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To cite this version:
Bertrand Lefebvre, Martina Nohejlová, Emmanuel L.O. Martin, Libor Kasicka, Ondřej Zicha, et al.. New Middle and Late Ordovician cornute stylophorans (Echinodermata) from Morocco and other peri-Gondwanan areas. The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco, 2022, 9781786204073. hal-03764421

HAL Id: hal-03764421
https://hal.science/hal-03764421
Submitted on 30 Aug 2022

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New Middle and Late Ordovician cornute stylophorans (Echinodermata)
from Morocco and other peri-Gondwanan areas
to the memory of Rudolf J. Prokop

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Abbreviated title: Ordovician cornute stylophorans
Abstract: Cornute stylophorans are a minor, though typical component of Middle–Late Ordovician echinoderm assemblages adapted to soft siliciclastic substrates, in high latitude peri-Gondwanan regions. All previously reported occurrences of Darriwilian–Katian cornutes from Czech Republic, France, Morocco and Spain are revised and their plate homologies reassessed. The genera Beryllia and Juliaecarpus are reinterpreted as junior synonyms of Domfrontia, and Thoralicystis is synonymised with Bohemiaecystis. Several Mediterranean scotiaecystids previously assigned to Bohemiaecystis and/or Scotiaecystis are placed within Thoralicarbus gen. nov., and cornute taxa originally left in open nomenclature by Chauvel are formally described as Bohemiaecystis chouberti sp. nov. (AVI) and Destombesicarpus izeguirenensis gen. et sp. nov. (AVIII). Other new Mediterranean taxa include Arauricystis clariondi sp. nov., Destombesicarpus budili gen. et sp. nov., Milonicystis reboulorum sp. nov., Thoralicarbus bounemrouensis gen. et sp. nov., and T. prokopi gen. et sp. nov. The six cornute genera identified in Darriwilian–Katian Moroccan echinoderm Lagerstätten are also present in coeval assemblages of at least one other Mediterranean region, thus supporting the existence of strong faunal affinities between the Anti-Atlas, the Armorican Massif, the Barrandian area and the Iberian Peninsula.

Keywords: Cornuta, Stylophora, Echinodermata, Ordovician, Mediterranean Province

Stylophorans are a class of vagile, benthic Palaeozoic echinoderms, which thrived on soft sea-floors over 200 my, from the Wuliuan (Miaolingian, middle Cambrian) to the Bashkirian (Pennsylvanian, late Carboniferous) (see e.g. Kolata et al. 1991; Zamora et al. 2013a). They consist of a single appendage (aulacophore) inserted into a flattened, asymmetrical to almost bilaterally symmetrical test (theca) (Fig. 1). Recently, the Lower Ordovician Fezouata Lagerstätte, in the central Anti-Atlas of Morocco yielded stylophoran specimens with
exceptionally preserved soft parts within their appendage (Lefebvre et al. 2019a; Saleh et al. 2020). This discovery confirmed that the distal part of the aulacophore was a feeding structure containing a single ambulacral canal and its lateral extensions (podia) (see e.g. Ubahgs 1961, 1968, 1970; Nichols 1972; Chauvel 1981; Parsley 1988; Sprinkle 1992; Sumrall 1997; David et al. 2000; Lefebvre & Fatka 2003; Guensburg et al. 2020).

Stylophorans are traditionally subdivided into the two orders Cornuta and Mitrata (see e.g. Jaekel 1918; Chauvel 1941; Gill & Caster 1960; Ubahgs 1968, 1970, 1991, 1994; Parsley 1988; Lefebvre & Vizcaíno 1999; Lefebvre 2001, 2003a). Cornutes are characterised by a relatively stiff distal aulacophore, with flat, undifferentiated interossicular articulations. Their theca was lightly built, with large polyplated integumentary areas framed by delicate skeletal elements: adorals and marginals (Fig. 1; Ubahgs 1968, 1970; Jefferies 1968; Parsley 1988; Cripps 1991; Lefebvre and Vizcaíno 1999; Lefebvre 2001). In contrast, the distal appendage of mitrates had complex, well-differentiated interossicular articulations. It formed a highly flexible structure, which could be recurved over the theca, in a vertical plane (Parsley 1988; Lefebvre 2003a). Moreover, the mitrate theca was typically made of a reduced number of large, massive skeletal elements (adorals, marginals) delimiting small integumentary areas (Jaekel 1918; Chauvel 1941, 1981; Ubahgs 1968, 1970; Jefferies 1968; Parsley 1988; Kolata et al. 1991; Lefebvre 2001, 2003a).

Recent findings in the late Guzhangian (Peng et al. 2020) and the Furongian of South China (Zamora et al. 2013b; Zhu et al. 2016) suggest that the earliest mitrates more likely derived from 'Phyllocystis' jingxiensis-like, regular boot-shaped cornutes (Lefebvre & Ausich 2021) rather than from heavily plated Ceratocystis-like early stylophorans (see e.g. Lefebvre & Vizcaíno 1999; Lefebvre 2001). This implies that the order Cornuta is a paraphyletic assemblage, with some of its members more closely related to mitrates than to other cornutes (e.g. Jefferies & Prokop 1972; Derstler 1979; Cripps 1989a, 1991; Parsley 1997). In this
paper, 'Cornuta' will thus be used as an informal taxonomic unit corresponding to all non-mitrute stylophorans.

Cornutes originally diversified on soft substrates during the Miaolingian, with two distinct morphotypes: heavily-plated ('armoured') *Ceratocystis*-like forms in proximal settings, and lightly built, boot-shaped taxa in more distal environments (e.g. *Archaeocothurnus*, *Ponticulocarpus*) (see Ubaghs 1967; Jefferies et al. 1987; Ubaghs & Robison 1988; Sprinkle 1992; Sumrall & Sprinkle 1999; Lefebvre 2003a, 2007a; Lefebvre & Fatka 2003; Zamora et al. 2013a; Noailles 2016). From this middle Cambrian stock of early cornutes, stylophorans underwent a major diversification in the Furongian–Floian time interval, with the onset of all major clades: Amygdalothecidae, Chauvelicystidae, Cothurnocystidae, Hanusiidae, Mitrata, Phyllocystidae, and Scotiaecystidae (Lefebvre & Ausich 2021). Cornutes were a major component of the relatively cosmopolitan late Cambrian–Early Ordovician echinoderm assemblages (Sprinkle & Guensburg 1997; Sumrall et al. 1997; Guensburg & Sprinkle 2000; Lefebvre & Fatka 2003; Lefebvre et al. 2013; Zamora et al. 2013a). In the Furongian–Floian time interval, cornutes were palaeobiogeographically widespread, with occurrences in Laurentia (Ubaghs 1963; Sprinkle 1976, 1992; Sumrall et al. 1997, 2009), Siberia (Rozova et al. 1985), and in many (peri)Gondwanan areas, such as Argentina (Nohejlová et al. 2018), Australia (Smith & Jell 1999), Avalonia (Daley 1992; Martí Mus 2002; Botting et al. 2015; Lefebvre et al. 2015b), France (Thoral 1935; Ubaghs 1970, 1983, 1991, 1994, 1998; Lefebvre & Vizcaíno 1999), Iran (Rozhnov & Parsley 2017), Korea (Lee et al. 2005), Morocco (Chauvel 1966, 1971; Martin et al. 2015; Lefebvre et al. 2016a, 2019a), and South China (Han & Chen 2008; Zamora et al. 2013b; Zhu et al. 2016). With rare exceptions (e.g. the Lady Burn starfish bed in Scotland; see Bather 1913; Jefferies 1968), cornutes were a minor component of all younger stylophoran assemblages, dominated by kirkocystid and/or mitrocystitid mitrates (Lefebvre 2007a; Lefebvre et al. 2013). Cornutes did not survive the
Hirnantian biodiversity crisis, whereas mitrates were less impacted and eventually briefly re-
diversified in the Early Devonian (Lefebvre et al. 2006; Lefebvre 2007a; Lefebvre & Ausich
2021).

In Early Ordovician times, the high-latitude Mediterranean Province, on the western south
polar margin of Gondwana (see Destombes et al. 1985; Álvaro et al. this volume), was an
outstanding biodiversity hotspot for cornutes (Vizcaíno & Lefebvre 1999; Vizcaíno et al.
2001; Sprinkle & Guensburg 2004; Lefebvre et al. 2013, 2016a). The central Anti-Atlas
(Morocco) and the Montagne Noire (France) yielded relatively similar, high diversity
assemblages, comprising, in each region, around 20 taxa belonging to the six main cornute
clades: Amygdalothecidae (*Amygdalotheca, Nanocarpus*), Chauvelicystidae (e.g. *Ampelocarpus, Chauvelicystis, Lyricocarpus*), Cothurnocystidae (e.g. *Procothurnocystis*),
Hanusiidae (e.g. *Galliaecystis*), Phyllocystidae (*Phyllocystis*), and Scotiaecystidae
(*Bohemiaecystis, Proscotiaecystis*). In marked contrast, very few cornute remains were
described from younger Ordovician deposits (Darriwilian–Katian) in the whole
Mediterranean Province: in Czech Republic (Ubaghs 1968; Jefferies & Prokop 1972; Cripps
1989a, b), France (Chauvel & Nion 1977; Chauvel 1986; Cripps & Daley 1994; Lefebvre &
Vizcaíno 1999), Morocco (Chauvel 1971; Ruta 1999a), and Spain (Gil Cid et al. 1996d).

However, in the last 20 years, numerous cornute remains were discovered in Middle and
Upper Ordovician strata of these regions, and in particular in the eastern Anti-Atlas of
Morocco (Gutiérrez-Marco et al. 2003; Lefebvre & Gutiérrez-Marco 2007; Lefebvre et al.

Consequently, the aim of this paper is to provide a relatively exhaustive review of
Darriwilian–Katian cornutes from the Mediterranean Province, based on the revision of most
previously known occurrences and on the description of several new taxa. Hanusiids were not
included in this study, because almost no new significant material was collected since their
original descriptions in Bohemia (Jefferies & Prokop 1972; Cripps 1989a, b). All other
cornute specimens were considered, including incomplete ones, thus providing a more
accurate picture of their original diversity and palaeobiogeographic affinities. A phylogenetic
analysis of cornutes is beyond the scope of this mostly taxonomic contribution. With at least
18 species belonging to nine genera and five families, the fossil record of cornutes in the
Mediterranean Province (Czech Republic, France, Morocco, and Spain) now appears as the
most diverse in the world for the Middle–Late Ordovician interval. This suggests that
cornutes maintained, at least in this region, a relatively high diversity, almost up to their
extinction in the Hirnantian.

Mid–Late Ordovician cornutes

With some notable exceptions (e.g. Cothurnocystis elizae and Scotiaecystis curvata, known
from hundreds of specimens from the same locality in Scotland), cornutes are generally rare
fossils in Middle and Upper Ordovician deposits (Bather 1913; Regnéll 1960; Jefferies &
Daley 1996; Lefebvre 2007a). This rarity possibly results from a strong taphonomic bias.
Cornutes are typical 'type 1 echinoderms' sensu Brett et al. (1997): their delicate, lightly built
thecae rapidly disarticulated into hundreds of skeletal elements, probably within days or
weeks after death and decay (Lefebvre 2007a; Martin et al. 2015). Although some of their
isolated plates show diagnostic features (see e.g. Rozhnov 1990; Pisera 1994; Lee et al.
2006), the fossil record of cornutes almost exclusively relies on intact or at least partly
articulated skeletons. The preservation of fully articulated individuals thus requires that they
were buried alive or soon after death by a sudden influx of sediments (e.g. tempestites,
turbidites), as this was the case e.g. in most cornute occurrences in the lower part (late
Tremadocian) of the Fezouata Shale, Morocco (Martin et al. 2015; Lefebvre et al. 2016a),
and also in some Upper Ordovician 'starfish beds' from the Tafilalt area (see e.g. Lefebvre et al. 2007, 2008, 2010a; Hunter et al. 2010; Nardin & Régnault 2015; Gutiérrez-Marco et al. a this volume).

Ordovician cornutes occurred exclusively on soft substrates, but in a relatively wide spectrum of palaeoenvironmental conditions, ranging from proximal settings (shoreface), typical of the 'kirkocystid biofacies' (Lefebvre 2007a) to relatively distal, low energy environments (offshore), where they can represent the dominant echinoderm group ('cornute biofacies'; Lefebvre 2007a; Botting et al. 2013). Their palaeobiogeographic distribution suggests that Ordovician cornutes were probably psychrospheric organisms, i.e. restricted to the most distal (and coolest) settings (Lefebvre 2007a). In high latitude areas (e.g. Mediterranean Province), they are found in both shoreface and offshore environments, whereas in lower latitude regions (e.g. Avalonia, Laurentia) they are apparently restricted to the most distal settings (Lefebvre 2007a). Their absence in North America in the Darriwilian–Katian time interval is probably original, but coeval deposits from other parts of the world have been little investigated for cornute occurrences (e.g. Australia, Siberia, Sibumasu). Finally, their rarity in most Mid–Late Ordovician 'echinoderm Lagerstätten' sensu Smith (1988), where many other type 1 echinoderms are preserved (e.g. eocrinoids, glyptocystitid rhombiferans, mitrates, ophiuroids, solutans) possibly also indicates an originally reduced contribution of cornutes to echinoderm diversity, compared to Furongian–Floian assemblages (Lefebvre et al. 2013).

**Mediterranean Province**

**Anti-Atlas (Morocco).** In Morocco, the first remains of Middle–Late Ordovician cornutes were collected by J. Destombes in the 1960s during field work for the 1:200.000 geological
maps of Jbel Saghro-Dades (localities 755 and 756; Destombes 2006a) and Todrha-Maīder (locality 1826; Destombes 2006b). This material was briefly described and figured by Chauvel (1971) as genera indet. AVI, AVII, and AVIII (with 'A' standing for 'Anti-Atlas'). The description of AVI was based on a single slab containing several incomplete and partly overlapping individuals from the Guezzart Formation (late Darriwilian). These specimens were correctly interpreted as boot-shaped cornutes by Chauvel (1971). The two other forms were each known from a single individual. They were described as a probable kirkocystid mitrate (AVII; base of the Lower Second Bani Formation, latest Katian) and a possible juvenile individual of mitrate indet. (AVIII; Izegguirene Formation, early Sandbian) (Chauvel 1971, 1978).

In subsequent works, affinities with a Lyricocarpus-like chauvelicystid cornute were repeatedly suggested for AVIII (see e.g. Ubaghs 1994; Lefebvre & Vizcaíno 1999; Gutiérrez-Marcò et al. 2003; Lefebvre & Fatka 2003; Lefebvre et al. 2007). Based on abundant new material collected by J. Destombes, R. Jefferies and J. Savill in 1990, Ruta (1999a) described the youngest known cornute, Juliaecarpus milnerorum, from the same level and locality as AVII (Destombes' locality 756). Ruta (1999a, p. 53) mentioned the possibility that AVII and J. milnerorum may correspond to the same original taxon. Lefebvre (2001) considered Juliaecarpus as a junior synonym of Nanocarpus and assigned it to the family Amygdalothecidae (see also Lefebvre 2003a, 2007a; Lefebvre et al. 2007). Scotiaecystid affinities for Chauvel's AVI (1971) were suggested by Lefebvre & Fatka (2003).

Based on new material collected by J. Destombes, R. Jefferies and J. Savill in 1990 in the same locality as AVIII (Izegguirene Formation), Gutiérrez-Marcò et al. (2003) briefly mentioned the occurrence of Scotiaecystis-like cornutes in the early Sandbian of the central Anti-Atlas (see also Lefebvre et al. 2007). The occurrence of scotiaecystids in the Izegguirene Formation was later confirmed by Lefebvre et al. (2008), based on additional specimens from
Bou Nemrou, in the Tafilalt area (see also Lefebvre et al. 2010a). The presence of two other cornutes (Cothurnocystis and Milonicystis) in the same locality (Bou Nemrou) was also briefly mentioned by Lefebvre et al. (2008, 2010a). In summary, in the late 2010s, six cornute occurrences were known in the Middle and Upper Ordovician of the Anti-Atlas, but only a single one had been formally described (N. milnerorum). They were documented from three distinct stratigraphic levels: the Guezzart (AVI), Izegguiren (AVIII, Cothurnocystis sp., Milonicystis sp., Scotiaecystis sp.), and Lower Second Bani formations (AVII = N. milnerorum).

In this study, the original material of AVI, AVII and AVIII originally reported by Chauvel (1971) is reexamined and formally described. New specimens collected from the same locality and horizon as AVI made it possible to assign it to a new species of scotiaecystids (Bohemiaecystis chouberti sp. nov.). Reexamination of AVII confirms that it is conspecific with Nanocarpus milnerorum (see Ruta 1999a). However, a new late Katian locality in the eastern Tafilalt yielded numerous better-preserved specimens of this small amygdalothecid cornute, suggesting that it more likely belongs to Domfrontia, rather than to Nanocarpus. The long suspected chauvelicystid affinities of AVIII (see Ubaghs 1994; Lefebvre & Vizcaíno 1999) are confirmed, and the specimen originally described by Chauvel (1971) is designated herein as holotype of a new taxon (Destombesicarpus izegguirenensis gen. et sp. nov.). In this study, the three other cornute taxa reported in the Upper Ordovician of the Anti-Atlas by Gutiérrez-Marco et al. (2003) and Lefebvre et al. (2007, 2008, 2010a) are also described, based on all available material (Arauricystis clariondi sp. nov., Milonicystis reboulorum sp. nov. and Thoralicarpus bounemrouensis gen. et sp. nov.). Finally, two specimens of a previously unreported scotiaecystid cornute collected in 1986 by J. Destombes in the Tachilla Formation (middle Darriwilian) of Agadir area (western Anti-Atlas) is also preliminary described herein as Bohemiaecystis? sp.
Armorican Massif (France). Cornutes are particularly rare fossils in Ordovician rocks of western France (Brittany and Normandy). In spite of intensive field work since the mid 19th century (e.g. Rouault 1851, 1883; Tromelin & Lebesconte 1876; Tromelin 1878; Kerforne 1901), no cornute remains were mentioned by Chauvel (1941) in his extensive monograph on Armorican carpoids and cystoids. The first Armorican cornutes were described by Chauvel & Nion (1977), based on material collected by J. Nion and M. Robardet in the Le Pissot Formation (late Darriwilian) of Normandy (Reticulocarpos pissotensis) and the lower part of the Traveusot Formation (middle Darriwilian) of eastern Brittany (Reticulocarpos sp.). Soon after, the upper part of the Traveusot Formation (late Darriwilian) yielded three additional specimens, which were assigned by Chauvel (1986) to a new species of mitrates, Milonicystis kerfornei.

