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***Pleolobites* (Decapoda: Brachyura) from the Paleogene of Africa revisited, with
implications on taxonomy of fossil portunoid crabs**

***Pleolobites* (Decapoda : Brachyura) du Paléogène d'Afrique et implications sur la
taxonomie des crabes portonoïdes fossiles**

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Abstract

Since its first description in 1960, the brachyuran crab genus *Pleolobites* was restricted to the Eocene (Ypresian) strata of Ivory Coast. Here, we report newly collected specimens that indicate its presence in the Paleocene (Thanetian) of Togo. This monotypic genus has been classified within various higher taxa, including Portunidae,

Macropipidae, and Carcinidae, depending on the concurrent classification of portunoid crabs. Through the re-examination of the type material of *Pleolobites erinaceus*, the most recent assignment of *Pleolobites* within the subfamily Polybiinae of the family Carcinidae is disputed herein. Nevertheless, we refrain from assigning *Pleolobites* to any family and opine for its placement as Portunoidea *incertae sedis*. Additionally, the crab genus *Rhachiosoma*, morphologically similar to *Pleolobites*, is also removed from Polybiinae and placed in Portunoidea *incertae sedis*. It is further argued that *Palaeoxanthopsis*, *Paraverrucoides*, *Parazanthopsis*, and *Verrucoides* currently classified within the family Palaeoxanthopsidae of the superfamily Carpilioidea show striking similarities with *Pleolobites* and *Rhachiosoma*, including the morphology of dorsal carapace, thoracic sternum and pleon. Additionally, chelipeds with a spiny propodal margin and multi-lobed serial finger-teeth, otherwise characteristic for Portunoidea are found in *Parazanthopsis* and *Palaeoxanthopsis*. It remains to be investigated whether these resemblances are the result of evolutionary convergence or close phylogenetic relationships.

Key words

Paleocene, Eocene, Portunoidea, Palaeoxanthopsidae, Togo, evolutionary convergence.

Résumé

Depuis sa première description en 1960, le genre de crabe brachyoure *Pleolobites* était limité à l'Eocène inférieur (Yprésien) de Côte d'Ivoire. Ici, nous rapportons des spécimens nouvellement collectés qui indiquent sa présence dans le Paléocène (Thanétien) du Togo. Ce genre monotypique a été classé au sein de différentes familles, notamment les Portunidae, les Macropipidae et les Carcinidae, en fonction de

l'évolution des classifications des crabes portunoïdes. Grâce au réexamen du matériel type de *Pleolobites erinaceus*, nous contestons la récente attribution de *Pleolobites* au sein de la sous-famille Polybiinae (famille des Carcinidae). Néanmoins, nous nous abstenons d'attribuer *Pleolobites* à une famille précise et considérons ce genre comme un Portunoidea *incertae sedis*. De plus, le genre de crabe *Rhachiosoma*, morphologiquement similaire aux *Pleolobites*, est aussi retiré des Polybiinae et placé parmi les Portunoidea *incertae sedis*. Nous notons également que les genres *Palaeoxanthopsis*, *Paraverrucoides*, *Parazanthopsis* et *Verrucoides*, actuellement classés dans la famille des Palaeoxanthopsidae (superfamille des Carpilioidea), présentent des similitudes frappantes avec *Pleolobites* et *Rhachiosoma*, notamment la morphologie de la carapace dorsale, du sternum thoracique et du pléon. De plus, la présence de chélipèdes avec une marge propodale épineuse et de dactylus avec une série de dents multilobées, caractéristique des Portunoidea, se retrouvent aussi chez *Parazanthopsis* et *Palaeoxanthopsis*. Il reste à savoir si ces ressemblances sont le résultat d'une convergence évolutive ou d'étroites relations phylogénétiques.

Mots clés

Paléocène, Eocène, Portunoidea, Palaeoxanthopsidae, Togo, convergence évolutive

1. Introduction

Systematic placement of extinct decapod genera may be difficult but is very important when testing relationships among various decapod groups and tracing origins of currently living higher taxa. Unfortunately, fossil material usually only offers limited number of morphological characters to be evaluated. In brachyuran crabs, dorsal

carapace morphology may be misleading due to widespread convergence (Ng et al. 2008: 9; Chu et al. 2015: 800). In this respect, characters present on the sternum and the pleon are in general considered as more informative than those on the dorsal carapace (Guinot et al. 2013; Davie et al. 2015a). Recently, the importance of selected characters on chelipeds, often prone to convergences (Schäfer 1954), has been demonstrated to be useful for attribution to higher level taxa (Spiridonov et al. 2014).

