	Achguig
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Walliserops sp A	Walliserops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Khaldi Crônier Hainaut Abbacke Mehadjji 2016 Geol Mag	Walliserops sp B	Walliserops	Acastidae	Phacopida	Erg Djemel	Ougarta basin	Emsian	upper Emsian	1	Chefar el Ahmar
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Walliserops hammii	Walliserops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	3	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Walliserops tridens	Walliserops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Morzadec 2001 PalaeontA	Walliserops trifurcatus	Walliserops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	4	Timrhamhart
vanViersen 2004 GEA	Walliserops trifurcatus	Walliserops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	1	Timrhamhart
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Walliserops trifurcatus	Walliserops	Acastidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	2	Timrhamhart
Chatterton Gibbs 2010 Jpal	Walliserops lindoei	Walliserops	Acastidae	Phacopida	Jbel Issoumour SW	Maider	Emsian	upper Emsian	1	El Otfal
Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana	Wendorfia calvus	Wendorfia	Homalonotidae	Phacopida	Jbel Gara el Zguilma	Draa Valley	Emsian	upper Emsian	6	Timrhamhart
Alberti 1969 SenckNaturGesell	Xiphogonium trautenbergensis crassus	Xiphogonium	Tropidocoryphidae	Proetida	El Atrous	Tafilalt	Emsian	lower Emsian	4	Seheb el Rhassel