Based on new material collected by A. Cripps and R. Jefferies in 1988 in the Le Pissot Formation and the original specimens of Chauvel & Nion (1977), Cripps & Daley (1994) revised the morphology of R. pissotensis and assigned it to a new genus, Domfrontia. They also suggested that a second, distinct cornute (Beryllia miranda) was co-occurring with D. pissotensis in the same locality and levels. Cripps & Daley (1994) also correctly decided that Milonicystis was not a mitrate, but a cornute stylophoran. In the late 1990s, a single, almost complete specimen of scotiaecystid cornute was discovered by C. Guillou in the late Darriwilian of eastern Brittany (upper part of the Traveusot Formation), and described as a new species (Scotiaecystis guilloui) by Lefebvre & Vizcaíno (1999). Consequently, in the late 2010s, four cornute taxa were known from the late Darriwilian of Brittany (Milonicystis kerfornei, Scotiaecystis guilloui) and Normandy (Beryllia miranda, Domfrontia pissotensis) (Lefebvre 2000a; Lefebvre & Fatka 2003; Lefebvre et al. 2015a), and additional cornute
remains (*Reticulocarpos* sp.) were documented from mid-Darriwilian deposits (Chauvel & Nion 1977; Chauvel 1981; Lefebvre *et al*. 2015a).

In recent years, the discovery of new specimens of small amygdalothecid cornutes in a new early Sandbian locality of eastern Brittany prompted the reevaluation of *Beryllia* and *Domfrontia*. In this study, the reexamination of all available material suggests that these two taxa are conspecific and that, consequently, *B. miranda* is a junior synonym of *D. pissotensis*. All isolated occurrences of Darriwilian amygdalothecids from Brittany are tentatively assigned to *Domfrontia*. The morphology of the two other Armorican cornutes *Milonicystis kerfornei* and *Scotiaecystis guilloui* is also reinvestigated, with the scotiaecystid here assigned to *Thoralicarpus* gen. nov. (*T. guilloui*; see below).

**Bohemia** (*Czech Republic*). Similar to the situation in the Armorican Massif, cornutes remained long unrecorded in the Ordovician of Bohemia (see e.g. Havlíček & Vaněk 1966), in spite of extensive field work and the vigorous palaeontological activity of Barrande (1887). Caster (*in* Ubaghs 1968) described the first Ordovician cornute from the Prague Basin (*Bohemiaecystis bouceki*), based on a handful of well-preserved specimens from the Šárka and Dobrotivá formations (middle Darriwilian–earliest Sandbian). In the following years, several closely related hanusiid cornutes were described based on material collected by F. Hanuš and M. Mergl in the Middle Ordovician of Bohemia (Jefferies & Prokop 1972; Cripps 1989a, b). The Šárka Formation (middle Darriwilian) yielded *Hanusia obtusa, H. sarkensis*, and *Reticulocarpos hanusi*, whereas two more taxa (*H. prilepensis* and *Prokopicystis mergli*) were reported from the overlying Dobrotivá Formation. In the last 30 years, no new cornute taxa were described in Bohemia, but Lefebvre & Vizcaïno (1999) considered that *Bohemiaecystis* should be synonymised with *Thoralicystis* (see also Lefebvre 2001, 2007a; Lefebvre & Fatka 2003). The first report of cornute remains (*Scotiaecystis* sp.) in the Upper
Ordovician of Bohemia (Letná and Vinice formations) was briefly mentioned by Noailles et al. (2014). In the late 2010s, with six taxa belonging to four genera and two families (Hanusiidae and Scotiaecystidae), the Prague Basin had yielded the most diverse assemblage of Middle Ordovician cornutes (Prokop & Petr 1999; Lefebvre & Fatka 2003; Lefebvre 2007a).

In this study, this high diversity is further enhanced with the first report of cothurnocystids (Arauricystis clariondi sp. nov.) in the Dobrotivá Formation, whereas scotiaecystids from the Šárka Formation are assigned to Thoralicarpus cf. prokopi gen et sp. nov. (see below). Moreover, the reexamination of the morphology of Middle Ordovician Czech scotiaecystids confirms that they belong to the same genus as Lower Ordovician taxa from Morocco and the Montagne Noire (see e.g. Ubaghs 1970; Chauvel 1971; Lefebvre & Vizcaíno 1999; Lefebvre et al. 2016a, 2019a). However, contrary to Lefebvre & Vizcaíno (1999), we consider herein that Thoralicystis Chauvel, 1971 should be synonymised with Bohemiaecystis Caster in Ubaghs, 1968, and not the reverse (see below). More significantly, abundant and diverse cornute remains are described herein for the first time in the Upper Ordovician of the Prague Basin. Four new taxa belonging to three families are documented from the Letná (Thoralicarpus jefferiesi and T. prokopi gen et sp. nov.), Vinice (T. prokopi gen. et sp. nov.), Zahořany (Destombesicarpus budili gen. et sp. nov. and Domfrontia aff. milnerorum), Bohdalen (D. aff. milnerorum), and Králův Dvůr formations (D. aff. milnerorum).

Iberian Massif (Spain). Compared to the situation in other Mediterranean regions, the fossil record of Ordovician cornutes is extremely scarce in Spain. They were first documented by Gil Cid et al. (1996d), who described several incomplete specimens of a new scotiaecystid (Bohemiaecystis jefferiesi) from the middle Berounian (late Sandbian–early Katian) Cantera Shale in the southern Central Iberian Zone (see also Gutiérrez-Marco et al. 2018). Lefebvre &
Vizcaïno (1999) pointed out that this cornute should be assigned to the genus *Scotiaecystis* (see also Lefebvre 2000a, 2001; Lefebvre *et al.* 2008), but it more likely belongs to *Thoralicarpus* gen. nov. (*T. jefferesi*; see below). Finally, the presence of poorly preserved cornute remains in the middle Darriwilian noduliferous shales of the Valle syncline of the Ossa Morena Zone was briefly mentioned by Lefebvre & Fatka (2003) and Lefebvre & Gutiérrez-Marco (2007).

In this study, the morphology of *T. jefferesi* is reexamined, based on the reevaluation of the original type material of Gil Cid *et al.* (1996d), and a preliminary description as *Domfrontia*? sp. from the two incomplete specimens from Ossa Morena is provided.

**Other regions**

*Avalonia* (Wales). Before its rifting away from the western Gondwanan margin in Early Ordovician times (opening of the Rheic ocean), Avalonia was palaeogeographically close to most other high-latitude regions of the Mediterranean Province (Verniers *et al.* 2002; Fortey & Cocks 2003; Servais & Sintubin 2009; Torsvik & Cocks 2013). Consequently, middle Cambrian–Early Ordovician cornute faunas from Avalonia were very similar to coeval ones from the Anti-Atlas, Bohemia, the Iberian Massif, and the Montagne Noire (see Lefebvre & Fatka 2003; Lefebvre 2007a). Examples of Mediterranean cornute assemblages from Avalonia were found in the Middle Menevian Beds (Drumian; Jefferies *et al.* 1987) and the Dol-cyn-Afon Formation of Wales (middle Tremadocian; Botting *et al.* 2015; Lefebvre *et al.* 2015b), and the Shineton Shale (late Tremadocian) of Shropshire (Daley 1992; Martí Mus 2002).

Probably derived from this Mediterranean original stock, low-diversity cornute faunas persisted in distal settings off Avalonia, when it drifted away from Gondwana in Middle and
Late Ordovician times (Jefferies 1987; Lefebvre 2007a; Botting et al. 2013). For example, Mediterranean affinities are still present in the assemblage briefly reported by Jefferies (1987) in the Pontyfenni Formation (Dapingian) of Wales. Three distinct cornutes were preliminary identified by Jefferies (1987) as Cothurnocystis sp., Reticulocarpos sp. 1, and R.? sp. 2. The cothurnocystid was subsequently formally described as Procothurnocystis owensi (Woods & Jefferies 1992). The two other taxa, each represented by a single specimen, are still awaiting formal description. The first of these (Reticulocarpos sp. 1′) was probably correctly identified by Jefferies (1987) as a hanusiid (see e.g. Lefebvre & Fatka 2003). The second specimen (Reticulocarpos? sp. 2′) more likely corresponds to a small chauvelicystid rather than to a hanusiid. Finally, locally abundant remains of Galliaecystis sp. were reported from several horizons within the Llanfawr Formation (late Darriwilian–earliest Sandbian) of central Wales (Botting et al. 2013).

**Baltica (Poland and Russia).** In Cambrian times, Baltica was located at relatively high palaeolatitudes in the southern hemisphere, not far away from the western margin of Gondwana (Fortey & Cocks 2003; Cocks & Torsvik 2005; Torsvik & Cocks 2013). Consequently, middle Cambrian echinoderm faunas from Baltica share many taxa with the Anti-Atlas, Bohemia, the Montagne Noire and/or Spain. For example, Mediterranean taxa such as the cornute Ceratocystis, the eocrinoid Cigara and the edrioasteroid Stromatocystites occur in the Wulian of Sweden (Lefebvre 2007a; Zamora et al. 2013a, 2015). No stylophoran remains have been described from Furongian–Early Ordovician deposits of Baltica (Lefebvre 2007a; Lefebvre et al. 2013). In Ordovician times, this palaeocontinent drifted from high to low, equatorial latitudes (see references above).

In Baltica, the fossil record of Middle–Late Ordovician cornutes is particularly scarce (Lefebvre et al. 2005, 2013; Lefebvre 2007a). In the Saint-Petersburg area (Russia), Rozhnov...
(1990) described isolated skeletal elements of cornutes (*Babinocystis dilabida*) occurring in relatively high energy, cool-water, storm-dominated deposits of the Volkhov regional stage (Dapingian). The recent discovery of a fully articulated specimen in the same levels (S. Rozhnov, pers. comm., Oct. 2019) will probably help elucidate the affinities of Dapingian cornutes from the Saint-Petersburg area. In Russia, additional cornute fragments (*Babinocystis* sp.) were also found in younger deposits (Lasnamägi regional stage, late Darriwilian) of the Pskov area (Rozhnov 1990). In the Holy Cross Mountains (Poland), numerous isolated cornute elements were also reported by Pisera (1994), from several stratigraphic levels of the Mójcza Formation (Uhaku, Kukruse and Idavere regional stages, i.e. late Darriwilian–Sandbian). Cornute plates occur in condensed, cool-water limestones deposited on a palaeo-high on the southwestern margin of Baltica (Dzik & Pisera 1994; Trela 2005).

 Laurentia (*northwestern Ireland and Scotland*). In Cambro-Ordovician times, Laurentia was a large continent, palaeogeographically very stable at near tropical to equatorial latitudes (Fortey & Cocks 2003; Cocks & Torsvik 2011; Torsvik & Cocks 2013). In North America (e.g. Nevada, Utah), cornutes were regularly present in Wulian–Tremadocian echinoderm assemblages (e.g. Ubaghs 1963; Sprinkle 1976, 1992; Ubaghs & Robison 1988; Sumrall *et al.* 1997, 2009; Sumrall & Sprinkle 1999; Lefebvre & Fatka 2003; Lefebvre 2007a; Zamora *et al.* 2013a; Lefebvre *et al.* 2019b). No stylophoran remains have been reported in the Middle Ordovician of Laurentia. In the latest Sandbian, the reappearance of mitrates in North America coincides with a major faunal shift (Mohawkian invasion) and the sudden arrival of cool-adapted taxa, such as bivalve molluscs and solutuan echinoderms (see e.g. Sprinkle 1982; Babin 1993; Cope & Babin 1999; Lefebvre 2007a, b; Lefebvre *et al.* 2013).
Although cornutes are absent from Late Ordovician shoreface settings of North America, they sometimes occur massively in offshore environments of the then-southern Laurentian margin (Bather 1913; Cripps 1988; Jefferies & Daley 1996; Lefebvre 2007a; Lefebvre et al. 2013). In the Midland Valley of Scotland (Girvan area), the Lady Burn Starfish Bed (South Threave Formation, late Katian) yielded abundant remains of two distinct cornutes, originally described as Cothurnocystis elizae and C. curvata by Bather (1913). Cothurnocystis curvata was subsequently assigned to a distinct genus (Scotiaecystis) and a new family (Scotiaecystidae) by Ubaghs (1968) (see also Jefferies, 1967, 1968; Jefferies & Daley, 1996). In northwestern Ireland (Pomeroy area), another scotiaecystid (S. collapsa) was described by Cripps (1988) in the Killey Bridge Formation (late Katian). This cornute was closely related to, though morphologically distinct from and slightly older than, S. curvata.

**Morphology and plate homologies in cornutes**

*Cornute morphology*

Main morphological features of cornutes were summarised by Ubaghs (1963, 1968, 1970), and the terminology he introduced to describe their anatomy will be largely followed here (see also Lefebvre & Vizcaíno 1999; Lefebvre 2003a). For clarity, all descriptive terms used in the systematic section are briefly reviewed and explained below.

*General organization and orientation* (Fig. 2). All cornutes display the typical morphology of stylophorans, with a single flexible feeding appendage (aulacophore) inserted into a flattened test (theca) (e.g. Ubaghs 1963, 1968, 1970; Nichols 1972; Chauvel & Nion 1977; Chauvel 1986; Parsley 1988; Sprinkle 1992; Sumrall *et al.* 1997; Ruta 1999b; Sumrall & Sprinkle...
In terms of orientation, the aulacophore, which hosts the mouth, marks the anterior pole of the organism, whereas the theca, which bears the anus, is posterior (Ubaghs 1963). The aulacophore is bilaterally symmetrical (e.g. Bather 1913; Jaekel 1918). The appendage midline and its intersection with the anterior extremity of the theca are generally used as morphological landmarks (e.g. Bather 1913; Ubaghs 1968, 1970).

Along this longitudinal 'main axis', structures are defined as 'proximal' or as 'distal', depending on their relative position close to, or away from, respectively, the aulacophore insertion (e.g. Bather 1913; Thoral 1935; Ubaghs 1963, 1968; Chauvel 1966; Parsley 1988; Ruta 1999a; Lefebvre 2003a). Based on the main axis, the terms 'adaxial' and 'abaxial' are also used to express if a structure is close to, or away from it, respectively (Ubaghs, 1968). The aulacophore and the flattened theca of cornutes both show contrasted surfaces. The portions of the organism originally in permanent contact with the sea floor are designated as 'lower', whereas those away from it and facing the water column are 'upper' (e.g. Bather 1913; Ubaghs 1963, 1968, 1970; Chauvel 1966, 1986; Jefferies 1968, 1969; Parsley 1988; Ruta 1999b; Lefebvre 2003a).

**Theca.** Thecal outlines of cornutes are plesiomorphically asymmetrical and boot-shaped (e.g. Archaeothurnus, Ceratocystis, Drepanocarpos, Nevadaecystis, Ponticulocarpus) (e.g. Bather 1913; Jefferies & Prokop 1972; Cripps 1991; Parsley 1997; Lefebvre 2001). However, a trend towards more bilaterally symmetrical thecal morphologies can be seen within most cornute lineages (e.g. Chauvelicystidae, Hanusiidae, Scotiaecystidae; Lefebvre 2001). In most cornutes, lateral edges of the theca are made of a series of delicate, relatively narrow skeletal elements: the 'marginals' (Figs 1, 3b–f, 4b–f) (see e.g. Bather 1913; Jaekel 1918; Ubaghs 1963; Chauvel 1966; Jefferies 1968; Parsley 1988; Cripps 1991; Sumrall et al. 1997; Lefebvre...
& Vizcaïno 1999; Ruta 1999a). However, in Ceratocystis (Figs 3a, 4a) and other early 'armoured' cornutes (e.g. Protocystites), lateral thecal walls consist of thick and wide marginals, largely expanding on the lower and/or the upper thecal surface (Jaekel 1918; Ubaghs 1967; Jefferies 1969; Jefferies et al. 1987; Lefebvre & Vizcaïno 1999). At the anterior extremity of the theca, the aulacophore insertion is typically framed by two marginals and, above them, by a delicate arch made of two or three narrow skeletal elements: the 'adorals' (Figs 1b, 4b, d, f) (e.g. Ubaghs 1963, 1968, 1970; Chauvel & Nion 1977; Parsley 1997; Lefebvre & Vizcaïno 1999; Martí Mus, 2002; Sumrall et al. 2009). Adorals and marginals form together the 'marginal frame' of the theca (Figs 1, 3b–f, 4b–f). In cornutes, this frame can form a continuous structure (plesiomorphic condition), posteriorly closed by two marginals at the distal extremity of the lower (Fig. 3c; e.g. Archaeoarthurnus, Persiarcarpos, Ponticulocarpus) or the upper thecal surface (Fig. 4d; e.g. Drepanocarpos, Galliae cystis).

However, in many taxa, posterior marginals are lost or no longer in contact with each other, and the marginal frame is thus posteriorly open (Figs 3b, d–f, 4e–f; e.g. Amygdalotheca, Chauvelicystis, Flabellicarpus, Nanocarpus) (Lefebvre & Vizcaïno 1999; Lefebvre 2001).

In all cornutes, the number of adorals and marginals does not change during ontogeny, and represents a key diagnostic feature for the definition of genera. Examples of allometric development of marginals can be documented in some taxa, when sufficiently large populations are available (e.g. Ceratocystis perneri, Cothurnocystis elizae; B. Lefebvre, pers. obs.). Anterior marginals are generally thicker and more massive than posterior ones. In boot-shaped cornutes, the lower surface of anterior and antero-abaxial marginals typically bear strong protuberances, knobs, and/or posteriorly directed spikes (Figs 1a, c, 3a, c) (e.g. Ceratocystis, Cothurnocystis, Galliae cystis, Phyllocystis, Scotiaecystis; see e.g. Bather 1913; Ubaghs 1963, 1967, 1968, 1970; Jefferies 1968, 1969; Cripps 1988, 1989b; Lefebvre 2003a; Ware & Lefebvre 2007). In these taxa, some posterior marginals can bear a long, flattened
spike (e.g. 'spinal' in the right posterior thecal corner; Fig. 3a, c–d) or be themselves modified into posterior blade-like processes (e.g. 'digital' and 'glossal' on the left and on the right of the anal opening, respectively; Fig. 3a, c) (see Jaekel 1918; Ubaghs 1963, 1968, 1970; Lefebvre & Vizcaíno 1999; Lefebvre 2003a). This ornamentation (protuberances, knobs, spikes, posterior blades) probably helped anchor or stabilize boot-shaped cornutes on the surface of soft substrates (e.g. Parsley 1988; Lefebvre 2003a; Noailles 2016).