Within the last decades, advances in the understanding of decapod evolution had a major impact on higher level classification of brachyuran crabs, especially on superfamilial and familial levels (Martin & Davis 2001; Ng et al. 2008; Schweitzer et al. 2010; Davie et al. 2015b; Luque et al. 2019), further influencing the assignment of extinct crab genera. The example presented here is a monotypic brachyuran genus *Pleolobites* Rémy, 1960, which has been classified within various higher taxa depending on constantly changing classification of Portunoidea (Karasawa et al. 2008; Schubart & Reuschel 2009; Spiridonov et al. 2014; Evans 2018; Spiridonov 2020; Schweitzer et al. 2021). Herein, we argue that the current placement of *Pleolobites* within the subfamily Polybiinae (Schweitzer et al. 2021) is untenable. The aim of this contribution is twofold: 1) report of the stratigraphically oldest occurrence of *Pleolobites erinaceus* from the Thanetian of Togo; and 2) revise the genus *Pleolobites* based on the re-examination of the type material and its removal from the subfamily Polybiinae (family Carcinidae).

2. Geographical and geological settings

Ivory Coast: The original and type material of *P. erinaceus* comes from the area near Fresco (Rémy, 1960). The type locality was indicated as Region JK, sea cliff under the Laga-Ghirobo hill, whereas other localities yielding remains of *P. erinaceus* were

Regions CD, EF, JK and MN, Laga-Ghirobo and Kraïébouén (Rémy, 1960). Specimens originate from glauconitic levels of the Falaise de Fresco (Rémy's "Level 5") with a probable Eocene age as suggested by Rémy (1960). Recently, this Ypresian age estimation was confirmed by Dibo et al. (2021, 158, 159, fig. 2a-d).

Togo: Newly collected specimens of *P. erinaceus* described herein originate from the WACEM cement quarry located 6 km northeast of the city of Tabligbo (Fig. 1A), southern Togo (Maritime Region). This region is part of the Togolese coastal sedimentary basin, which consists of a thick Upper Cretaceous to Neogene monoclinial sequence dipping south. The series outcropping in the WACEM quarry consists of a carbonate-dominated Paleogene sequence (Johnson et al. 2000; Da Costa et al. 2013a). This sequence includes various Upper Cretaceous to Paleocene clastic facies, which all belong to the Tabligbo Group, and precedes Ypresian shales, clays, and phosphorite series (Johnson et al. 2000). The lower part of the Paleocene series (Fig. 1B) consists of a four-meter-thick unit of bioclastic limestone containing abundant remains of the echinoderm *Togocyamus seefriedi* Oppenheim, 1915 in its upper part. Evidence based on both invertebrate and vertebrate associations suggests a Thanetian age for this lower unit (Amoudji et al. 2021). The upper part of the formation is about two-meter thick and comprises a compact oyster-rich limestone containing frequent nautilid remains and is overlain by a thin glauconitic series. The glauconitic series reaches a thickness of about one-meter and is composed of a lower glauconitic biomicrite overlain by a 20-cm thick glauconitic sandstone. Abundant bioturbations mark the boundary between the glauconitic biomicrite and the glauconitic sandstone. The Ypresian shaly series rest unconformably over the glauconitic unit. The age of the glauconitic unit has been debated but recent data on benthic foraminifers and elasmobranch assemblages suggest

a late Thanetian age (Guinot et al. 2020). This agrees with previous conclusions based on planktic foraminifera (Johnson et al. 2000; Da Costa et al. 2013b).

3. Material and methods

The crab specimens studied herein includes the original material of Rémy (1960) and newly collected specimens from Togo. The latter were collected from the glauconitic unit on top of the carbonate-dominated Paleogene sequence (coordinates: 06°35'34.7''N, 1°33'25.8''E). The specimens were found within burrows forming the bioturbations at the boundary between the glauconitic biomicrite and the glauconitic sandstone (Fig. 1B). Specimens were prepared using pneumatic and manual needles. All studied specimens were documented photographically (Canon 5DSR mounted with a Canon 100mm macro lens) either dry and uncoated or whitened with ammonium chloride sublimate (see figure captions for more details). The terminology used for cheliped dentition follows Spiridonov et al. (2014).

Repositories: MNHN.F – Collection de Paléontologie, Muséum National d'Histoire Naturelle de Paris, France. ULDG – Collections of Geology Department of the University of Lomé, Togo.

4. Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Brachyura Latreille, 1802

Section Heterotremata Guinot, 1977

Superfamily Portunoidea Rafinesque, 1815

Family *incertae sedis*

Genus *Pleolobites* Rémy, 1960

Type species. *Pleolobites erinaceus* Rémy, 1960 by original designation and monotypy.