In some other cornutes (e.g. Amygdalotheca, Chauvelicystis, Domfrontia, Lyricocarpus, Milonicystis, Reticulocarpos), anterior knobs and spikes are absent and the marginal frame is more lightly built (e.g. Ubaghs 1970, 1983, 1994; Jefferies & Prokop 1972; Chauvel & Nion 1977; Chauvel 1986; Daley 1992; Cripps & Daley 1994; Ruta 1999a; Lefebvre 2003a). In some of these taxa, lateral and posterior marginals sometimes bear a fringe of articulated spines (Figs 3e,f, 4e, f) (e.g. Ampelocarpus, Chauvelicystis) and/or are themselves modified into large spikes (Figs 3f, 4f) (e.g. Prochauvelicystis, Sokkaejaecystis) (e.g. Chauvel 1966; Ubaghs 1970, 1983; Daley 1992; Lefebvre & Vizcaíno 1999; Lee et al. 2005). In still other cornutes (e.g. Amygdalotheca, Flabellicarpus, Milonicystis, Reticulocarpos), abaxial edges of lateral and posterior marginals are modified into a wide flattened peripheral flange (Fig. 3b) (e.g. Ubaghs 1970; Jefferies & Prokop 1972; Chauvel 1986; Cripps & Daley 1994; Martí Mus 2002)

In most cornutes, the lower thecal surface is divided into two unequal fields (left and right 'infracentral areas') by an asymmetrical skeletal strut (the 'zygal bar' or 'septum'), extending diagonally from left of the aulacophore insertion (anteriorly) to right of the anal opening (posteriorly) (Figs 1a, c, 2a, 3b–f) (e.g. Ubaghs 1963, 1968, 1970; Chauvel & Nion 1977; Parsley 1997; Sumrall et al. 1997, 2009; Lefebvre et al. 1998; Lefebvre & Vizcaíno 1999; Lee et al. 2005; Noailles 2016; Rozhnov & Parsley 2017). In Ceratocystis and other early 'armoured' cornutes (e.g. Protocystites), the strut is present, but marginals are so wide that the
right infracentral area is absent, whereas the left one is reduced to one or two skeletal elements (Fig. 3a) (see Lefebvre & Vizcaíno 1999; Lefebvre 2001). In many taxa (e.g. *Chauvelicystis, Cothurnocystis, Phyllocystis, Scotiae cystis*), the strut results from the adjoining of two delicate parts branching from two opposite marginals (Figs 1a, c, 2a, 3c–f) (e.g. Ubaghs 1963, 1968, 1970; Parsley 1997; Lefebvre *et al.* 1998; Lefebvre 2001).

However, in some cases, the zygal bar is made of three skeletal elements, with one of them in central position (Fig. 3b) (e.g. *Amygdalotheca, Milonicystis, Nano carpus*; Ubaghs 1970, 1991; Chauvel 1986; Cripps & Daley 1994; Lefebvre & Vizcaíno 1999). In some cornutes (*Domfrontia, Prokopicystis, Reticulocarpos*), the strut was described as 'incomplete' and not reaching, posteriorly, the opposite portion of the marginal frame (Jefferies & Prokop 1972; Cripps 1989a; Cripps & Daley 1994). This interpretation is not confirmed by the reexamination of the type material of these taxa, which demonstrates that, as in most other cornutes, the strut was made of two plates, and was posteriorly in contact with the marginal frame (see below; see also Cripps 1989a, fig. 6d; Ruta 1999a, b).

In most cornutes, the left and right infracentral areas are made of a high number of tessellate, polygonal, unorganised skeletal elements: the 'infracentrals'. They are much thinner than marginals and their external (lower) surface is invariably flat and smooth. In some cornute clades, the acquisition of more bilaterally symmetrical thecal outlines is achieved through a drastic reduction of their right infracentral area (e.g. *Ampelocarpus, Prochauvelicystis*), and in some cases, through its total loss (e.g. *Destombesicarpus* gen. nov., *Lyricocarpus*) (see below; Daley 1992; Ubaghs 1994; Lefebvre & Vizcaíno 1999; Lefebvre 2001).

A single polyplated integumentary area is present on the upper thecal surface: the 'supracentral area'. In the early 'armoured' cornute *Ceratocystis* (Fig. 4a), this surface is rigid and made of a limited number of thick, large skeletal elements, tightly sutured to adorals and
marginals (see Jackel 1901; Bather 1913; Ubaghs 1967, 1968; Jefferies 1969; Lefebvre & Vizcaíno 1999). The supracentral area of Ceratocystis and some other early cornutes (e.g. Nevadaecystis, Protocystites) is reinforced by a strong triradiate ridge (Fig. 4a) (see Jaekel 1901; Bather 1913; Ubaghs 1963, 1967; Jefferies 1969; Jefferies et al. 1987; Lefebvre & Vizcaíno 1999). In all other cornutes, the supracentral area is a flexible, thin, polyplated membrane made of tessellate and generally polygonal skeletal elements: the 'supracentrals' (Figs 1b, d, 2b, 4c, f). In some taxa (e.g. Arauricystis primaeva, Cothurnocystis elizae, Procothurnocystis owensi), strongly convex and almost rounded supracentrals are also present (see e.g. Jefferies 1968; Ubaghs 1970; Woods & Jefferies 1992). The external (upper) surface of supracentrals is frequently smooth (e.g. Galliaecystis, Phyllocystis, Reticulocarpos), but it can sometimes bear a central knob (Fig. 4c) (e.g. Chauvelicystis spinosa, Procothurnocystis courtessolei), or a mushroom-like tubercle (Fig. 4f) (e.g. Amygdalotheca, Flabellicarpus, Milonicystis, Sokkaejaecystis) (see Ubaghs 1970; Jefferies & Prokop 1972; Chauvel 1986; Cripps & Daley 1994; Martí Mus 2002; Lee et al. 2005). In some taxa (e.g. 'Cothurnocystis' fellinensis, Procothurnocystis owensi), spines can be articulated to the supracentral area (Fig. 1b, d) (see Ubaghs 1970; Woods & Jefferies 1992). In Nevadaecystis, the star-shaped morphology of supracentrals results from the presence of numerous sutural pores (epispires), identical to those occurring in many other echinoderm taxa (e.g. Camptostroma, gogiids, lepidocystids, Stromatocystites) (Ubaghs 1963, 1968; Sprinkle 1973).

However, the widespread occurrence of sutural pores on the upper thecal surface of Nevadaecystis represents the exception to the rule. When present in cornutes, respiratory structures are generally restricted to the right anterior corner of the supracentral area (Figs 1b, d, 2b, 4a–c). In Ceratocystis (Fig. 4a) and related early forms (e.g. Protocystites), they consist of a single series of sutural pores (see Ubaghs 1967; Jefferies 1969; Lefebvre & Vizcaíno 1999). In taxa with a more thinly plated and flexible supracentral area, numerous isolated
Sutural pores sometimes occur in the right anterior corner of the upper thecal surface \((Phyllocystis crassimarginata;\) Thoral 1935; Ubaghs 1968, 1970; Lefebvre & Vizcaño 1999; Ware & Lefebvre 2007). However, sutural pores are more frequently gathered into small clusters delimited by two opposite U-shaped plates: the 'cothurnopores' (Figs 1b, d, 2b, 4c, 5a) (e.g. Chauvelicystis, Cothurnocystis, Nevadaecystis, Phyllocystis blayaci, Ponticulocarpus; see Ubaghs 1963, 1968, 1970; Lefebvre & Vizcaño 1999). In some other taxa (e.g. Flabellicarpus, Proscotiaecystis), numerous adjoining cothurnopore U-shaped plates form together an elongate rhombic structure: the 'proto-lamellate organ' (Fig. 5b) (Lefebvre \textit{et al.} 2017b). In these cornutes, each pair of opposite U-shaped plates delimits an elongate, slit-like sutural pore (Ubaghs 1983, 1994; Lefebvre & Vizcaño 1999; Martí Mus 2002). In some scotiaecystids (\textit{Bohemiaecystis}, \textit{Scotiaecystis}, \textit{Thoralicarpus} gen. nov.), adjacent U-shaped plates are so tightly packed that their fused lateral walls ('lamellae') separate long, narrow slits: the 'lamellipores' (see Ubaghs 1968, 1970; Lefebvre & Vizcaño 1999; Lefebvre \textit{et al.} 2017b). Scotiaecystid lamellipores and lamellae form together a rhombic, elongate 'lamellate organ' (Figs 4b, 5c–d) (e.g. Ubaghs 1968, 1970; Lefebvre & Vizcaño 1999).

In spite of a wide morphological disparity, respiratory structures of cornutes are thus fundamentally all sutural pores (see Ubaghs 1968; Parsley 1988; Lefebvre & Vizcaño 1999). They are generally absent in all small-sized taxa (e.g. \textit{Ampelocarpus}, \textit{Bohemiaecystis ubaghsi}, \textit{Destombesicarpus} gen. nov., \textit{Domfrontia}, \textit{Lyricocarpus}, \textit{Nanocarpus}) (see below; Chauvel & Nion 1977; Ubaghs 1991, 1994; Cripps & Daley 1994; Lefebvre & Vizcaño 1999; Ruta 1999a). Pore-structures are also secondarily lost in some cornute clades (e.g. Hanusiidae), even in large-sized taxa (e.g. \textit{Galliaecystis}). In these cornutes, respiration was possibly achieved directly through their thinly plated, reticulate upper supracentral area.

In cornutes, the anal opening is located either in lateral (terminal) position at the distalmost extremity of the theca (Fig. 3, 4a, c–f) (e.g. \textit{Amygdalotheca}, \textit{Ceratocystis}, \textit{Cothurnocystis}, ...
*Chauvelicystis, Galliaecystis*, or in the left posterior extremity of the supracentral area (Figs 2b, 4b) (e.g. *Phyllocystis, Bohemiaecystis, Scotiaecystis*) (see e.g. Bather 1913; Thoral 1935; Ubaghs 1967, 1968, 1970, 1983; Jefferies 1968, 1969; Chauvel 1971; Cripps 1988; Gil Cid *et al.* 1996; Lefebvre & Vizcaïno 1999). The anus is sometimes slit-like (Figs 3a, 4a) (e.g. *Ceratocystis*; see Ubaghs 1967), but it more frequently occurs at the summit of a small cone-shaped pyramid or periproct (Figs 2b, 3c, f, 4c, f) (see Bather 1913; Ubaghs 1968, 1970; Jefferies 1968; Parsley 1988; Lefebvre & Vizcaïno 1999).

In most taxa, the hydropore corresponds to a small orifice (the 'right adoral orifice'; Fig. 6a) situated very close to, and right of the aulacophore insertion, along the suture between the right adoral and the underlying anterior marginal (Ubaghs 1968, 1970, 1991; Parsley 1997; Lefebvre & Vizcaïno 1999; David *et al.* 2000; Lefebvre 2003; Lefebvre *et al.* 2019a). The right adoral orifice opens into a small underneath cavity, located on the upper surface of the right anterior marginal: the 'infundibulum' (Fig. 6b–c) (Ubaghs 1968, 1970). The infundibulum is connected both to the lumen of the proximal aulacophore by a narrow 'anterior oblique groove' and to the main intrathecal cavity by the 'anterior transverse groove' (Fig. 6b–c; Ubaghs 1968, 1970). Comparison with other echinoderms suggests that the anterior oblique groove, which connects the right adoral orifice (hydropore) to the aulacophore (containing the ambulacral canal) could have housed the stone canal.

The intrathecal cavity of cornutes is anteriorly in contact with the lumen of the proximal aulacophore (Ubaghs 1968; David *et al.* 2000; Lefebvre *et al.* 2019a). In *Ceratocystis* and possibly some other 'armoured' early taxa, both internal cavities were widely communicating with each other (see Ubaghs 1967, 1968; Lefebvre & Vizcaïno 1999). However, in all other cornutes, this communication was strongly reduced by two high anterior walls emitted by the two anterior-most marginals, posteriorly to the appendage insertion: the 'aulacophore apophyses' (Fig. 6a) (Ubaghs 1968, 1970; Parsley 1988; Lefebvre & Vizcaïno 1999; Lefebvre...
The two apophyses formed an anteriorly concave, cup-shaped structure, which probably served for the attachment of the powerful muscles housed in the proximal aulacophore (Ubaghs 1968, 1970; Parsley 1988; Clausen & Smith 2005; Lefebvre et al. 2019a). Consequently, communication between the intrathecal cavity and the lumen of the proximal appendage was only possible through the narrow, transversely elongate opening located between adorals (above) and apophyses (below) (Fig. 6a). Exceptionally preserved soft parts in late Tremadocian cornutes from the Fezouata Shale (Morocco) indicate that the gut extended into the theca via this orifice, and was extending posteriorly into the periproct (see Lefebvre et al. 2019a).

Aulacophore. In all stylophorans, the feeding appendage consists of two distinct parts: the proximal and the distal aulacophore (Figs 1c, 2a, 7). Although it is functionally part of the appendage, the proximal region is, anatomically, a cylindrical outward expansion of the theca housing both powerful muscles and the esophagus (David et al. 2000; Lefebvre 2003a; Lefebvre et al. 2019a). Exceptionally preserved soft parts in late Tremadocian cornutes from the Fezouata Shale (Morocco) provided evidence of the presence of an elongate, spindle-shaped fore-gut within the proximal aulacophore (Fig. 8b) (Lefebvre et al. 2019a). The esophagus connects anteriorly to the mouth (see below), and is posteriorly constricted (Lefebvre et al. 2019a). The observed posterior pinching of the gut above the apophyses coincides with its course through the narrow, transversely elongate neck separating the wide lumen of the proximal aulacophore and the intrathecal cavity (see above; Figs 6a, 8b).

In the early cornute Ceratocystis, the proximal aulacophore is a simple tube-like, highly flexible structure, which could be moved in almost any direction. Its lateral walls are made of numerous, imbricate, scale-like elements forming more or less regular 'rings' of plates (Ubaghs 1967, 1968, 1987; Jefferies 1969; Lefebvre & Vizcaíno 1999; Lefebvre 2003a;
In other cornutes, the proximal appendage is organised into regular, tetramerous, telescopic and bilaterally symmetrical rings (Figs 1–2, 7, 8a) (e.g. Bather 1913; Jaekel 1918; Thoral 1935; Ubaghs 1963, 1968, 1970, 1981, 1983; Jefferies 1968; Chauvel & Nion 1977; Cripps 1988, 1991; Parsley 1988, 1997; Sumrall et al. 1997, 2009; Lefebvre & Vizcaïno 1999; Martí Mus 2002; Lefebvre 2003a). Each proximal ring consists of a pair of 'inferolaterals' contributing to its lower and lateral portions, and of a pair of smaller 'tectals' forming the upper portion of the ring (Figs 1, 2, 7–8). Each ring overlaps the proximal region of the next, more distal one. The proximal-most ring attaches tightly to the anterior extremity of the theca, so as to fit perfectly against the apophyses and within the more or less rounded insertion area defined by the adorals (above) and the two most anterior marginals (below). The distal-most ring partly overlaps the proximal portion of the funnel-shaped, most posterior ossicle: the 'stylocone' (Figs 1, 7, 8) (Ubaghs 1963, 1968, 1970; Lefebvre 2003a). In some cornutes (e.g. Amygdalotheca, Sokkaejaecystis), spines are articulated to proximal rings of the aulacophore (see Ubaghs 1970; Lee et al. 2005).

Exceptionally preserved soft parts associated to the water-vascular system (ambulacral canal, podia) were recently described in the distal aulacophore of cornutes from the Fezouata Lagerstätte (Lower Ordovician) of Morocco (Lefebvre et al. 2019a; Saleh et al. 2020). This discovery confirms Ubaghs' interpretation (1961, 1963, 1967, 1968, 1970, 1981, 1983, 1987, 1991, 1994) that this portion of the appendage represents a feeding structure (Figs 8b, 9) (see also e.g. Chauvel 1971, 1986; Chauvel & Nion 1977; Parsley 1988, 1997; Ubaghs & Robison 1988; Sumrall et al. 1997, 2009; Lefebvre & Vizcaïno 1999; Ruta 1999a, b; Sumrall & Sprinkle 1999; David et al. 2000; Lefebvre 2001, 2003a, 2007a; Martí Mus 2002; Lee et al. 2005; Ware & Lefebvre 2007; Han & Chen 2008; Clark et al. 2020). In all cornutes, the distal aulacophore consists of a lower series of relatively massive uniserial 'ossicles' and, above them, two longitudinal sets (left and right) of movable ambulacral 'cover plates' (Figs 7–9).
Interossicular articulations are flat, suggesting that the distal aulacophore formed a relatively rigid structure. However, the occurrence of distally coiled appendages in some taxa (e.g. *Archaeocothurnus* and *Ponticulocarpus*) suggests that their anterior extremity was possibly more flexible and could be recurved in a vertical plane (Parsley 1988; Ubahgs & Robison 1988; Sumrall & Sprinkle 1999; Lefebvre 2003a). The morphology of the most proximal ossicle (styrocone; see above) is markedly different from that of all more anterior uniserial skeletal elements (Fig. 7). The stylocone and its associated cover plates are often designated as the 'median aulacophore', because they form the transition between the large and short proximal region, and the narrower and usually much longer distal part of the appendage (e.g. Ubahgs 1963, 1968, 1970). The anterior portion of the stylocone is morphologically identical to all more distal ossicles. Its posterior part is wider and contains a deep, hollow proximal cavity, which contained the anterior portion of the esophagus (Fig. 8b) (see Lefebvre *et al.* 2019a). This larger, posterior region of the stylocone is generally overlapped by the most distal tetramerous ring of the proximal aulacophore (see e.g. Ubahgs 1968, 1970, 1981).

In most cornutes (e.g. *Ceratocystis, Chauvelicystis, Cothurnocystis, Phyllocystis, Scotiaecystis*), more distal ossicles are simple, semi-cylindrical skeletal elements, with a rounded lower surface, and a relatively flat upper side (Figs 7, 9) (e.g. Bather 1913; Thoral 1935; Ubahgs 1967, 1968, 1970, 1983, 1987; Jefferies 1968; Cripps 1988; Daley 1992; Lefebvre 2003a). However, in some taxa, the lower surface of the stylocone and proximal-most ossicles can bear a small knob (e.g. *Galliaecystis*), a low longitudinal crest (e.g. *Sokkaejaecystis*), and sometimes, a strong downward-directed spike (Fig. 8; e.g. *Domfrontia, Nanocarpus, Prokopicystis, Reticulocarpos*) (see Ubahgs 1970, 1991; Jefferies & Prokop 1972; Chauvel & Nion 1977; Cripps 1989a; Ruta 1999a; Lefebvre 2003a; Lee *et al.* 2005).

Strong ossicular spikes are generally occurring in small cornutes with a reduced thecal
ornamentation (e.g. knobs, protuberances, spikes). In these taxa, it is thus likely that ossicular spikes functioned as anchors (Fig. 8; Lefebvre 2003a).

The upper surface of ossicles bears a deep 'longitudinal median groove', which corresponds to the imprint of a single radial canal of the water-vascular system (Figs 1b, d, 2b, 7b, 9) (see Ubaghs 1963, 1968, 1970, 1981; Parsley 1988; David et al. 2000; Lefebvre 2003a; Lefebvre et al. 2019a). In some cornutes (e.g. Arauricystis, Cothurnocystis, Galliaecystis, Nanocarpus, Phyllocystis), this longitudinal median furrow is connected to lateral depressions by transverse channels (Fig. 7b) (e.g. Ubaghs 1968, 1970, 1981, 1991; Jefferies 1968). Exceptionally preserved soft parts in cornutes from the Fezouata Shale indicate that lateral depressions housed tube feet, which were connected to the single radial canal of the water-vascular system (longitudinal median groove) by lateral canals (transverse channels) (Figs 8b, 9; see Ubaghs 1968, 1970, 1981; Nichols 1972; Lefebvre & Vizcaíno 1999; David et al. 2000; Lefebvre et al. 2019a). In some other cornutes (e.g. Ceratocystis, Bohemiaecystis), the upper surface of ossicles does not preserve any evidence of transverse channels connecting the longitudinal ambulacral groove and lateral podial basins (see Ubaghs 1967, 1968; Jefferies 1969; Lefebvre & Vizcaíno 1999).

Proximally, the longitudinal median furrow ends in a deep notch on the upper surface of the stylocone (Figs 7b, 8b) (Ubaghs 1968, 1970, 1981; Parsley 1988; David et al. 2000; Lefebvre 2003a). This orifice, which is situated at the contact between the external food groove and the internal body cavity, corresponds to the mouth (Ubaghs 1961, 1963, 1968, 1970, 1981; Nichols 1972; Parsley 1988; David et al. 2000; Lefebvre 2003a; Lefebvre et al. 2019a). This interpretation was recently confirmed by the observation of exceptionally preserved soft parts in cornutes (Lefebvre et al. 2019a). In all specimens preserving the esophagus, its anterior extremity was pinched into the stylocone cavity and ending at the stylocone notch (Fig. 8b). In late Tremadocian cornutes from the Fezouata Shale, Lefebvre et
al. (2019a) documented a second putative longitudinal canal, extending across all ossicles and situated below the longitudinal median groove. This internal structure, previously reported in some mitrates (e.g. *Mitrocystites*; see Jefferies 1968), could have housed a coelomic canal or nerve.

Cornute cover plates (Figs 1, 2, 7–9) are generally delicate, wing-like to fan-shaped elements, frequently displaying a typical radiating fibrillar ornamentation (see e.g. Ubaghs 1970, 1983, 1991, 1994; Pisera 1994; Dzik 1999; Lefebvre & Vizcaíno 1999; Martí Mus 2002; Lefebvre 2003a; Lee et al. 2005). Their base consists of a rounded articulatory apophysis made of denser stereom (see Ubaghs 1970; Dzik 1999). In some Cambrian cornutes (e.g. *Archaeocothurnus, Ponticulocarpus*), cover plates are elongate, narrow, scale-like skeletal elements, with a forked upper margin (see Ubaghs & Robison 1988; Sumrall & Sprinkle 1999). Within a same longitudinal series, cover plates are imbricate: the distal margin of each element is overlapping the proximal portion of the next, more anterior one (see e.g. Ubaghs 1968, 1970; Parsley 1988; Ubaghs & Robison 1988; Sumrall & Sprinkle 1999; Lefebvre 2003a). In most cornutes (e.g. *Cothurnocystis, Phyllocystis, Scotiaecystis*), two pairs of opposite cover plates are articulated to the upper surface of the stylocone, and a single pair to each, more distal ossicle (Figs 1–2, 7; Ubaghs 1968, 1970, 1981; Parsley 1988; Lefebvre & Vizcaíno 1999; Lefebvre 2003a). This regular one-to-one correspondence between ossicles and pairs of opposite cover plates does not occur in the distal appendage of some early taxa (Figs 8–9; e.g. *Ceratocystis*; see Ubaghs 1967; Jefferies 1969).

In cornutes, the two longitudinal series of cover plates roof the underlying ambulacral food groove and associated tube feet borne on the upper surface of ossicles (Figs 8, 9) (e.g. Ubaghs 1963, 1968, 1970, 1981; Parsley 1988; Dzik 1999; Lefebvre & Vizcaíno 1999; David et al. 2000; Lefebvre et al. 2019a). The imbricate pattern of cover plates suggests that each individual element could not move or open independently (Parsley 1988; Lefebvre 2003a).
Consequently, opening and closure of these plates probably involved movements of the whole lateral series. Ubaghs (1970) reported the occurrence of sites for both ligamentary and muscular articulation on cover plates. Ligaments were inserted abaxially, and they contributed to passively open the two opposite sheets (Ubaghs 1970). In contrast, Ubaghs (1970) described muscle insertions on the adaxial edges of cover plates, thus suggesting that their closure was actively controlled by the organism. It is possible that distal coiling of the aulacophore augmented closure of the two sets of imbricate elements (Parsley 1988; Lefebvre 2003a).

In cornutes, cover plates are often preserved as two open sheets lying on both sides of the distal appendage (Figs 1–2, 7) (see e.g. Ubaghs 1967, 1970, 1981; Parsley 1988; Woods & Jefferies 1992; Lefebvre & Vizcaïno 1999; Lefebvre 2003a; Lee et al. 2005; Han & Chen 2008; Sumrall et al. 2009; Martin et al. 2015). This preservation is generally interpreted as the original feeding posture, with the stiff distal appendage lying over the sea floor and their two sheets of ambulacral cover plates widely open on both sides, so as to expose the food groove (Ubaghs 1967; Parsley 1988; Lefebvre 2003a; Martin et al. 2015). However, fully articulated, complete cornute aulacophores are also sometimes preserved with their two opposite sheets of cover plates in closed position (Fig. 8) (see e.g. Ubaghs 1963; Sumrall & Sprinkle 1999). In the Bou Nemrou assemblage of the Tafilalt Lagerstätte (early Sandbian, Morocco), feeding appendages of most cornute specimens are preserved with tightly closed cover plates (see below). The taphonomy of Bou Nemrou cornutes and associated organisms suggests that they probably correspond to original communities suddenly killed and buried by obrution, storm-generated deposits (see below). Particularly long ambulacral tube feet, protruding beyond the upper margin of ajar cover plates are preserved in late Tremadocian cornutes from the Fezouata Lagerstätte (Fig. 8b) (Lefebvre et al. 2019a). These podia are very similar in
morphology to the long tube feet reported in exceptionally preserved Palaeozoic asteroids (Sutton et al. 2005) and ophiuroids (Glass & Blake 2004).

The preservation of cover plates still articulated to ossicles (taphonomic grade 1, sensu Martin et al. 2015) and in various positions (open, ajar, closed) clearly demonstrates that they were hinged. New fossil evidence from Ordovician Lagerstätten of Morocco suggests that the long tube feet of cornutes were still efficient, even if cover plates were closed or ajar. Their frequently observed open position possibly corresponds to the original feeding posture, but it could also represent a ligamentary-induced post-mortem artefact (see Ubaghs, 1970), similar to the taphonomic 'butterfly position' of bivalves (Polechová 2016).

The primary function of the cornute appendage was that of a feeding device (see Ubaghs 1963, 1968, 1970, 1981; Parsley 1988; David et al. 2000; Lefebvre 2003a). The occurrence of strong ossicular spikes in some taxa (Fig. 8) also suggests that it was also probably acting as an efficient anchoring device on soft substrates (Lefebvre 2003a). A locomotory function for the cornute appendage seems unlikely in most taxa (Ubaghs 1968, 1981; Lefebvre 2003a, 2007a). The aulacophore certainly helped for active reorientation or limited forward movement of the organism (Clark et al. 2020), but the presence of a strong ornamentation on the lower thecal surface in many taxa (anterior knobs, spikes, protuberances) probably hampered locomotion (Ubaghs 1968, 1970, 1981; Lefebvre 2003a).

**Thecal plate homologies in cornutes**

*Models of skeletal homologies.* The number and morphology of major thecal plates (adorals, marginals) represent, along with other characters related to integumentary areas, body openings (e.g. pore structures), and the aulacophore, key diagnostic features for the systematics of cornutes. Since Bather (1913), several terminologies have been proposed to
identify their major skeletal elements (e.g. Ubaghs 1963; Jefferies 1967; Jefferies & Prokop 1972; Parsley 1997; Lefebvre & Vizcaïno 1999). However, some of these systems are descriptive and do not imply homology: plates are simply named following their position on the theca (e.g. Bather 1913; Ubaghs 1963; Parsley 1997). The first attempt at identifying homologous skeletal elements in cornutes was provided by Jefferies (1967, 1968, 1969, 1986), who proposed a new plate terminology largely inspired from the one elaborated for mitrates by Jaekel (1918). In this system, the aulacophore insertion was used as a morphological landmark for plate identification: on both sides of it, left (M_L) and right marginals (M_R) were numbered 1–n away from the origin, with sometimes an additional letter indicating whether the plate was extending on the lower ('V' for 'ventral') or the upper thecal surface ('D' for 'dorsal'): e.g. M_3LV corresponds to the third marginal away from the aulacophore insertion, on the left side of the lower thecal surface (Jefferies 1967, 1968, 1969, 1986; Rahman et al. 2010).

The identification of homologies in cornutes was subsequently further elaborated by Jefferies & Prokop (1972), who defined a new terminology. In their system, the posterior zygal plate was chosen as a morphological landmark and designated as plate 'a' (Jefferies & Prokop 1972). Similarly to Bather's (1913) clockwise numbering of marginals (1–11), all major skeletal elements considered as homologous were designated by letters, in alphabetical order and clockwise around the theca (Jefferies & Prokop 1972). This system of plate homologies, which relied on detailed comparison of cornute plate patterns, was progressively emended and improved over the years (see e.g. Jefferies et al. 1987; Cripps 1988, 1989a, b, 1991; Daley 1992; Woods & Jefferies 1992; Cripps & Daley 1994; Gil Cid et al. 1996d; Martí Mus 2002). Initially defined for cornutes (Jefferies & Prokop 1972), this system of skeletal homologies was also applied to mitrate stylophorans (see e.g. Jefferies, 1973; Jefferies & Lewis 1978; Craske & Jefferies 1989; Cripps 1990; Beisswenger 1994; Ruta
1997; Ruta & Theron 1997; Domínguez et al. 2002a). However, because of theoretical requirements of the 'calcichordate' interpretation of stylophorans as early chordates, skeletal elements of the lower thecal surface of cornutes were erroneously identified by Jefferies (1973) as homologous to those of the upper side of mitrates (see e.g. Chauvel 1981; Ubaghs 1981; Parsley 1988, 1997; Kolata et al. 1991; Lefebvre et al. 1998; Lefebvre & Vizcaño 1999; Ruta 1999b; David et al. 2000; Lefebvre 2000b, 2001, 2003a; Martí Mus 2002).

Consequently, although agreeing with most homologies identified in cornutes by tenants of the calcichordate theory, Lefebvre & Vizcaño (1999) proposed a third model of skeletal homologies, which could be also applied to mitrates (see Lefebvre 2000b, c, 2001, 2003b; Lefebvre & Gutiérrez-Marco 2003; Lee et al. 2004; Lefebvre et al. 2006, 2010b; Lefebvre & Botting 2007; Scheffler et al. 2019; Lefebvre & Ausich 2021). In this system, the identification of thecal plates was largely inspired from previous terminologies (Jaekel 1918; Ubaghs 1963), but with the major difference that skeletal elements bearing the same name were considered as homologous, independently of their position (Lefebvre & Vizcaño 1999; Lefebvre 2000b, 2001). Marginals were numbered 1–n away from the aulacophore insertion, both on the left (M' series) and on the right (M series), with the exception of plates originally designated as the digital (D), the glossal (G), and the posterior zygal plate (Z) by Ubaghs (1963), and generally considered as homologous in all cornutes (see e.g. Ubaghs 1968; Jefferies, 1968, 1969; Jefferies & Prokop, 1972; Ubaghs & Robison, 1988; Cripps, 1991; Lefebvre 2000b, 2001; Lee et al. 2005; Ware & Lefebvre 2007; Sumrall et al. 2009). Similarly, on the upper thecal surface, adorals were designated as A₀ (median adoral), A₁' (left adoral), and A₁ (right adoral). Skeletal homologies in cornutes were identified by Lefebvre & Vizcaño (1999) based on the detailed comparison of their plate patterns with that of the early stylophoran Ceratocystis (see also Lefebvre 2001; Lefebvre et al. 2006).
However, when Lefebvre & Vizcaïno (1999) proposed their model of plate homologies, the fossil record of cornutes was largely dominated by diverse assemblages (about 20 taxa) from the Lower Ordovician of the Montagne Noire (Thoral 1935; Ubaghs 1970, 1983, 1991, 1994; Cripps 1989b; Daley 1992; Lefebvre & Vizcaïno 1999) and, to a lesser extent, by younger occurrences (Middle–Upper Ordovician) from the Anti-Atlas (Ruta 1999a), the Armorican Massif (Chauvel & Nion 1977; Chauvel 1986; Cripps & Daley 1994; Lefebvre & Vizcaïno 1999), Bohemia (Ubaghs 1968; Jefferies & Prokop 1972; Cripps 1989a, b), the Iberian Massif (Gil Cid et al. 1996d), northern Ireland (Cripps 1988), Russia (Rozhnov 1990), Scotland (Bather 1913), and Wales (Woods & Jefferies 1992). Most of these Ordovician cornutes displayed relatively derived plate patterns, typical of their respective clades (amygdalotheccids, chauvelicystids, cothurnocystids, hanusiids, phyllocystids, and scotiaecystids). In the late 1990s, a strong morphological and stratigraphic gap separated Ordovician taxa from the few middle Cambrian (Miaolingian) documented cornutes (Archaeocothurnus, Ceratocystis, Ponticulocarpus, Protocystites; see Pompeckj 1896; Jefferies et al. 1987; Ubaghs & Robison 1988; Sumrall & Sprinkle 1999).

In the last 20 years, this ‘Furongian–mid Tremadocian gap’ in knowledge (see Smith 1988) was partly filled with the description of numerous and diverse cornute remains in Australia (Smith & Jell 1999), France (Ubaghs 1998), Iran (Rozhnov & Parsley 2017), Korea (Lee et al. 2005), South China (Han & Chen 2008; Zamora et al. 2013b; Zhu et al. 2016), Spain (S. Zamora, pers. comm., 2016), and the USA (Sumrall et al. 1997, 2009). Important new findings were also made in the late Tremadocian of Argentina (Nohejlová et al. 2018), Britain (Martí Mus 2002), Korea (Lee et al. 2006) and mostly, in the Fezouata Shale of Morocco (Lefebvre & Fatka 2003; Martin et al. 2015; Lefebvre et al. 2016a, 2019a). Many of these recently documented Furongian–Tremadocian cornutes are displaying previously unrecorded
plate patterns, and are thus prompting a reevaluation of their skeletal homologies (see Ware & Lefebvre 2007; Lefebvre & Ausich 2021).

These abundant new data were incorporated by Lefebvre & Ausich (2021) in their critical revision of plate homologies in early stylophorans and mitrates. Their nomenclature system is the same as the one originally defined by Lefebvre & Vizcaíno (1999), with A for adorals, D for digital, G for glossal, M_{1-n} for right marginals, M'_{1-n} for left ones, and Z for the zygal plate. The revised scheme of stylophoran skeletal homologies proposed by Lefebvre & Ausich (2021) will be followed here, and applied to cornutes (Figs 10–16). This model of plate homologies relies on the detailed comparison of thecal patterns and it largely agrees with most previous identifications of homologous skeletal elements in cornutes (e.g. Jefferies 1969; Jefferies & Prokop 1972; Cripps 1988, 1991; Daley 1992; Parsley 1997; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002; Lee et al. 2005; Ware & Lefebvre 2007; Sumrall et al. 2009).

Widely agreed plate homologies. All thecal plates forming the aulacophore insertion (M', M, A', A_0 and A_1) are universally considered as homologous in cornutes (Figs 10–16). In all taxa, the two anterior-most marginals M_1 and M'_1 occupy the same position, each bearing one of the two anterior apophyses, the left marginal forms the anterior part of the zygal bar, and the right one bears the infundibulum. Similarly, the homology of adorals relies on their similar positions and morphologies in all cornutes (they form a delicate arch above the aulacophore insertion), the occurrence of the hydropore on A_1, and their close association with always the same two underlying marginals, M'_1 and M_1 (see e.g. Ubaghs 1968; Jefferies 1969; Jefferies & Prokop 1972; Jefferies et al. 1987; Cripps 1988, 1989a, b, 1991; Daley 1992; Woods & Jefferies 1992; Parsley 1997; Lefebvre & Vizcaíno 1999; Ruta 1999b; Smith...
The two marginals located on both sides of the anal lobe and at the distal extremity of the left infracentral area are widely considered as homologous in all cornutes (Figs 10–15, 16a, c, d). They were originally designated as the digital (D) and the glossal (G) by Ubaghs (1963). However, they were sometimes identified as distinct skeletal elements, depending on whether they were part of the marginal frame (M's and M5) or modified into posterior spines articulated to it (D and G) (see e.g. Ubaghs 1967, 1991, 1994; Chauvel 1986; Parsley 1997; Ruta 1999a; Rozhnov & Parsley 2017). Following Lefebvre & Ausich (2021) and most authors, D and G are interpreted herein as homologous in all cornutes, independently of their shape, and of their participation to the marginal frame. This identification largely relies on similarities in position and on identical contacts with surrounding thecal plates (see Thoral 1935; Jefferies 1967, 1969; Jefferies et al. 1987; Ubaghs & Robison 1988; Cripps 1988, 1989a, b; Rozhnov 1990; Daley 1992; Woods & Jefferies 1992; Cripps & Daley 1994; Sumrall et al. 1997, 2009; Lefebvre & Vizcaíno 1999; Smith & Jell 1999; Sumrall & Sprinkle 1999; Lefebvre 2001; Martí Mus 2002; Lee et al. 2005; Ware & Lefebvre 2007).