Emended diagnosis: Carapace wider than long, length about 75 percent maximum width; front bifid, with pronounced inner orbital teeth giving tetra-lobed appearance; orbits deep, with medial fissure and notch near outer orbital tooth, fronto-orbital width about half maximum carapace width; anterolateral margins with five teeth including outer orbital teeth, second and third teeth broadly triangular, fourth tooth situated nearly on base of fifth, very long, laterally directed tooth; posterolateral margins slightly convex; posterior margin nearly straight; protogastric, hepatic, epibranchial, and branchial regions with large tubercles centrally; sternum wide, with maximum width at level of sternite 5; sterno-pleonal cavity deep, reaching end of sternite 4; male pleon weakly subtriangular, all somites free; telson subtriangular; pleonal somite 6 subtrapezoidal, twice as long as somite 5; chelipeds with long and robust chelae, propodus with two parallel longitudinal keels at mid-height; fingers with serial conical teeth.

Remarks: Remy (1960) classified *Pleolobites* within Portunidae. Glaessner (1969: R573) further assigned the genus into the subfamily Carcininae MacLeay, 1838. Such placement was questioned by Karasawa & Fudouji (2000: 244). Later, Karasawa et al. (2008: 100) included *Pleolobites* within the redefined Macropipidae Stephenson & Campbell, 1960; this placement was followed by Schweitzer & Feldmann (2010) and Schweitzer et al. (2010). However, the family Macropipidae was recognized as polyphyletic when molecular analyses showed that genera such as *Bathynectes*

Stimpson, 1871, *Liocarcinus* Stimpson, 1871, *Macropipus* Prestandrea, 1833, and *Polybius* Leach, 1820, are closely related to each other (Schubart & Reuschel 2009; Spiridonov et al. 2014). Evans (2018) proposed these taxa to be included within the subfamily Polybiinae Ortmann, 1893 of the family Carcinidae. Feldmann et al. (2018) and Schweitzer et al. (2021) presented a diagnosis of Polybiinae based on morphological characters with a potential to be preserved in fossils and listed all fossil genera within this subfamily, including *Pleolobites*. Spiridonov (2020: 158) noted that because of major changes in higher-level classification of Portunoidea, such as the reduction in the number of constituent families, fossil genera formerly placed within Macropipidae (*sensu* Karasawa et al. 2008) could return to an uncertain status rather than being classified within the subfamily Polybiinae. We concur with this assertion. Moreover, we opine that classifying the genus *Pleolobites* within the currently revised Polybiinae is not supported by the morphological features (see Discussion further below) of its type species, *Pleolobites erinaceus*. The placement of *Pleolobites* as portunoid has never been disputed and we do not dispute it either. Therefore, we refrain from assigning *Pleolobites* to any family and present its placement as Portunoidea *incertae sedis*.

***Pleolobites erinaceus* Rémy, 1960**

Figures 2, 3

1960 *Pleolobites erinaceus* Rémy, p. 59, text-figs. 4, 5; figs. 10, 11 of the plate.

1969 *Pleolobites erinaceus* Rémy; Glaessner, p. R513, fig. 321.3

2008 *Pleolobites erinaceus* [sic!] Rémy; Karasawa et al., p. 101.

2010 *Pleolobites erinaceus* [sic!] Rémy; Schweitzer & Feldmann, p. 410, fig. 2E, F

2010 *Pleolobites erinaceus* Rémy; Schweitzer et al., p. 108.

2020 *Pleolobites erinaceus* [sic!] Rémy; Sasaki, p. 9220.

2021 *Pleolobites erinaceus* Rémy; Schweitzer et al., p. 11, fig. 6,2a–b.

Diagnosis: As for genus.

Material examined (Ivory Coast): Holotype MNHN.F R03782 (Fig. 2C): near-complete female individual with cephalothorax, pleon, both chelae, and partially preserved walking legs. Paratype MNHN.F A70125 (Fig. 2E): male individual with cephalothorax, pleon, right chela, and partially preserved walking legs. Paratype MNHN.F A70126 (Fig. 2A): individual with cephalothorax, both chelae, and partially preserved walking legs. Paratype MNHN.F A70127 (Fig. 2B): male individual with cephalothorax and pleon (without chelae nor walking legs). Paratype MNHN.F A70128 (Fig. 2D): individual with cephalothorax, both chelae, and partially preserved walking legs. In all specimens, the cephalothorax is preserved with dorsal carapace and sternum.

Material examined (Togo): ULDG TAB3-6 (Fig. 3B): individual with dorsal carapace, sternum, and both chelae. ULDG TAB3-7 (Fig. 3A): near-complete dorsal carapace with prominent muscle scars. ULDG TAB3-8 (Fig. 3C): dorsal carapace fragment. ULDG TAB3-9 (Fig. 3D): fragmentary dorsal carapace with left chela.