Similarly, M2 and the left series of marginals M'2, M'3, and M'4 are almost universally identified as homologous skeletal elements in all cornutes (Figs 10–16). However, the homology of left marginals was questioned by Cripps (1988) in scotiaecystids (Fig. 11), because in some of them (e.g. Scotiaecystis collapsa, S. curvata), the left anterior corner of the theca was not framed by the second left marginal (as in most other cornutes), but by the third one. Consequently, Cripps (1988) suggested that a supernumerary, autapomorphic marginal 'r' was present between M'1 and M'2 in Scotiaecystis (see also Cripps 1991; Gil Cid et al. 1996d). However, as demonstrated by Lefebvre & Vizcaíno (1999), the apparently unusual plate pattern displayed by some highly derived scotiaecystids simply results from the
anterior shift of all left marginals, consecutively to the displacement of the glossal into the left posterior extremity of the thecal frame (Fig. 11; see also Lefebvre 2001; Martí Mus 2002). Consequently, as already suggested by most authors, the four marginals M₂, M'_2, M'_3 and M'_4 are herein considered as homologous in all cornutes (Figs 10–16) (see e.g. Bather 1913; Thoral 1935; Ubaghs 1963; Jefferies 1969; Chauvel & Nion 1977; Cripps & Daley 1994; Parsley 1997; Sumrall et al. 1997; Lefebvre & Vizcaíno 1999; Ruta 1999a; Smith & Jell 1999; Martí Mus 2002; Lee et al. 2005; Han & Chen 2008; Rozhnov & Parsley 2017).

Revised plate homologies around the right infracentral area. Cornutes display a particularly wide morphological disparity in plate patterns on their right thecal side (i.e. all marginals located between M₁ and G). Their interpretation has long been challenging in the absence of transition forms between Ceratocystis, generally considered as displaying the most plesiomorphic organization in stylophorans (Fig. 12a–c), and more lightly framed, 'typical' Ordovician cornutes (Figs 10–11, 13–16). In the last twenty years, the description of several Furongian–Tremadocian stylophorans with previously unrecorded skeletal patterns provided invaluable clues to decipher thecal plate homologies in cornutes (Lefebvre & Ausich 2021).

These taxa (e.g. Archaeocothurnus, Drepanocarpos, Flabellicarpus, Persiacarpos, 'Phyllocystis' jingxiensis, Ponticulocarpus) confirmed that the Early Ordovician burst in cornute taxonomic diversity was preceded by a Furongian peak in morphological disparity (Lefebvre et al. 2006).

In Ceratocystis (Wuliuan–Drumian; Czech Republic, France, Germany, Morocco, Spain, and Sweden), both thecal surfaces are entirely made of large adjoining skeletal elements (Fig. 12a–c; see e.g. Jaekel 1901; Bather 1913; Ubaghs 1967; Jefferies 1969; Lefebvre & Vizcaíno 1999; Rahman et al. 2010). By comparison with other cornutes, most of them can be identified unambiguously as A₀ (median adoral), A'_1 and A₁ (lateraladors), M₁ and M'_1.
(anterior marginals at the aulacophore insertion), M₂ (forming the right anterior corner), M'₂, M'₃ and M'₄ (left marginal series), D and G (posterior marginals on both sides of the anal opening) (Fig. 12a–c; e.g. Jefferies 1969; Jefferies et al. 1987; Cripps 1991; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Rahman et al. 2010; Lefebvre & Ausich 2021). *Ceratocystis* does not show any evidence of right infracentral area. The large central plate anteriorly in contact with M'₁ and posteriorly sutured to G can be reasonably interpreted as homologous to the posterior zygal plate, which shows the same position and contacts as in all other cornutes (Fig. 12a, c; e.g. Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Lefebvre & Ausich 2021). Similarly, the marginal plate located in between M₂ (anteriorly) and Z (posteriorly) certainly represents M₃ (Fig. 12a, c; Ubaghs 1967, 1987; Jefferies 1969; Jefferies et al. 1987; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Lefebvre & Ausich 2021). As in many other cornutes, M₃ bears a well-defined posterior spike: the spinal blade (Fig. 12a, c). The thecal plate sutured to both G (posteriorly and on the upper thecal surface) and to the abaxial margin of Z (on the lower side of the theca) is interpreted herein as equivalent to M₄ (Fig. 12a–c; see also Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Lefebvre & Ausich 2021). When present in other cornutes, this skeletal element occupies a similar position on the thecal frame and shows the same narrow association with both G and Z (Figs 10b, 12f, 13b, d, 14, 15a–c). The closely related 'armoured' stylophoran *Protocystites* (Drumian; Wales) displays an almost identical plate pattern on the right side of the theca (Fig. 12e–f; see Jefferies et al. 1987; Lefebvre & Vizcaïno 1999; Lefebvre 2001).

*Ponticulocarpus* (Fig. 13a–b), from the Spence Shale (Wulian) of Utah, is the earliest known cornute with a lightly built theca and extensive polyplated integumentary areas (Sprinkle 1976; Sumrall & Sprinkle 1999). However, the plate pattern of its right thecal side is very similar to that of *Ceratocystis* and *Protocystites* (Fig. 12), with the only difference that
all major skeletal elements are separated by an extensive right infracentral area (Fig. 13a). This integumentary surface is framed by M'₁ and M₁ (anterior marginals, forming the aulacophore insertion), M₂ (at the right anterior thecal corner), M₃ (spinal-bearing marginal, at the right posterior thecal edge), and Z (posterior zygal plate) (Fig. 13a). Marginal M₄ is present above Z, closely sutured to it, and also in contact with both M₃ and G (Fig. 13b). The interpretation of the morphology of the right thecal side of *Ponticulocarpus* presented here is slightly different from its original reconstruction (see Sumrall & Sprinkle 1999, fig. 1), in which a small additional plate was figured abaxially to M₁, and no marginal was identified above Z. However, the detailed examination of the specimens illustrated in Sumrall & Sprinkle (1999, fig. 3) suggests that the putative additional anterior marginal more likely represents the abaxial portion of M₁ extending laterally beyond the overlying right adoral (Fig. 13b). Moreover, a L-shaped M₄ is clearly present above Z in all specimens (see Sumrall & Sprinkle 1999, figs 3.2, 3.4, 3.6).

*Persiacarpos jefferesi* (Fig. 13c–d) from the Mila Formation (latest Guzhangian) of Iran was originally described as a *Phyllocystis*-like cornute, with a rounded, posteriorly closed marginal frame (Rozhnov & Parsley 2017). This interpretation is not confirmed by the morphology of the original type specimens (see Rozhnov & Parsley 2017, fig. 3, pl. 6), which clearly indicates that *Persiacarpos* is a boot-shaped cornute morphologically close to *Ponticulocarpus* (see Lefebvre & Ausich 2021). The plate pattern of *P. jefferesi* (Fig. 13c–d) is apparently identical to that of *'Cothurnocystis' fellinensis* (late Tremadocian, Montagne Noire; Fig. 10), and it is very likely that the latter belongs to the same genus (see discussion below). The main difference between *P. jefferesi* and *P. fellinensis* is the wider aspect of marginals in the former. As in *Ponticulocarpus* (Fig. 13a–b), the right infracentral area of *Persiacarpos* is delimited by M'₁ and M₁ (anterior marginals), M₂ (at the right anterior corner), M₃ (spinal-bearing marginal, at the right posterior corner), and Z (posterior zygal
Marginal M₄ is the L-shaped element above Z and in contact with both G and M₃ (Fig. 13d). However, Persiacarpos differs from Ponticulocarpus in the presence of one additional marginal inserted in between M₂ and M₃ (Fig. 13c–d). This plate pattern is not unique to Persiacarpos, but it also occurs in many Ordovician cornutes (e.g. Chauvelicystis, Cothurnocystis, Flabellicarpus, Phyllocystis, Procothurnocystis; Figs 10, 14a–b, 15c–d, 16).

Most authors consider that this supernumerary skeletal element, which was designated either as 't' (Jefferies et al. 1987) or as Mc ('cothurnocystid marginal'; Lefebvre & Vizcaíno 1999), is homologous in all cornute taxa (see e.g. Cripps 1988, 1991; Daley 1992; Woods & Jefferies 1992; Cripps & Daley 1994; Lefebvre 2001; Martí Mus 2002; Lee et al. 2005; Ware & Lefebvre 2007; Sumrall et al. 2009; Lefebvre & Ausich 2021). Comparison with the plate pattern of Ceratocystis (Fig. 12b) suggests that Mc is possibly homologous to the large supracentral element abaxially sutured to both M₂ and M₃, and variously designated as S₃ (Ubaghs 1967, 1987), Cₚₖ (Jefferies 1969; Rahman et al. 2010) or plate 1 (Jefferies et al. 1987).

Drepanocarpos (Fig. 14a–b) was initially described in the Furongian of Queensland (Australia), based on several poorly preserved specimens (Smith & Jell 1999). Its original identification as a Phyllocystis-like cornute is not supported by the presence of an obvious M₄-M′₄ posterior bar at the distal extremity of its supracentral area (Fig. 14b), which clearly indicates hanusiid affinities (Zamora et al. 2013a). This hanusiid affiliation was confirmed by the preliminary report of abundant remains of better-preserved specimens of Drepanocarpos in the Furongian Guole Lagerstätte (Guangxi, South China; Zamora et al. 2013b; Zhu et al. 2016). As in Persiacarpos (Fig. 13a), the right infracentral area of Drepanocarpos is framed by M₁ and M₁ (anterior marginals), M₂ (at the left anterior corner), Mc, M₃ (spinal-bearing marginal, at the right posterior corner), and Z (posterior zygal plate) (Fig. 14a). Marginal M₄ is present above Z, closely associated to it, and also in contact with M′₄, M₃ and G (Fig. 14a–
b). Consequently, the plate pattern of *Drepanocarpos* (Fig. 14a–b) suggests that early hanusiids possessed a cothurnocystid marginal, and that Mc was secondarily lost in younger taxa (e.g. *Galliaecystis, Hanusia, Prokopicystis, Reticulocarpos*). Moreover, contrary to the situation in *Drepanocarpos, Persiacarpos and Ponticulocarpus*, the posterior zygal plate of younger hanusiids is not Y-shaped and occurs only in central position (loss of its lateral branch, abaxially sutured to M₃). Consequently, in *Galliaecystis* (Fig. 14c–d) and related forms, the right infracentral area is posteriorly delimited by M₃ and M₄ (Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002).

As in *Galliaecystis* (Fig. 14c), the right infracentral area of a yet undescribed late Tremadocian cornute from the Fezouata Shale, Morocco ('Cornuta indet. n. gen., n. sp. 2' in Lefebvre et al. 2016a; herein informally designated as the 'Tizagzaouine cornute'; Fig. 15c) is framed by M’₁ and M₁ (anteriorly), M₂ (at the right anterior corner), Mc, M₃ (spinal-bearing marginal), M₄ (posteriorly), and Z (posterior zygal plate, in central position) (see also Ware & Lefebvre 2007; Martin et al. 2015).

A similar situation also occurs in *Archaeocothurnus* (Fig. 15a–b) from the Wheeler Formation of Utah (Drumian) and the Lincoln Peak Formation of Nevada (Paibian) (see Ubaghs & Robison 1988; Sumrall et al. 1997). As in *Galliaecystis* and the Tizagzaouine cornute, the posterior zygal plate of *Archaeocothurnus* is not Y-shaped (no contact with M₃) and it is occupying a central position on the lower thecal surface (Fig. 15a–b; Sumrall et al. 1997). The anterior branch of Z forms the posterior portion of the zygal bar, whereas its posterior part is closely associated to M₄, along the posterior margin of the left infracentral area (Fig. 15a–b; Sumrall et al. 1997). As in *Ceratocystis* (Fig. 12a–c), *Drepanocarpos* (Fig. 14a–b), *Galliaecystis* (Fig. 14c–d), *Persiacarpos* (Fig. 13c–d), *Ponticulocarpus* (Fig. 13a–b), and the Tizagzaouine cornute (Fig. 15c), Z and M₄ are both posteriorly in contact with G in *Archaeocothurnus* (Fig. 15b). Comparison with other cornutes suggests that, on the right
thecal side of *Archaeocothurnus*, the cothurnocystid marginal is absent between M$_2$ and M$_3$ (see Ubaghs & Robison 1988; Sumrall *et al.* 1997). Moreover, the right infracentral area of *Archaeocothurnus* is posteriorly delimited by a long, narrow marginal inserted between M$_4$ (on the left) and M$_3$ (on the right) (Fig. 15b; see Ubaghs & Robison 1988; Sumrall *et al.* 1997). This skeletal element, which also occurs in all scotiaecystid cornutes (Fig. 11), has no equivalent in the morphology of *Drepanocarpos, Persiacarpos, Ponticulocarpus* or the Tizgagzaouine cornute. Its occurrence in between M$_3$ and M$_4$ falsifies the interpretation suggested by several authors that this plate could be homologous to M$_3$ or to M$_4$ (e.g. Jefferies 1969; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Ware & Lefebvre 2007). On the other hand, comparison with *Ceratocystis* (Fig. 12b) suggests that this supernumerary marginal is possibly equivalent to the large supracentral skeletal element inserted between M$_3$ and M$_4$ in this early stylophoran, and variously designated as S$_7$ (Ubaghs 1967, 1987), M$_{3LD}$ (Jefferies 1969; Rahman *et al.* 2010), or 'u' (Jefferies *et al.* 1987). Several authors have considered this additional plate ('s' in Cripps 1988) as an autapomorphy of scotiaecystid cornutes (see e.g. Cripps 1991; Daley 1992; Gil Cid *et al.* 1996d; Martí Mus 2002). This interpretation is accepted here, and this 'scotiaecystid marginal' is thus designated Ms (Figs 11, 15a–b).

In Guangxi Province (South China), the Guole Lagerstätte (Furongian) yielded not only early hanusiids (see above), but also abundant remains of a second cornute, which was originally described as *Phyllocystis jingxiensis* (Chen & Han 2008). However, its plate pattern is markedly different from that of *Phyllocystis* (Zamora *et al.* 2013b; Zhu *et al.* 2016; Lefebvre & Ausich 2021). *Phyllocystis* (Figs 2, 16b) was originally described in the late Tremadocian of the Montagne Noire (France; Thoral 1935; Ubaghs 1968, 1970, 1981; Ware & Lefebvre 2007). This genus occurs also in the Lower Ordovician of Morocco (Gigout 1954; Lefebvre & Fatka 2003; Lefebvre *et al.* 2016a). A single specimen of cornute from the upper part of the Chupino Formation (early Floian; Sennikov *et al.* 2018) of Siberia was also
tentatively identified as *P. salairica* (Rozova et al. 1985). However, its morphology is poorly
known, and its assignment to *Phyllocystis* still remains to be confirmed. The right infracentral
area of *Phyllocystis* is delimited by six marginals (Fig. 16b; see Thoral 1935; Ubaghs 1970;
Ware & Lefebvre 2007): M$'_1$ and M$_1$ (anteriorly, forming the aulacophore insertion), M$_2$ (at
the right anterior corner), Mc, M$_3$ (retaining a short spinal in some specimens of *P. crassimarginata*), and Z (posterior zygal plate, in marginal position). Digital, glossal and M$_4$
are absent in *Phyllocystis* (Fig. 16b; see e.g. Cripps 1988, 1991; Daley 1992; Parsley 1997;
Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Ware & Lefebvre 2007). The
right infracentral area of 'P.' *jingxiensis* (Fig. 16a) is framed by the six same marginals (M$'_1$,
M$_1$, M$_2$, Mc, M$_3$, and Z), but contrary to the situation in Montagne Noire and Moroccan
specimens, its Y-shaped posterior zygal plate is in central position (see Chen & Han 2008;
Zamora et al. 2013b; Zhu et al. 2016; Lefebvre & Ausich 2021). In 'P.' *jingxiensis*, the central
position of Z results from the contact, posteriorly to it, of the particularly wide processes
formed by the spinal (M$_3$) and the glossal (G) (Fig. 16a; Lefebvre & Ausich 2021). Moreover,
the left infracentral area of 'P.' *jingxiensis* is posteriorly closed by adjoining digital and
glossal (Fig. 16a). Consequently, the central position of Z, as well as the occurrence of both D
and G in 'P.' *jingxiensis* confirm that this cornute is different from *Phyllocystis* (Fig. 16b) and
should be assigned to a distinct, new genus (Zamora et al. 2013b; Zhu et al. 2016; Lefebvre &
Ausich 2021). A very similar (if not identical) plate pattern occurs in the cornute described as
'genus indet. form A' by Lee et al. (2005) in the Dongjom Formation (Tremadocian; Choi
2019) of Korea, and also in a yet undescribed late Tremadocian cornute from the Fezouata
Shale, Morocco ('Cornuta indet. n. gen. n. sp. 1' in Lefebvre et al. 2016a).

The morphological features displayed by all these Furongian–Tremadocian 'P.' *jingxiensis-
like cornutes (e.g. peripheral flange around the theca, Z in central position and posteriorly in
contact with both M$_3$ and G, presence of D, loss of M$_4$) are also occurring in amygdalothecids
This observation questions the possibility that early amygdalothecids (e.g. *Amygdalotheca, Nanocarpus*) were derived from 'P.' jingxiensis'-like cornutes. If this interpretation is correct, then the right infracentral area of amygdalothecids would be delimited by M'_1 and M_1 (anterior marginals), M_2 (at the right anterior corner), Mc, M_3 (posteriorly sutured to G), and Z (posterior zygal plate, in central position) (Fig. 16c; Lefebvre & Ausich 2021). This revised identification of thecal plates in amygdalothecids will be adopted here. It is markedly different from all previous interpretations, which considered that Mc was absent in amygdalothecids (see e.g. Jefferies & Prokop 1972; Cripps 1991; Cripps & Daley 1994; Parsley 1997; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002).

Revised plate homologies around the left infracentral area. The left infracentral area of *Ponticulocarpus* (Fig. 13a) is delimited by Z and M'_1 (the two plates forming the zygal bar), M'_2 (at the left anterior corner), M'_3, and two small posterior skeletal elements (Sumrall & Sprinkle 1999). These two plates form a short transverse strut, closing distally the left infracentral area and separating it from a distinct, posterior infracentral area flanked by D (on the left) and G (on the right) (Fig. 13a). The left element of the posterior strut is abaxially sutured to M'_4 and anteriorly, to M'_3. The right plate of the posterior bar is in contact with both G and Z (see Sumrall & Sprinkle 1999, fig. 2.2). This situation, with a left infracentral area closed by a short transverse strut formed by two skeletal elements is not unique to *Ponticulocarpus* (Fig. 13a): the same plate pattern occurs e.g. in *Auricystis, Cothurnocystis, Persiacarpos, Procothurnocystis,* and *Protocystites* (Figs 1b, 10a, 12d, 13c; see e.g. Bather 1913; Thoral 1935; Ubags 1968, 1970, 1994; Jefferies 1968; Jefferies et al. 1987; Woods & Jefferies 1992; Lefebvre & Vizcaíno 1999; Parsley & Rozhnov 2017). In these taxa, the two posterior plates are universally considered as homologous (see e.g. Jefferies & Prokop 1972;
Following Lefebvre & Vizcaíno (1999), these two skeletal elements are designated here M’5 and M5. Their occurrence is some of the earliest known cornutes (e.g. *Ponticulocarpus*, *Protocystites*) suggests that the posterior closure of the left infracentral area very likely represents a plesiomorphic feature, which was secondarily lost in all stylophorans with a posteriorly open marginal frame on the lower thecal surface (Figs 14, 15c–d, 16c–d; e.g. *amygdalothecids, chauvelicystids, Flabellicarpus, hanusiids, mitrates, Tizagzaouine cornute*) (Lefebvre & Ausich 2021).

In *Ceratocystis* (Fig. 12a, c), the identification of M5 and M’5 is more problematic. A small skeletal element inserted between Z and G (‘I2’ in Ubaghs 1967) on the lower thecal surface of *Ceratocystis* was frequently considered as possibly homologous to M5 (see e.g. Jefferies *et al.* 1987; Cripps 1988, 1991; Daley 1992; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002; Lefebvre & Ausich 2021). Similarly, the small posterior marginal of *Ceratocystis*, in contact with D and M’4 (on the left), Z (anteriorly), and G and M5 (on the right) was often identified as M’5 (see e.g. Jefferies 1969; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002; Lefebvre & Ausich 2021). Although this identification is plausible, an alternative interpretation is also possible (Fig. 12c). In all cornutes with a posterior M5-M’5 strut, M’3 is posteriorly sutured to both M’4 (on the left) and M’5 (on the right), whereas Z is posteriorly in contact with both M5 (on the left) and G (on the right). In *Ceratocystis*, M’3 is posteriorly in contact with two plates: M’4 (on the left), and a small skeletal element designated either as I3 (Ubaghs 1967), Ip (Lefebvre & Vizcaíno 1999) or Cv (Rahman *et al.* 2010). Consequently, this small skeletal element, which is generally interpreted as an isolated infracentral plate, could be equivalent to M’5 in other cornutes. If this identification is correct, then M5 could be homologous to any of the two distal elements in contact with both G and Z in *Ceratocystis*. 
The posterior margin of the left infracentral area is poorly preserved in *Archaeocothurnus* (Fig. 15a–b), and it is not clear if one or two plates are present (see Ubaghs & Robison 1988; Sumrall & Sprinkle 1999). However, the occurrence of two plates posteriorly sutured to M'3 confirms that at least M'5 occurs in *Archaeocothurnus* (Fig. 15a–b). The presence of M5 is also very likely (Fig. 15a–b; see Sumrall & Sprinkle 1999: figs 6.1-2, 7.3-4), but it still needs to be confirmed by better-preserved specimens. Several Furongian cornutes (e.g. *Acuticarpus*, *Nevadaecystis*) are too incompletely preserved to document, whether their marginal frame was posteriorly closed or open (see e.g. Ubaghs 1963; Sumrall *et al.* 1997).

In scotiaecystids (Fig. 11), the left infracentral area is delimited by six marginals: Z and M'1 (forming together the zygal bar), M'2, M'3, M'4 (abaxially articulated to the digital, in both *Proscotiaecystis* and *Bohemiaecystis*), and a single posterior skeletal element. The identification of this marginal situated between M'4 and Z is problematic (see e.g. Jefferies 1969; Cripps 1988, 1991; Daley 1992; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002). Contrary to the situation in other cornutes with a closed infracentral area, M'3 is not posteriorly sutured to two plates (M'4 and M'5), thus suggesting that M'5 was probably lost in scotiaecystids (Fig. 11). Consequently, the posterior marginal, which is also sutured to both G and Z in most scotiaecystids, probably corresponds to M5 (Fig. 11; e.g. Jefferies & Prokop 1972; Lefebvre & Vizcaíno 1999; Lefebvre 2001).

A relatively similar situation occurs in *Phyllocystis* (Fig. 16b; see Thoral 1935; Ubaghs 1970; Ware & Lefebvre 2007; Clark *et al.* 2020). As in scotiaecystids, the left infracentral area is framed by six plates (Fig. 16b). Four of them can be readily identified as Z and M'1 (forming together the zygal bar), M'2 (at the left anterior corner), and M'3. However, in the absence of D and G, the identification of the two posterior skeletal elements situated between M'3 and Z is ambiguous (see Martí Mus 2002; Ware & Lefebvre 2007). They could be homologous either to M'3 and M5 ('Cothurnocystis-like' configuration; e.g. Ware & Lefebvre ...
2007) or to M'4 and M5 ('Scotiaecystis-like' pattern; e.g. Lefebvre & Vizcaïno 1999; Lefebvre 2001). In *Phyllocystis*, the absence of the digital suggests that, contrary to the situation in scotiaecystids, M'4 was probably lost (Ware & Lefebvre 2007). Consequently, the two posterior marginals of *Phyllocystis* more likely correspond to M'5 and M5. This 'Cothurnocystis-like' configuration is in good agreement with the thecal plate pattern of the right side of *Phyllocystis* (Fig. 16b), with a cothurnocystid marginal (Mc), but no scotiaecystid marginal (Ms).

**Implications for cornute systematics.** Since the original designation of Cornuta as a distinct suborder (Jaekel 1901) and order (Jaekel 1918), successive descriptions of new plate patterns throughout the 20th century have prompted the identification of several taxonomic subdivisions (families, subfamilies) within this group of early echinoderms: Ceratocystidae (Jaekel 1901), Cothurnocystidae (Bather 1913), Scotiaecystidae (Ubaghs 1968), Amygdalothecidae (Ubaghs 1970), Phyllocystidae (Derstler 1979), Hanusiidae (Cripps 1991), Chauvelicystidae (Daley 1992), and Reticulocarpidae (Cripps & Daley 1994). In the last 50 years, the identification of thecal plate homologies (see above) has yielded a wealth of skeletal-based characters useful for phylogenetic analyses of cornutes (see e.g. Cripps 1988, 1991; Daley 1992; Parsley 1997; Lefebvre & Vizcaïno 1999; Lefebvre 2001, 2005; Martí Mus 2002; Ruta 2003; Lee *et al.* 2005). Producing a new phylogenetic analysis of cornutes is beyond the scope of this paper, as it would require taking into account the plate patterns of several late Cambrian–Early Ordovician taxa pending description (e.g. Tizagzaouine cornute) or redescription (e.g. *Drepanocarpos, Persiacarpos jefferesi, 'Phyllocystis jingxiensis*).

Although still incompletely known, the morphologies of these new cornutes help partly filling the morphological and stratigraphic gaps between the few early stylophorans known from the Miaolingian and the more abundant and better-documented Ordovician taxa. Thecal plate
homologies could be dramatically revised based on the previously undocumented plate patterns of these new cornutes (see above; Lefebvre & Ausich 2021).

The new fossil evidence accumulated in the last 20 years confirms the long-suspected paraphyly of Cornuta (see e.g. Jefferies 1967, 1969; Jefferies & Prokop 1972; Cripps 1988, 1991; Parsley 1988, 1991, 1997; Daley 1992; Woods & Jefferies 1992; Cripps & Daley 1994; Ruta 1999a, b, 2003). The earliest known mitrates were originally described as cornutes (Nanocarpus guoleensis) in the Furongian of Guangxi, South China (Chen & Han 2013; but see Zamora et al. 2013a, b; Zhu et al. 2016; Lefebvre & Ausich 2021). Similar-looking undescribed early mitrates are also possibly present in the late Guzhangian of Yunnan, South China (Peng et al. 2020) and the Furongian of Korea (Lefebvre 2007a; Lefebvre et al. 2016b). Their morphology does not confirm previous suggestions that mitrates may derive from cornutes close to Amygdalotheca (Parsley 1988), Ceratocystis (Lefebvre & Vizcaíno 1999; Lefebvre 2001, 2005), Domfrontia (Jefferies et al. 1987; Cripps 1988; Parsley 1997), Nanocarpus (Parsley 1997; Ruta 2003), Phyllocystis (Jefferies 1969), Prokopicystis (Cripps 1989a, 1989b, 1991; Daley 1992), or Reticulocarpos (Jefferies & Prokop 1972; Parsley 1991). Although they are probably closely related (sister-group?) to amygdalothecids, early mitrates more likely derive from a 'Phyllocystis' jingxiensis-like ancestor (Lefebvre & Ausich 2021).

The reevaluation of plate homologies in cornutes confirms the validity of most family-level clades already established in former classifications and/or phylogenies (e.g. Jaekel 1918; Ubaghs 1968, 1970; Jefferies 1969; Derstler 1979; Cripps 1988, 1991; Daley 1992; Cripps & Daley 1994; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002; Ware & Lefebvre 2007). The family Ceratocystidae is a small clade incorporating the most plesiomorphic stylophorans (Ceratocystis spp.; see e.g. Ubaghs 1968, 1987; Rahman et al. 2010). Closely related, more derived taxa (e.g. Protocystites) are excluded so as to avoid the paraphyly of
ceratocystids. Cothurnocystidae have long been an ill-defined group including all cornutes not assigned to another family (e.g. *Chauvelicystis, Nevadaecystis, Phyllocystis*; see Bather 1913; Thoral 1935; Chauvel 1966, 1971; Ubaghs 1963, 1968, 1970; Derstler 1979). This family is here restricted to the small clade uniting *Cothurnocystis* and related forms (e.g. *Arauricystis, Procothurnocystis*; see Cripps 1988, 1991; Parsley 1997; Lefebvre & Vizcaíno 1999; Martí Mus 2002; Ware & Lefebvre 2007). Since their identification as a distinct family (Ubaghs 1968), Scotiaecystidae (*Bohemiaecystis, Proscotiaecystis, Scotiaecystis, Thoralicarpus* gen. nov.) form a well-defined clade (see e.g. Jefferies 1969; Ubaghs 1970, 1983; Chauvel 1971; Cripps 1988, 1991; Daley 1992; Gil Cid *et al.* 1996d; Parsley 1997; Lefebvre & Vizcaíno 1999; Martí Mus 2002; Ware & Lefebvre 2007). Originally described by Ubaghs (1970) to include all cornutes with both a posteriorly open marginal frame and a posterior zygal plate in central position, the family Amygdalothecidae has been regularly emended (e.g. Derstler 1979; Cripps 1988; Ubaghs 1991; Daley 1992; Martí Mus 2002), before being split into two distinct clades: Amygdalothecidae (*Amygdalotheca, Domfrontia, Nanocarpus*; Lefebvre & Vizcaíno 1999; Lefebvre 2001) and Hanusiidae (*Drepanocarpos, Galliaecystis, Hanusia, Prokopicystis, Reticulocarpos*; Cripps 1991; Parsley 1997; Lefebvre & Vizcaíno 1999; Ruta 1999a; Lefebvre 2001). In this context, the family Reticulocarpidae, created by Cripps & Daley (1994) to include both *Reticulocarpos* and 'Beryllia' (i.e. *Domfrontia*, see below), is not retained here because its members belong either to amygdalothecids (*Domfrontia*) or to hanusiids (*Reticulocarpos*) (see also Ruta 1999a). Various taxa have been assigned to the family Phyllocystidae (e.g. Chauvelicystinae, *Drepanocarpos, Lobocarpus*; see e.g. Cripps 1988, 1991; Daley 1992; Ubaghs 1998; Smith & Jell 1999). This small well-defined clade is restricted here to its original definition (*Phyllocystis* spp.) by Derstler (1979) (see also, Lefebvre & Vizcaíno 1999; Lefebvre 2001; Ware & Lefebvre 2007). Chauvelicystidae (e.g. *Ampelocarpus, Chauvelicystis, Lyricocarpus, Prochauvelicystis, Sokkaeaecystis*) have been
regularly identified as a distinct (sub)fam
ily of spiny cornutes (see e.g. Cripps 1988, 1991;
Daley 1992; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Lee et al. 2005; 
Ware & Lefebvre 2007).

The major subdivision of cornutes into the two suborders Amygdalothecida (with Z in
central position and no marginal Mc) and Cothurnocystida (with Z in marginal position, and a
Mc element) suggested by Lefebvre & Vizcaïno (1999) is not confirmed by the reevaluation
of stylophoran plate homologies based on the new thecal patterns discovered in the last 20
years (Figs 13c–d, 14a–b, 15c, 16a; Lefebvre & Ausich 2021). A Mc marginal is present in
the earliest known member of hanusiids, Drepanocarpos (Fig. 14a–b; see above), suggesting
that this plate was secondarily lost in later taxa. The central position of the posterior zygal
plate was acquired independently and through different mechanisms in amygdalothecids
(expansion and joining of G and M₃) and hanusiids (loss of the Z-M₃ contact). This different
origin explains why Z is posteriorly sutured to two marginals (M₃ and G) in amygdalothecids
(Fig. 16c), but only to M₄ (along a very long suture) in hanusiids (Fig. 14). New fossil
evidence suggests that amygdalothecids have a Mc marginal and derive from 'Phyllocystis'
ingxiensis-like cornutes (see above; Lefebvre & Ausich 2021). Conversely, the reevaluation
of plate homologies in cornutes suggests that some taxa, which do not possess a Mc marginal
(Figs 11, 15a–b; e.g. Archaeocothurnus, Scotiaecystidae) were erroneously identified by
Lefebvre & Vizcaïno (1999) as Cothurnocystida (see also Lefebvre 2001, 2005; but see Ware
& Lefebvre 2007). Consequently, in this work, cornutes are retained as an informal,
paraphyletic group of early stylophorans. Their subdivision into two orders (Amygdalothecida
and Cothurnocystida) is abandoned. Pending a new phylogenetic of stylophorans being
performed, seven well-defined and widely-agreed, family-level clades of cornutes are
retained: Amygdalothecidae, Ceratocystidae, Chauvelicystidae, Cothurnocystidae,
Hanusiidae, Phyllocystidae, and Scotiaecystidae (Table 1).
**Geological setting**

**Anti-Atlas, Morocco**

Main features of the geological context and Ordovician faunal associations of the Anti-Atlas were summarised by Destombes (1962, 1970, 1971), Destombes *et al.* (1985) and Álvaro *et al.* (this volume) and will not be repeated here (see also Gutiérrez-Marco *et al.* 2003; Destombes 2006a, b, c). All fossiliferous localities yielding Middle and Late Ordovician cornutes in the Anti-Atlas (Morocco) are listed below, in stratigraphical order (see also Chauvel 1971, 1978; Ruta 1999a; Gutiérrez-Marco *et al.* 2003; Lefebvre *et al.* 2007, 2008, 2010a; Hunter *et al.* 2010; Álvaro *et al.* this volume).

*Tachilla Formation.* The Tachilla Formation (early–middle Darriwilian) is the uppermost unit of the Outer Feijas Group (Destombes 1962, 1970, 1971; Destombes *et al.* 1985; Gutiérrez-Marco *et al.* 2003; Álvaro *et al.* this volume). In 1986, two specimens of cornutes were collected by J. Destombes in the Tachilla Formation, in Tiznit area (western Anti-Atlas), about 78 km south of Agadir, west of the small village of Aït Waziz, on the eastern flank of Jbel Ouarzemine (J. Destombes' locality 2410; Fig. 17.1). Together with Jbel Tachilla (to the north), Jbel Ouarzemine corresponds to the Ordovician core of a NNE-SSW elongate and narrow syncline (Bigot & Dubois 1931; Bourcart 1933; Ségaud 1933; Ségaud & Termier 1933; Destombes 1962). In the Tiznit area, the Tachilla Formation is particularly thick and unconformably overlies the middle Cambrian sandstones of the Tabanite Group (Destombes 1962, 1970, 1971; Destombes *et al.* 1985; Álvaro *et al.* this volume). In Jbel Ouarzemine, the Tachilla Formation consists of ~1,200 m of dark blue to grey shales and fine siltstones, with
some sandstone intercalations. In both Jbel Ouarzemine and Jbel Tachilla, low diversity
Darriwilian assemblages consisting of acritarchs, rare aristocystid diploporites (*Calix segaudii*), chitinozoans (e.g. *Desmochitina bulla*), graptolites (e.g. *Corymbograptus retroflexus*, *Haddingograptus?* sp.) and very rare trilobites (*Selenopeltis macrophthalma*) were reported from other fossiliferous levels of the Tachilla Formation (e.g. Bigot & Dubois 1931; Destombes 1962; Chauvel 1966; Elaouad-Debbaj 1984; Destombes *et al.* 1985; Gutiérrez-Marcos *et al.* 2003).

In Destombes' locality 2410, two small slabs of fine grey micaceous siltstones yielded two individuals of a scotiaecystid cornute, herein described as *Bohemiaecystis?* sp. (see below). Each specimen corresponds to an incomplete, partly disarticulated theca, with the proximal aulacophore attached to it. Fragments of the distal aulacophore are present nearby. This preservation corresponds to taphonomic grade 3 (*sensu* Martin *et al.* 2015). It corresponds to the burial of *in situ* decaying individuals, in relatively low energy environmental conditions, probably several days or a few weeks after death.