Emended description: Carapace transversely hexagonal, almost twice as wide as long, maximum width at mid-length of carapace; vaulted longitudinally, slightly vaulted transversely; carapace surface with fine, even granulations, elevated parts of regions more densely granulated. Front bilobed, lobes bifid (with prominent inner orbital teeth

giving tetra-lobed appearance), with median notch, slightly downturned, protruding beyond orbits. Orbits wide, subrectangular in outline; supraorbital margin with closed fissure medially, and notch present near outer orbital tooth; infraorbital margin entire except for fissure below outer orbital tooth; eyestalks well-calcified, as long as orbital length; outer orbital tooth subtriangular in outline. Anterolateral margins convex, with four subtriangular teeth excluding outer orbital tooth, last (epibranchial) tooth conical, elongate. Posterolateral margins weakly convex, convergent posteriorly, with rounded edge. Posterior margin straight, rimmed; re-entrant visible in posterior view. Carapace regions well-marked, defined with rounded swellings. Hepatic region inflated. Mesogastric region slender and weakly defined anteriorly, posterior portion wider, bearing two contiguous swellings. Metagastric region not defined. Protogastric lobes swollen, each with central tubercle. Urogastric region narrow, widely V-shaped, separated from meso- and metagastric regions by cervical groove. Cardiac regions wide and inflated. Epibranchial regions forming line of sigmoidal swellings ending at last anterolateral spine; mesobranchial region with prominent tubercle; metabranchial region smooth. Intestinal region not defined. Pterygostome subtrapezoidal, margin finely rimmed with granules.

Male thoracic sternum elongated, slightly ovate, maximum width at level of sternite 5; sternite 2 inverted subtriangular in outline, with shallow longitudinal groove; sternites 4–7 subtrapezoidal in outline; sternite 4 slightly vaulted, lateral margins rounded, medially crossed by deep sterno-pleonal cavity, with shallow grooves paralleling lateral margins. Episternites 4–6 with visible suture. Suture 2/3 complete; suture 3/4 visible laterally, forming V-shaped groove; sutures 4/5, 5/6, and 6/7 laterally complete. Sterno-pleonal cavity deep, reaching margin of sternite 4. Press button present on sternite 5, located on edge of sterno-pleonal cavity just above suture 5/6.

Male pleon weakly subtriangular in outline, all somites free; telson subtriangular; pleonal somite 6 subtrapezoidal, twice as long as somite 5; somite 5 subrectangular, transversely elongate.

Female thoracic sternum slightly wider than that in male; lateral margins of sternite 4 rounded. Female pleon very wide, covering almost entire posterior portion of sternum; somite 6 subrectangular with rounded lateral margins, twice as long as somite 5; sternites 5–3 subrectangular, transversely elongate.

Chelipeds (pereiopods 1) strong. Merus stout, with rounded edges, outer margin with two distal spines, articulated freely from basis-ischium. Carpus stout, outer margin rounded, inner margin with acute rimmed spine. Chelae long, robust, dactyli as long as fixed fingers. Propodus subtrapezoidal in outline, higher distally; outer surface smooth, with two parallel longitudinal keels at mid-height; upper margin sharp-edged, proximal half ending in blunt spine, distal half ending in spine directed distally; lower margin rounded, slightly convex. Dactylus of right chela with a proximal knobstick molariform tooth followed by serial conical teeth; pollex with serial conical teeth. Both fingers of left chela with serial conical teeth. Walking legs (pereiopods 2–4) of similar size, long, smooth, slightly flattened; pereiopod 5 slightly shorter.

Remarks: The newly collected material from the Thanetian strata of Togo conforms with the original material from the Ypresian of Ivory Coast in every aspect. The only observable difference is in the preservation; the original material shows virtually all cuticular surfaces with well-preserved ornamentation, whereas in specimens from Togo the cuticle is only partially, if at all, preserved. In at least one specimen, upper layers of cuticle are missing entirely showing muscle scars (compare with Klompaker et al. 2019: figs. 13, 14).

Occurrence: Thus far, *Pleolobites erinaceus* have been reported from the Paleocene (Thanetian) of Togo and lower Eocene (Ypresian) of Ivory Coast.