**Guezzart Formation.** In the western Maïder area (eastern Anti-Atlas), about 12 km south of Alnif (Fig. 17.2,3), two small excavations within the same fossiliferous level at the top of the Guezzart Formation (late Darriwilian) yielded abundant remains of very well-preserved scotiaecystid cornutes (*Bohemiaecystis chouberti* sp. nov.). The Guezzart Formation, which is the third main subdivision of the First Bani Group, consists of white-green sandstones and quartzites (Destombes *et al.* 1985; Gutiérrez-Marcos *et al.* 2003; Álvaro *et al.* this volume). In the Alnif area, its ~6 m thick uppermost level corresponds to dark, ferrugineous quartzitic sandstones, which constitute a well-defined unit (Destombes 2006b), which is exploited by local fossil dealers for well-preserved trilobites (e.g. *Ectillaenus benignensis*, *Placoparia cf. africana*, *Selenopeltis* sp.).
The first excavation corresponds to Destombes' locality 1826 (Fig. 17.2; Chauvel 1971, 1978; Gutiérrez-Marco et al. 2003; Destombes 2006b; Rábano et al. 2020). It is located on the western flank of Jbel Bou Isidane, about 9 km E of Taichoute. This site is the type locality of the diplopore Isidalocystis furca (Chauvel 1978; Destombes 2006b). It yielded numerous other echinoderm remains, including Calix sp., Phlyctocystis granulata and the cornute indet. reported by Chauvel (1971) as genus AVI (Chauvel 1978; Gutiérrez-Marco et al. 2003; Lefebvre & Fatka 2003). Chauvel's original material of Bohemiaecystis chouberti sp. nov. (AVI) corresponds to a small (~8 x 10 cm) slab of dark, massive sandstones containing more than 20, partially overlapping individuals (Fig. 18c). Although most of them are fully articulated, they are so densely packed that their precise thecal outlines are often difficult to distinguish (Chauvel 1971). All individuals on the slab, but one, are preserved in upper aspect.

The second excavation is located less than 200 m north of Destombes' locality 1826, in the same dark ferruginous quartzitic sandstone unit forming the top of the Guezzart Formation. This site (TA-F5; Fig. 17.3) is defined herein as the type locality of Bohemiaecystis chouberti sp. nov. (see below). The holotype occurs on a relatively large (~15 x 20 cm) slab (part and counterpart) of beige-green sandstones with ten other more or less strongly superimposed individuals, preserved in various orientations, and with some of them upside-down (Fig. 18b). Most specimens are fully articulated, and in many of them, the aulacophore is intact, connected to the theca, and with the delicate ambulacral cover plates still attached to underlying ossicles (taphonomic grade 1 sensu Martin et al. 2015). This preservation is very similar to that described by Martin et al. (2015) in a cornute-dominated lens from the lower part of the Fezouata Shale (late Tremadocian) in the Zagora area. In both cases, such relatively dense accumulations of complete cornute specimens, preserved in various orientations and on top of each other, probably result from the burial of para-autochthonous
living assemblages by storm deposits, closely matching the taphofacies IIC defined by Brett et al. (1997). Consequently, the exceptional taphonomic conditions prevailing at the top of the Guezzart Formation in Alnif area suggest that these levels can be interpreted as an echinoderm Lagerstätte *sensu* Smith (1988).

**Izegguirene Formation.** The Izegguirene Formation (earliest Sandbian) represents the uppermost unit of the First Bani Group (see Destombes et al. 1985; Gutiérrez-Maro et al. 2003; Álvaro et al. this volume). Particularly abundant and diverse cornute remains were found in two distinct localities within the Izegguirene Formation. The first one corresponds to the type locality of this stratigraphic unit: Jbel Izegguirene (Fig. 17.4). The type section is located about 15 km NW of Tazarine, 17 km SE of Nkob, and south of the R108 road connecting these two cities. In this area, the Izegguirene Formation represents a ~140 m thick succession, with fine micaceous white to pinkish siltstones at the base, and a thick quartzitic level at the top (Destombes, 2006a). The fossiliferous level is located about 55 m above the base of the Izegguirene Formation, along the gentle northern slope of Jbel Izegguirene (Gutiérrez-Maro et al. 2003; Destombes 2006a). This site, which corresponds to Destombes’ localities 755 and 2479, has yielded a particularly diverse assemblage comprising echinoderms (asterozoans indet., *Calix* sp., ophiuroids, and stylophorans), gastropods, graptolites (*Dendrograptus* sp.), hyolithids, inarticulate brachiopods, ostracods, and various trilobites (e.g. Asaphidae indet., *Degamella princeps princeps*, *Eoharpes* sp., *Morgatia*? sp., *Placoparia* sp., *Selenopeltis macrophthalmalma*) (Gutiérrez-Maro et al. 2003; Destombes 2006a).

At least three distinct stylophoran taxa were reported from this locality: a small-sized chauvelicystid (genus AVIII in Chauvel 1971), a scotiaecystid cornute, and a kirkocystid mitrate (*Anatifopsis* sp.) (see Chauvel 1971, 1978; Destombes et al. 1985; Gutiérrez-Maro et
Stylophorans are preserved in relatively fine, micaceous, light grey siltstones. Chauvel's original specimen of AVIII is designated herein as the holotype of the chauvelicystid cornute *Destombesicarpus izegguirenensis* gen. et sp. nov., with Destombes' locality 755 as its type locality. This specimen corresponds to a fully articulated theca in upper aspect, with several delicate spines still articulated to its marginal frame (Fig. 18d). Its aulacophore is largely disarticulated, and only some scattered ossicles are preserved, anteriorly to the theca. Scotiaecystids collected in the same levels are here assigned to *Thoralicarpus bounemrouensis* gen. et sp. nov., as they are morphologically identical to the more numerous and better preserved specimens from the western Tafilalt area (Bou Nemrou locality, see below).

The second locality, Bou Nemrou (Fig. 17.5), corresponds to several deep excavations intensively quarried by collectors in the last 20 years at the top of the First Bani Group, in sandstone levels correlated to the Izegguirene Formation (see Van Roy 2006a, 2011; Lefebvre *et al.* 2008; Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al.* a this volume). The quarries are situated at the summit of one of the hills forming the Jbel Tijarfaïouine Massif, not far away from the village of Ksar Tamarna, E of the Oued El Caïd Rami valley, and about 30 km SW of Erfoud. The coarse, micaceous, purple-reddish sandstones of Bou Nemrou have yielded fully marine diverse assemblages, comprising both skeletonised and soft-bodied taxa forming together the Tafilalt Biota (Van Roy 2011; Gutiérrez-Marco & Garcia-Bellido 2015; Gutiérrez-Marco *et al.* 2020, a this volume). In these levels, exceptional preservation probably results from the sudden burial of autochthonous communities by storm-generated obrution deposits and their subsequent sealing by microbial mats on the sea-floor (Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al.* a this volume). The presence of microbial mats is supported by the widespread occurrence of typical 'elephant-skin' and Kinneyia structures (Gutiérrez-Marco *et al.* 2020, a this volume). The most
spectacular elements of the Bou Nemrou Lagerstätte comprise large paropsonemid eldonioids
(Discophyllum peltatum), aglaspidid and cheloniellid arthropods (Duslia sp., Triopus sp.),
hydrozoans (Webbyites? sp.), palaeoscolecid worms (Gamascolex vanroyi), and trilobites with
ever preservation internal soft parts (see e.g. Van Roy 2006a, 2011; Lefebvre et al.
2008; Gutiérrez-Marco & García-Bellido 2015; MacGabhann et al. 2019; Gutiérrez-Marco et
al. 2020, a, b this volume). Other faunal elements include agglutinated tubes (Onuphionella
corusca; Muir et al. this volume), conulariids (Sumrall & Zamora 2011), dendroid graptolites
(Dendrograptus sp., Ptilograptus aff. glomeratus; Gutiérrez-Marco et al. b this volume), and
diverse trilobites (Cekovia cf. goetzi, Crozonaspis cf. primula, Degamella cf. princeps,
ingens, Placoparia africana, Selenopeltis macrophalma, S. cf. buchi, Uralichas tardus;
Gutiérrez-Marco et al. a this volume).

Echinoderms are a major component of Bou Nemrou assemblages, and the dominant group
in several levels (Van Roy 2006a; Lefebvre et al. 2007, 2008, 2010a; Régnault 2007; Hunter
et al. 2010; Nardin & Régnault 2015; Gutiérrez-Marco et al. 2020, a this volume). In this
locality, starfish beds are dominated by eocrinoids (Ascocystites sp.), protasterid ophiuroids,
and diverse stylophorans. Additional echinoderm taxa include rare but diverse crinoids
(cincinnaticrinid? indet., Iocrinus ouzammoui, I. sp., Trichinocrinus? sp.; Botting this
volume), edrioasteroids attached to conulariids (Belochthus? chauveli, Isorophus africanus;
Sumrall & Zamora 2011), and the enigmatic Hexedriocystis inexpectatus (Sumrall & Zamora
2011, this volume). The possible occurrence of cyclocystoids in Bou Nemrou was mentioned
by Lefebvre et al. (2008, 2010a, 2013), but this information was not confirmed by Reich et al.
(2017), who demonstrated that these specimens originated from a distinct locality and a
stratigraphically older unit within the First Bani Group (Taddrist Formation; see also Sprinkle
et al. 2015).
Stylophorans are locally abundant and particularly diverse in Bou Nemrou, with at least seven occurring taxa (Lefebvre et al. 2008, 2010a). The three most common mitrates (Anatifopsis sp., Aspidocarpus discoidalis, and Eumitrocystella savilli) were also reported in the underlying Ouine-Inirne Formation at Tizi n'Tanekfoul (Destombes' locality 1698), in the Central Anti-Atlas (see e.g. Chauvel 1971; Cripps 1990; Beisswenger 1994; Gutiérrez-Marco et al. 2003; Destombes 2006a; Lefebvre 2007a). The anomalocystitid mitrate Diamphidiocystis regnaulti is only known from a handful of specimens (Lefebvre et al. 2008, 2010a, this volume). Bou Nemrou is also designated herein as the type-locality of three cornute taxa: Arauricystis clariondi sp. nov., Milonicystis reboulorum sp. nov. and Thoralicarpus bounemrouensis gen. et sp. nov. (see below). Within cornutes, T. bounemrouensis gen. et sp. nov. is relatively common in Bou Nemrou starfish beds, and frequently found associated with other echinoderms (e.g. Ascocystites, Aspidocarpus, Eumitrocystella; Fig. 18a) and/or trilobites (Lefebvre et al. 2007, 2008, 2010a; Hunter et al. 2010). In contrast, the two other cornutes are particularly rare, and known only from one (M. reboulorum) and three specimens (A. clariondi).

Most cornutes from Bou Nemrou are fully articulated, retaining particularly long, intact portions of their distal aulacophore (Fig. 18a). In some specimens, more than 40 ossicles are preserved with their two lateral sets of ambulacrural cover plates in anatomical connection. This remarkable preservation, which corresponds to taphonomic grade 1 in cornutes (sensu Martin et al. 2015), suggests that individuals were probably killed and buried in situ by a sudden influx of sediments (obrution deposits). This interpretation is further supported by the preservation of many other particularly delicate structures in co-occurring echinoderms. For example, most mitrates from Bou Nemrou have their complete, fully articulated aulacophore preserved in extended position (Lefebvre et al. 2008; Hunter et al. 2010). This position, which corresponds to their feeding posture, is seldom observed in the fossil record (Lefebvre 2003a;
Mitrates are generally preserved with their appendage recurved over the theca, resulting either from a distressed posture or a post-mortem contraction (see e.g. Parsley 1988, 1991; Ruta & Bartels 1998; Lefebvre 2003a). Consequently, their taphonomic posture in Bou Nemrou suggests that mitrates were buried alive. The preservation of particularly delicate structures such as the feeding arms of ophiuroids and the brachioles of most specimens of *Ascocystites* are also evidence of a rapid burial (Lefebvre *et al.* 2008, 2010a; Hunter *et al.* 2010; Nardin & Régnault 2015). This interpretation is further supported by the preservation of some ophiuroids 'caught in the act' of feeding on small eocrinoids (Lefebvre *et al.* 2008; Nardin & Régnault 2015; Gutiérrez-Marco *et al.* 2020). Burial was thus probably fast and deep enough to prevent vagile epifaunal invertebrates (e.g. mitrates, ophiuroids, trilobites) to escape (Lefebvre *et al.* 2008, 2010a).

Biostratinomic analysis of eocrinoid assemblages indicates that limited transport may have nevertheless occurred (Lefebvre *et al.* 2008, 2010a; Nardin & Régnault 2015). Distal portions of eocrinoid stems (and their putative anchoring structures) are always missing, and most individuals are generally similarly oriented and probably current-aligned (Hunter *et al.* 2010; Nardin & Régnault 2015). In both cornutes (*Thoralicarpus bouemrouensis* gen. et sp. nov.) and eocrinoids (*Ascocystites* sp.), the preservation of a wide range of sizes and thus, of ontogenetic stages, suggests the absence of size-sorting, and supports the view that most preserved assemblages correspond closely to original, para-autochthonous populations (see below; Régnault 2007; Nardin & Régnault 2015). All these observations confirm that cornutes and associated echinoderms from Bou Nemrou were probably autochthonous to para-autochthonous assemblages suddenly killed and buried by storm deposits in a fully marine, relatively proximal environment, at or slightly above storm-wave base (Lefebvre *et al.* 2008, 2010a; Hunter *et al.* 2010; Gutiérrez-Marco & Garcia-Bellido 2015; Gutiérrez-
Marco et al. a this volume). However, contrary to other echinoderm Lagerstätten associated to similar environmental conditions (e.g. the Sandbian Bromide Formation or the Katian Brechin Lagerstätte; Sprinkle 1982; Brett et al. 1997; Cole et al. 2018), the particularly coarse grain of the Bou Nemrou micaceous sandstones prevents the preservation of fine anatomical details (see Botting, this volume). For example, in cornutes, precise plate patterns and boundaries are often obscured by the coarse lithology (see below).

*Upper Tiouririne Formation.* Abundant, fully articulated remains of *Domfrontia milnerorum* were found in a 40 m long trench excavated by local fossil dealers, about 15 km E of Erfoud, in the eastern Tafilalt (Khabt-el-Hejar section D in Destombes 2006c). This locality (Fig. 17.6), which was described as E2 by Van Roy (2006a), occurs stratigraphically below the basal unit of the bryozoan-dominated limestones of the late Katian Khabt-el-Hejar Formation (Ka3–Ka4; see Álvaro et al. this volume; Ernst, this volume). Comparison with the stratigraphic succession in the western Tafilalt suggests that the Khabt-el-Hejar Formation is a lateral equivalent of the Upper Ktaoua Formation (Álvaro et al. this volume; Colmenar et al. this volume; Villas & Colmenar this volume). Consequently, the alternations of micaceous shales and fine green sandstones occurring stratigraphically below the Khabt-el-Hejar Formation in locality E2 can be assigned to the Upper Tiouririne Formation (early Katian, Ka2), as this is the case for several other nearby fossiliferous sites (see Destombes et al. 1985; Van Roy 2006a; Sumrall & Zamora 2011; Van Iten et al. this volume; Villas & Colmenar this volume). In the eastern Tafilalt, the Upper Tiouririne Formation is variable in thickness (150–300 m). It consists of shales and sandstones preserving sedimentary structures (e.g. hummocky-cross stratifications) suggesting shoreface, environmental conditions (Van Iten et al. this volume). In the Khabt-el-Hejar area, these levels have yielded a relatively diverse fauna comprising aglaspidids (*Chlupacaris dubia*), rhynchonelliform brachiopods (e.g.
draboviids indet., *Hirnantia* sp., *Kiaeromena? chouberti*, plectambonitoids indet.,
rafinessquins indet., *Rostricellula termieri*, large conulariids (e.g. *Archaeoconularia* aff. *consobrina*, A. cf. *imperialis*), crinoids (e.g. *Rosfacrinus robustus*), edrioasteroids (e.g. *Streptaster nodosus*), ophiuroids, and trilobites (e.g. *Selenopeltis buchi*, *Onnia ultima*, *Calymenella* sp.) and large trace fossils (*Neoeione moniliformis*) (Destombes et al. 1985; Le Menn & Spjelknaes 1996; Destombes 2006c; Van Roy 2006a, b; Sumrall & Zamora 2011; Gutiérrez-Marco et al., 2019; Van Iten et al. this volume; Villas & Colmenar this volume).

With more than 130 specimens collected in locality E2, small-sized amygdalothecid cornutes (*D. milnerorum*) appear as one of the most common members of a relatively low diversity assemblage comprising cheloniellid arthropods (*Triopus* sp.; Van Roy 2006a), crinoids, edrioasteroids, ophiuroids, trilobites and numerous trace fossils. Almost all cornute specimens are fully articulated, with their delicate feeding appendage attached to the theca (taphonomic grades 1–2 *sensu* Martin et al. 2015). However, fine details of their morphology are obscured by the coarse grain size of the sandstones in which they are preserved (Fig. 18e).

Several specimens of *Domfrontia* frequently co-occur on a same slab. They are not aligned, and about half of them are preserved upside-down. Most individuals of *D. milnerorum* from locality E2 could be measured (thecal length TL, thecal width TW), and their size-distribution is normal (see Fig. 19), thus indicating the absence of any size sorting. Consequently, *Domfrontia*-rich layers in locality E2 probably result from the rapid burial of autochthonous to para-autochthonous original populations of gregarious cornutes by storm deposits. These taphonomic conditions (i.e. regular smothering of epibenthic communities by storm-generated obtrusion deposits) probably also partly explain the occurrence of exceptionally preserved lightly sclerotised arthropods (cheloniellids) and fully articulated ophiuroids in locality E2 (Van Roy 2006a).
Lower Second Bani Formation. Chauvel (1971) reported the occurrence of several stylophoran remains in Destombes' locality 756 (Fig. 17.7), which was tentatively assigned to the Upper Ktaoua Formation (see also Havlíček 1971; Chauvel 1978; Ruta 1999a). This locality is situated in the Central Anti-Atlas, about 8 km SW of Tazarine, at Tizi n'Takrit (Destombes 2006a). Its stratigraphic position was reevaluated by Destombes (2006a), who established that locality 756 did not occur at the top of the Upper Ktaoua Formation, but about 10 m above the base of the overlying Lower Second Bani Formation. Destombes (2006a) identified two marker horizons defining the boundary between these two lithostratigraphic units. In the Tazarine area, the uppermost part of the Upper Ktaoua Formation is characterised by the 'Flexicalymene ouzregui' bed (Destombes 2006a). The base of the overlying Lower Second Bani Formation corresponds to a ferrugineous marker bed ('G level' in Destombes 2006a) with an erosive, more or less conglomeratic base, containing the trilobite Dreyfussina strupei (see Colmenar et al. this volume). A latest Katian age (Ka4) was suggested for the lowermost part of the Lower Second Bani Formation (including locality 756), based on brachiopod and trilobite assemblages (Destombes 2006a; Colmenar et al. this volume).