5. Discussion

As noted above, the genus *Pleolobites* was classified within various (sub)families depending on changing higher classification of Portunoidea within the last decades. Unfortunately, the placement of the genus apparently has not been revised in respect to emended diagnoses of relevant higher taxa and actual morphology present in well-preserved fossils. According to the latest classification scheme presented by Schweitzer et al. (2021), *Pleolobites* would belong to Polybiinae. However, there are striking differences between the observed morphology of *Pleolobites erinaceus* and taxonomically important characters presented in the diagnosis of Polybiinae. The diagnosis of Polybiinae (Spiridonov et al. 2014: 422; Davie et al. 2015b: 1102; Feldmann et al. 2018: 2; Schweitzer et al. 2021: 6, 7) indicates the presence of a well-developed posterolateral re-entrant for insertion of last pereopods, whereas in *P. erinaceus* the re-entrant is barely marked dorsally and visible only in posterior view. In Polybiinae, a portion of male sternite 8 is visible, male pleonal somites 3-5 are fused, and the pleonal somite 3 is transversely keeled, while in *P. erinaceus* the sternite 8 is not visible, male pleonal somites 3-5 are free, and the pleonal somite 3 is only slightly vaulted. The epibranchial ridge, a character typical for Polybiinae, is not present in *P. erinaceus*. Most of the extant representatives of Polybiinae possess a wide thoracic sternum with the maximum width at the level of sternite 6 (Spiridonov 2020: 139), whereas in *P. erinaceus* the maximum width of the sternum is at the level of sternite 5. In Polybiinae, the lower margin of cheliped propodus is concave (Davie et al. 2015b:

1102), whereas it is slightly convex in *P. erinaceus*. In addition, the P5 of representatives of Polybiinae is usually paddle-like, and although it could not be verified, it does not seem to be the case in *Pleolobites* (Fig. 2C3). Most extant representatives of Polybiinae have a carapace outline and the fronto-orbital margin (with usually an uneven number of teeth) strikingly differing from that in *P. erinaceus*. In this respect, only *Bathynectes longispina* Stimpson, 1871, *B. maravigna* (Prestandrea, 1839), and *B. piperitus* Manning & Holthuis, 1981, have the frontal margin with four teeth and an extremely long last anterolateral tooth similar to *P. erinaceus*. Based on the differences discussed above, the genus *Pleolobites* should be removed from the subfamily Polybiinae.

Rhachiosoma Woodward, 1871 (Fig. 4), known from the Ypresian of England, also placed within Polybiinae (Schweitzer et al. 2021), shows striking with *Pleolobites*. However, *Rhachiosoma* differs from the latter in having small orbits, elongate chelae, and acute posterolateral corners (Woodward 1871: 91, 92, pl. 4, figs. 3, 5; Woodward 1873: 25–28, pl. 1, figs. 1–6; Collins et al. 2020: 46, fig. 10H; Schweitzer et al. 2021: figs. 7.3a, b). Therefore, *Rhachiosoma* is removed from Polybiinae to Portunoidea *incertae sedis*.

The dorsal morphology of *Pleolobites erinaceus* shows striking similarities with some Late Cretaceous and early Paleogene representatives of the family Palaeoxanthopsidae Schweitzer, 2003, within the superfamily Carpilioidea Ortmann, 1893: *Verrucoides* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer & Waugh, 2001a (figured in Collins & Wienberg Rasmussen 1992: fig. 21A-C; Vega et al. 2001: fig. 17.1-4; Schweitzer et al. 2018: fig. 7.3), *Palaeoxanthopsis* Beurlen, 1958 (figured in Beurlen 1958: fig. 3, pl. 1, figs. 1, 2; Luque et al. 2017: fig. 8E; Schweitzer et al. 2018: fig. 6.4; Vega et al. 2018: figs. 11.12–19), or *Paraverrucoides* Schweitzer, 2003

(figured in Rathbun 1935: pl. 20.3–16; Armstrong et al. 2010: fig. 6.5–8). These taxa and *Pleolobites erinaceus* share several features such as strong swellings in identical carapace areas, a long last anterolateral spine, the fronto-orbital margin with bilobed front with median notch giving a tetra-lobed aspect, and broad subrectangular orbits with two fissures in the supraorbital margin. Additionally, some palaeoxanthopsid taxa have chelipeds with spiny propodal margin and multi-lobed serial finger-teeth similar to those in modern portunoid crabs (Spiridonov et al., 2014). Detailed examination of high-resolution images of ventral aspects of *Parazanthopsis meyapaquensis* Vega, Feldmann, García-Barrera, Filkorn, Pimentel & Avendaño, 2001b, and *Palaeoxanthopsis cretacea* (Rathbun, 1902), figured in Vega et al. (2018: figs. 11.2, 19), show no significant differences when compared with the ventral features of *Pleolobites erinaceus*. Thus, some genera currently classified within Palaeoxanthopsidae might be removed from the respective family (and superfamily) and placed into Portunoidea upon closer inspection.

6. Conclusions

The diagnosis of the monotypic brachyuran crab genus *Pleolobites* is emended based on examination of the type and newly collected specimens. Herein, the new specimens from Togo expands the stratigraphic range for the genus into the Paleocene (Thanetian). The examination of characters of the thoracic sternum and pleon, *Pleolobites* is removed to Portunoidea *incertae sedis* from the subfamily Polybiinae of the family Carcinidae. It is further argued that *Palaeoxanthopsis*, *Paraverrucoides*, *Parazanthopsis*, and *Verrucoides*, currently classified within the family Palaeoxanthopsidae of the superfamily Carpilioidea, show striking similarities with portunoid crabs. It remains to be investigated whether these resemblances are the result

of evolutionary convergence or close phylogenetic relationships. The above mentioned palaeoxanthopsid genera are left within the respective family, pending revision of their relationships

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FIGURES

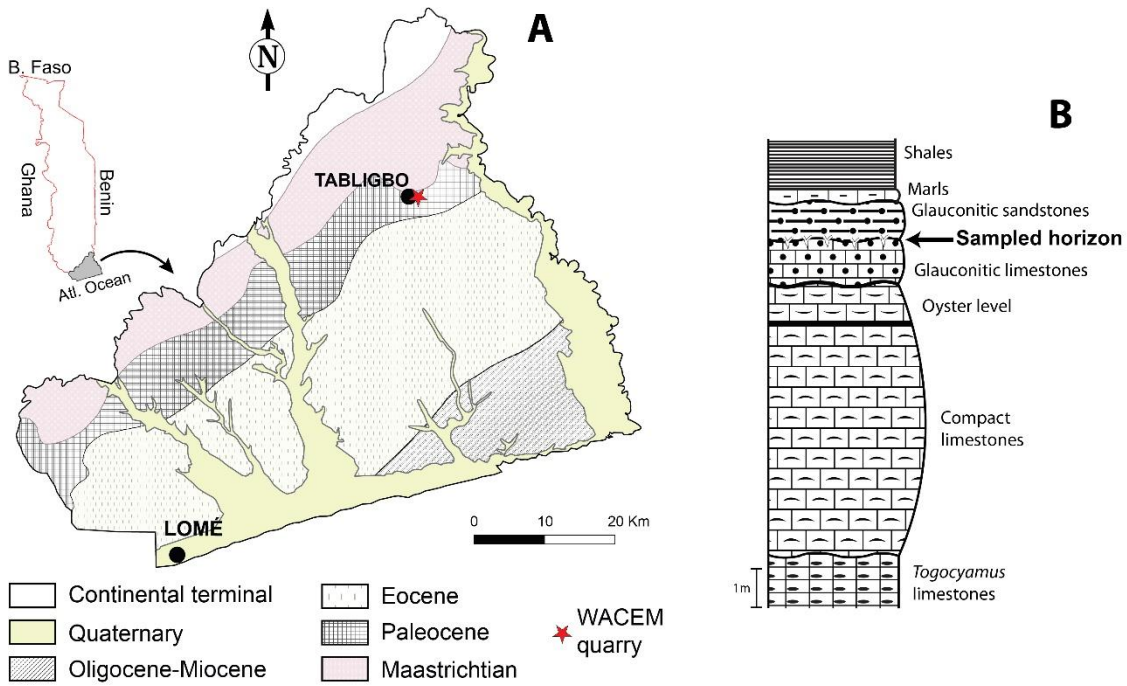


Figure 1. A, General geological map of the Coastal Sedimentary Basin in Southern Togo and localisation of the sampled site. **B**, synthetic sedimentary log of the geological section at WACEM quarry; modified after Guinot et al. (2020).

Figure 1. A, Carte géologique générale du Bassin Sédimentaire Côtier du sud Togo et localisation de la localité échantillonnée. **B**, log synthétique de la section géologique dans la carrière de WACEM ; modifié d'après Guinot et al. (2020).

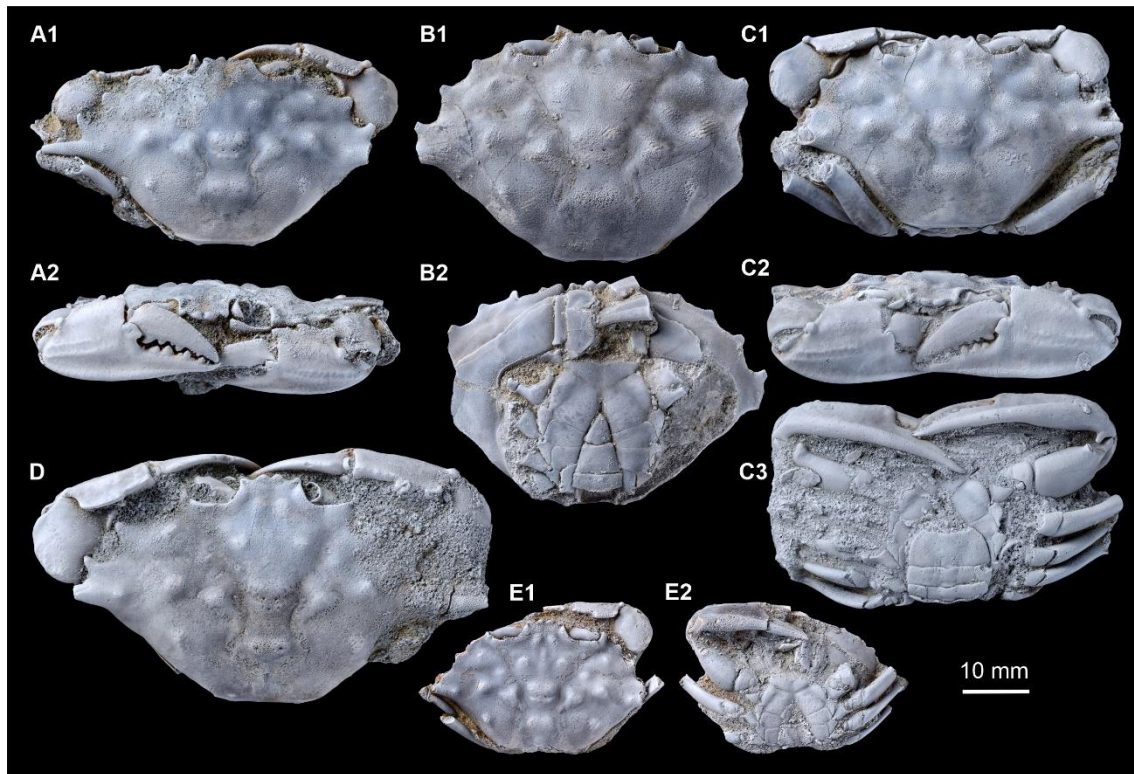


Figure 2. Type material of *Pleolobites erinaceus* Rémy, 1960; lower Eocene (Ypresian) of Ivory Coast. **A**, Paratype MNHN.F A70126. **B**, Paratype MNHN.F A70127. **C**, Holotype MNHN.F R03782. **D**, Paratype MNHN.F A70128. **E**, Paratype MNHN.F A70125. All specimens were whitened with ammonium chloride prior the photography. Specimens are to the same scale.

Figure 2. Spécimens types de *Pleolobites erinaceus* Rémy, 1960 ; Eocène inférieur (Yprésien) de Côte d'Ivoire. **A**, Paratype MNHN.F A70126. **B**, Paratype MNHN.F A70127. **C**, Holotype MNHN.F R03782. **D**, Paratype MNHN.F A70128. **E**, Paratype MNHN.F A70125. Tous les spécimens ont été blanchis au chlorure d'ammonium avant photographie. Les spécimens sont tous à la même échelle.

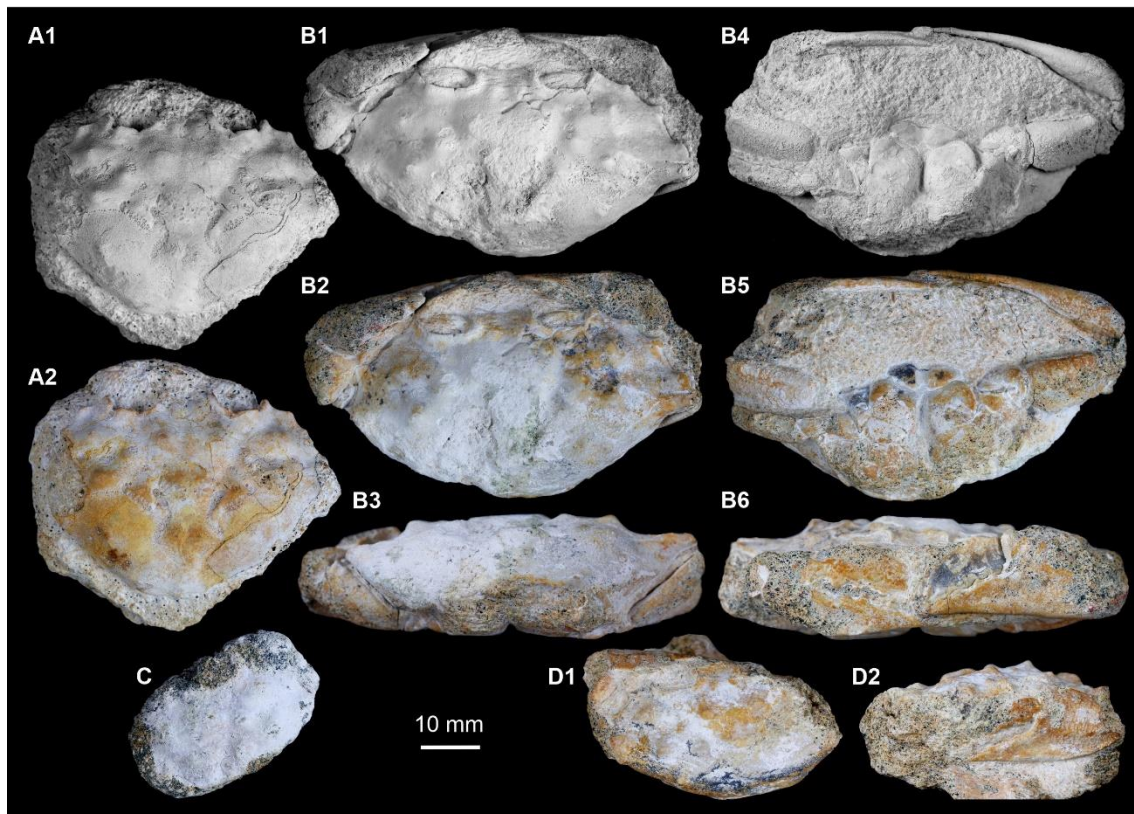


Figure 3. *Pleolobites erinaceus* Rémy, 1960; upper Paleocene (Thanetian) of Togo. **A**, ULDG TAB3-7, a near-complete dorsal carapace with prominent muscle scars. **B**, ULDG TAB3-6, specimen with dorsal carapace, sternum, and both chelae. **C**, ULDG TAB3-8, a dorsal carapace fragment. **D**, ULDG TAB3-9, fragmentary dorsal carapace with left chela. Specimens in A1, B1, and B4 were whitened with ammonium chloride prior the photography. All specimens are to the same scale.

Figure 3. *Pleolobites erinaceus* Rémy, 1960 ; Paléocène inférieur (Thanétien) du Togo. **A**, ULDG TAB3-7, carapace dorsale quasi-complète avec des marques musculaires proéminentes. **B**, ULDG TAB3-6, spécimen avec carapace dorsale, sternum, et les deux pinces. **C**, ULDG TAB3-8, fragment de carapace dorsale. **D**, ULDG TAB3-9, carapace dorsale fragmentaire avec pince gauche. Les spécimens A1, B1, et B4 ont été blanchis au chlorure d'ammonium avant photographie. Les spécimens sont tous à la même échelle.

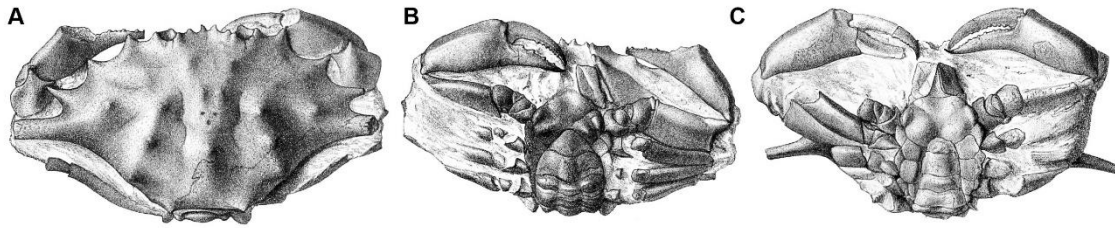


Figure 4. *Rhachiosoma bispinosa* Woodward, 1871; lower Eocene of England. **A**, NHMUK 59223 in dorsal view (digital copy of Woodward 1871: pl. 1, fig. 4). **B**, NHMUK 59223 in ventral view (digital copy of Woodward 1871: pl. 1, fig. 5). **C**, Near-complete individual in ventral view (digital copy of Woodward 1871: pl. 1, fig. 6).

Figure 4. *Rhachiosoma bispinosa* Woodward, 1871 ; Eocène inférieur d'Angleterre. **A**, NHMUK 59223 en vue dorsale (copie digitale de Woodward 1871 : pl. 1, fig. 4). **B**, NHMUK 59223 en vue ventrale (copie digitale de Woodward 1871 : pl. 1, fig. 5). **C**, individu sub-complet en vue ventrale (copie digitale de Woodward 1871 : pl. 1, fig. 6).