At Tizi n'Takrit, the fine, slightly micaceous, light grey argillites of locality 756 have yielded a particularly diverse fauna comprising bivalves (e.g. Palaeoneilo sp., Praenucula pojetai, Pterinea? sp.), brachiopods (e.g. Chonetoidea radiatula, Comatopoma sororium, lingulids, orbiculoids), machaeridians (Plumulites), nautiloid cephalopods, ostracods, stylophoran echinoderms, and trilobites (e.g. Brongniartella platynota marocana, cyclopygids, Dionide sp., Dreyfussina strupei, odontopleurids) (Destombes 1967, 2006a; Chauvel 1971, 1978; Havlíček 1971; Destombes et al. 1985; Babin & Destombes 1990; Ruta 1999a; Ebbestad et al. this volume).
Locality 756 is the type locality of the small amygdalothecid cornute *Domfrontia milnerorum*, originally reported as 'genus indet. AVII' by Chauvel (1971), based on a single disarticulated specimen originally collected by J. Destombes in 1961. In 1990, over 80 additional specimens were collected from the same locality and the same horizon by J. Destombes, R. Jefferies and J. Savill. This material was available for Ruta's (1999a) description of *Juliaeacarpus*. Contrary to the situation in most other Middle–Late Ordovician cornute occurrences in the Anti-Atlas, specimens from locality 756 do not occur in siltstones or sandstones, but in fine argillites. Consequently, extremely fine details are preserved, such as the delicate porous, labyrinthic microstructure of the stereom of integumentary platelets (see Ruta 1999a). However, very few specimens are fully articulated (see Ruta 1999a: p. 50–51). Most of them consist of proximal aulacophore rings inserted into partly to strongly disrupted thecae (Chauvel 1971; Ruta 1999a). Small portions of the distal appendage (stylocone and ossicles) are preserved in a handful of individuals. In Tizi n'Takrit, the preservation of most specimens of *D. milnerorum* complies with cornute taphonomic grade 3 (*sensu* Martin et al. 2015). This suggests that most individuals were probably already dead, decayed, and largely disarticulated, *in situ* and in quiet sea bottom conditions, when burial occurred.

Associated stylophoran remains consist of partly disarticulated anomalocystitid mitrates and isolated adorals of kirkocystids (*Anatifopsis* sp.) (Chauvel 1971, 1978; Destombes et al. 1985; Destombes 2006a). Anomalocystitids were tentatively assigned to *Placocystites bohemicus* by Chauvel (1971), mostly because of the presence of numerous cuesta-shaped ribs on both thecal sides (at least anteriorly). However, re-examination of Chauvel's (1971) original material of *P. bohemicus* suggests that, as this is also probably the case for Barrande's type specimens of *'Anomalocystites' bohemicus* (1887) from the late Katian of Bohemia
Králův Dvůr Formation, it more likely corresponds to *Barrandeocarpus* (see Lefebvre et al. this volume).

**Armorican Massif, France**

The structure of the Armorican Massif is largely inherited from the Hercynian orogeny. It results from the juxtaposition of two originally distinct geological domains: the Medio-North Armorican Domain (MNAD) and the South Armorican Domain (SAD), which are now in contact along a several hundred kilometer long major Variscan shear zone (Fig. 20; Robardet et al. 1994; Cartier et al. 2001; Ballèvre et al. 2009). North of this South Armorican Shear Zone (SASZ), the MNAD belongs to the same microplate as the Central Iberian Zone (CIZ), which drifted away from Gondwana in Early Ordovician times (Hammann 1976; Paris & Robardet 1977, 1994; Gutiérrez-Marco et al. 2002; Ballèvre et al. 2009). However, the persistence of strong affinities between Armorican and West-Gondwanan faunas from the Ordovician to the Devonian strongly suggests that they remained palaeogeographically very close to each other and were not separated by a large ocean (Gutiérrez-Marco et al. 2002; Robardet 2003; Servais & Sintubin 2009; Álvaro et al. this volume). South of the SASZ, the SAD corresponds to relics of deeper, oceanic settings, probably originally situated between the Armorican Massif and the Gondwanan margin (Ballèvre et al. 2009; Lefebvre et al. 2010b). All Ordovician occurrences of Armorican cornutes are from the MNAD.

**Traveusot Formation.** The Traveusot Formation (Darriwilian–early Sandbian) is a ~ 400 m thick unit largely exposed in the Martigné-Ferchaud syncline, in eastern Brittany. Cornute remains were found in at least five fossiliferous localities occurring in two distinct stratigraphic levels within the Traveusot Formation. In locality 'côte 85', about 17 km south of
of the lower part of the Traveusot Formation yielded numerous disarticulated skeletal elements belonging to small amygdalothecid cornutes (isolated marginals, cover plates, stylocones, integumentary plates), which were identified as *Reticulocarpos* sp. by Chauvel & Nion (1977) and are here tentatively assigned to *Domfrontia* (*D.?* sp.; see below). Relatively abundant, though often slightly tectonically distorted remains of other marine invertebrates were described in côte 85 and stratigraphically equivalent fossiliferous levels within the lower part of the Traveusot Formation (see e.g. Babin *et al.* 1976; Chauvel & Nion 1977; Henry 1980; Vannier 1986a, b). This fauna was dated from the middle Darriwilian (Dw2, *Didymograptus artus* graptolite Zone; see Henry 1980; Gendry *et al.* 2013). It comprises brachiopods, graptolites (*Didymograptus* cf. *artus*), ostracods (e.g. *Gracquina* aff. *hispanica*, *Klimphores vogelweidei*, *Rivillina henningsmoeni*, *Primitiella* sp.), and many trilobites (e.g. *Asaphidae*, *Bathycheilus* sp., *Colpocoryphe* sp., *Geragnostus* sp., *Neseuretus* sp., *Pateraspis* andegavus?, *Placoparia cambriensis*, *Retamaspis melendezi?*, *Uralichas* sp.).

The four other cornute localities all occur stratigraphically in the upper part of the Traveusot Formation. Three of them (le Domaine, la Saudrais and Traveusot) form a geographic cluster, about 1.5 km W of the côte 85 locality and about 3 km E of Guichen (Fig. 20.2–4). Le Domaine and la Saudrais are situated on the north side of the D39 road and they are less than 100 m distant from each other. The Traveusot locality corresponds to the field on the opposite (south) side of the D39. The micaceous siltstones and concretions of these three localities have yielded similar, abundant and diverse late Darriwilian (Dw3, *Hustedograptus teretiusculus* graptolite Zone) assemblages (see e.g. Chauvel 1941, 1980, 1981, 1986; Babin 1966; Mélou 1973, 1975; Babin *et al.* 1976; Henry 1980, 1989; Romano & Henry 1982; Vannier 1986a, b; Lefebvre & Vizcaíno 1999; Gendry *et al.* 2013; Lefebvre *et al.* 2015a; Blake *et al.* 2016). Faunas from the upper part of the Traveusot Formation include bivalves...
(e.g. *Redonia deshayesi*), brachiopods (e.g. *Aegiromena guichenensis*, *A. mariana*, *Heterorthina kerfornei*), cephalopods, crinoids (e.g. *Heviacrinus melendezii*), diploporite blastozoans (e.g. *Calix rouaulti*, *Oehlerticystis andouilleensis*, *Phlyctocystis* cf. *gigas*, *Tholocystis kolihai*), gastropods, graptolites (e.g. *H. cf. teretiusculus*), hyolithids, ostracods (e.g. *Aechmina? ventadorni*, *Euprimites* sp., *Ogmooopsis? arcedelti*, *Primitiella* sp., *Quadritia tromelini*, *Raimbautina hammanni*), stenuroid asterozoans (e.g. *Lehmannaster spinosus*), stylophorans, and trilobites (e.g. *Colpocoryphe rouaulti*, *Dionide mareki*, *Eccoptochile mariana*, *Ectillaenus giganteus*, *Eodalmanitina destombesi*, *Eoharpes guichenensis*, *Guichenia dufouri*, *Isabelinia glabrata*, *Neseuretus tristani*, *Nobiliasaphus nobilis*, *Panderia beaumonti*, *Phacopidina micheli*, *Placoparia tournemini*, *Prionocheilus mendax*, *Selenopeltis gallica*, *Uralichas* sp., *Zeliszkella lapeyrei*). The fourth locality (Beauséjour) is located about 29 km S of Rennes, immediately to the north of Bain-de-Bretagne (Fig. 20.5). The associated fauna is typical of the stratigraphically uppermost part of the Traveusot Formation (early Sandbian, Sa1), with rare brachiopods and echinoderms, various molluscs (bivalves, cephalopods, gastropods), and mostly trilobites (e.g. *Colpocoryphe grandis*, *Dalmanitina* sp., *Eodalmanitina destombesi*, illaenids indet., *Neseuretus* sp., *Panderia beaumonti*, *Phacopidina micheli*, *Placoparia* sp.).

Stylophorans are locally extremely abundant in the upper part of the Traveusot Formation. Most echinoderm assemblages are dominated by the mitrocystitid mitrate *Mitrocystella incipiens miloni* (several hundreds specimens collected), associated with relatively common kirkocystids (Chauvel 1941, 1981; Jefferies 1968; Lefebvre 2000a, 2007a; Lefebvre & Régnault 2009). Five other stylophoran taxa have been reported, but they represent very rare members of the assemblages: they include the mitrates *Diamphidiocystis regnaulti* and *Lagynocystis pyramidalis*, and the three cornutes *Domfrontia pissotensis*, *Milonicystis kerfornei*, and *Thoralicarpus guilloui* (see below; Chauvel & Nion 1977; Chauvel 1981;
Domfrontia pissoten is known from one almost complete individual and fragments of another one occurring on a single slab (no counterpart) collected by P. Courville at Beauséjour (see below; Fig. 21c). Milonicystis kerfornei (Fig. 21a) is documented from six almost complete, slightly disarticulated individuals: four of them were collected by J. Chauvel and J. Nion in its type locality (Traveusot), and two more ones, more recently, by C. Guillou, in a single concretion from the nearby locality of le Domaine (see below; Chauvel 1986; Cripps & Daley 1994). Thoralicarpus guilloui is known from a single slab (no counterpart; Fig. 21b) of micaceous silstone preserving a single, almost complete, large individual in upper aspect (see below; Lefebvre & Vizcaïno 1999; Lefebvre 2000a). This unique specimen was collected by C. Guillou at la Saudrais.

In terms of preservation, most specimens of Mitrocystella incipiens miloni, which is the most abundant stylophoran in the upper part of the Traveusot Formation, consist of a complete to slightly disarticulated theca, with their proximal aulacophore and stylocone still connected to it (Chauvel 1941, 1981). More distal portions of their feeding appendage (ambulacral cover plates, ossicles) are very seldom preserved (Jefferies 1968; Chauvel 1981). This preservation, which corresponds to stylophoran taphonomic grade 3 (sensu Martin et al. 2015), is also observed in the few available cornute specimens (see below; Chauvel 1986; Cripps & Daley 1994; Lefebvre & Vizcaïno 1999). Taphonomic features of stylophorans in the upper part of the Traveusot Formation suggest that most of them correspond to the in situ preservation of decayed and collapsed carcasses in a very quiet, well-oxygenated setting, probably at or more likely below storm wave base (Lefebvre 2007a). This interpretation is in good agreement with the occurrence of numerous intact trilobite exuviae in Traveusot: the preservation of such delicate structures requires very quiet sea bottom conditions (Henry 1980, 1989).
Le Pissot Formation. Relatively abundant cornute remains were collected in the concretions-bearing, micaceous siltstones of the uppermost part of the Le Pissot Formation (late Darriwilian, H. teretiusculus graptolite Zone), in Normandy (Chauvel & Nion 1977; Cripps & Daley 1994; Lefebvre 2000a). All specimens were found in a single locality (le Pissot, Fig. 20.6), which is situated N of Domfront, in the Domfront-Mortain syncline, about 58 km N of Laval and 68 km SW of Caen (see Chauvel & Nion 1977; Robardet 1981; Cripps & Daley 1994). In this area, the uppermost part of the Le Pissot Formation yielded a diverse fully marine assemblage comprising also bivalves, brachiopods, crinoids (e.g. Heviacrinus melendezi, H. tromelini), diplopore blastozoans (e.g. Calix sp.), rare graptolites, numerous ostracods (e.g. Aechmina? aff. ventadorni, Lardeuxella bussacensis, Marquezina moniquae, M. zohrae, Medianella sp., Quadritia tromelini, Reuentalina ribiriana), and many trilobites (e.g. Colpocoryphe rouaulti, Dionide mareki, Ectillaenus giganteus, Eodalanitina destombesi, Morgatia hupei, Neseuretus tristani, Nobliasaphus nobilis, Panderia beaumonti, Phacopidina micheli, Placoparia tournemini, Plaesiacomia oehlerti, Prionocheilus mendax) (see Babin et al. 1976; Chauvel 1980; Henry 1980; Robardet 1981; Vannier 1986a, b; Lefebvre et al. 2015a).

All cornute remains from le Pissot are here assigned to a single taxon (Domfrontia pissotensis; see discussion below). Six individuals were originally collected in this locality by M. Robardet and J. Nion in the 1970s, and 23 additional specimens were subsequently sampled by A. Cripps and R. Jefferies in 1988 (see Chauvel & Nion 1977; Cripps & Daley 1994). Most of this material (20 specimens) corresponds indeed to small slabs of siltstones containing isolated cornute skeletal elements. However, over ten almost complete individuals of D. pissotensis are preserved on the nine other rock samples (see Chauvel & Nion 1977; Cripps & Daley 1994). In most of them, the aulacophore is present (proximal rings, stylocone,
ossicles, and cover plates) and inserted into a fully articulated to slightly disarticulated theca (Chauvel & Nion 1977; Cripps & Daley 1994). Two distinct taphonomic grades (1 and 5, sensu Martin et al. 2015) can thus be observed in cornute specimens from le Pissot. Complete individuals were probably buried alive by storm-generated, obrution deposits, whereas isolated skeletal elements can be interpreted as fragments of already decayed individuals. These taphonomic features suggest shallower environmental conditions than in the upper part of the Traveusot Formation, probably at or more likely above storm-wave base. This interpretation is well-supported by independent conclusions reached using associated trilobites (see e.g. Henry 1980, 1989).

Bohemia, Czech Republic

The Ordovician rocks in the Bohemian Massif are mainly restricted to the Teplá-Barrandian area, namely the Prague Basin, which is an infilling of a tectonically predisposed, narrow linear depression (Havlíček 1981, 1982). The Prague Basin is situated in the central part of Czech Republic, between Pilsen and Prague (Fig. 22).

The Prague Basin exposes a continuous succession of sedimentary and volcanic rocks ranging from the Lower Ordovician (Tremadocian) to the Middle Devonian (Givetian) (Havlíček 1998). Its Ordovician succession is characterised by siliciclastic sedimentation (Havlíček 1998), while the Silurian one shows a gradual upward transition from siliciclastic to carbonate sedimentation (Kříž 1998). The Devonian record is mainly characterised by carbonate rocks (Chlupáč 1998). The sedimentation in the Prague Basin is associated to an extensional regime. From the Tremadocian to the Givetian, tectonic activity led to an extensive volcanism in Ordovician and Silurian, the segmentation of the Prague Basin and the
subsequent facies differentiation. The sedimentation ended with the onset of the Variscan orogeny (Chlupáč 1998).

The Ordovician series is represented by an unmetamorphosed, richly fossiliferous, continuous succession of different clastic sediments accompanied with volcanic rocks (Havlíček 1998).

**Šárka Formation.** The Šárka Formation represents the lower part of the Darriwilian Stage in the Prague Basin. This unit was formed during a time of transgression, deepening and strong regional volcanic activity (Havlíček 1998; Servais et al. 2008). The thickness of this formation ranges from several metres in the marginal parts of the basin to nearly 350 m in segments with supposedly rapid synsedimentary subsidence (Havlíček 1981, 1998; Servais et al. 2008). The Šárka Formation consists of clayey shales in the central part of the basin and of oolitic iron ore along the flanks of the basin (Havlíček & Vaněk 1966; Havlíček 1998; Mergl 2013). The Šárka Formation contains highly diverse skeletal fauna (e.g. brachiopods, molluscs, arthropods, echinoderms). Trilobites are the dominant and the most abundant fossil group (Budil et al. 2003; Mergl et al. 2008; Laiblová & Kraft 2014). Most of the museum material is preserved three-dimensionally in silicified concretions collected in fields without information about their exact stratigraphy. Fauna from shales is well documented only from few localities, mostly temporary excavations. This formation is divided into two graptolite biozones: the *Corymagnostus retroflexus* and *Didymagnostus clavulus* biozones (Kraft et al. 2001). However, in most localities concretions of both biozones are mixed together and sometimes also with those of the overlying Dobrotivá Formation.

The concretions of the Šárka Formation yielded a particularly rich and diverse echinoderm assemblage comprising asterozoans (e.g. *Archegonaster, Eophiura, Palaeura*), crinoids (e.g., *Ramseyocrinus*?), diploporites (e.g. *Archeocystis, Pyrocystites*), edrioasteroids, solutans (e.g.
Plasiacystis and stylophorans (Barrande 1887; Chauvel 1941; Spencer 1951; Plas & Prokop 1979; Prokop & Petr 1999, 2003; Lefebvre 2007a; Lefebvre et al. 2012; Zicha et al. 2019).

Mitrates are particularly abundant and diverse with kirkocystids (Anatifopsis, Balanocystites), lagynocystids (Lagynocystis) and mitrocystitids (Mitrocystites, Promitrocystites) (Barrande 1872, 1887; Chauvel 1941; Jefferies 1968, 1973; Parsley 1994, 2000; Henry et al. 1997; Lefebvre 1999, 2007a; Parsley et al. 2000). In the Šárka Formation, cornutes are rare elements of the assemblages. They consist mostly of hanusiids (Reticulocarpos hanusi, Hanusia obtusa, H. sarkensis; Jefferies & Prokop 1972; Cripps 1989a, b). Although the occurrence of the scotiaecystid Bohemiaecystis bouceki was regularly mentioned in the Šárka Formation (see e.g. Ubaghs 1968, 1970; Derstler, 1979; Domínguez et al. 2002b), none of the three specimens originally examined by Caster (in Ubaghs 1968) was actually collected in this unit (holotype and paratype deposited in the collections of the National Muzeum, Prague, and additional specimen from the collections of the Cincinnati Museum Center, Cincinnati).

A fourth specimen of scotiaecystid cornute from the Middle Ordovician of Bohemia was found recently in the collections of the Naturhistoriska Riksmuseet, Stockholm. The label of this well preserved specimen (part and counterpart) explicitly mentions that it was collected in the Šárka Formation, at locality Praha-Šárka. This cornute, morphologically close to both B. bouceki (from the overlying Dobrotivá Formation) and Thoralicarpus prokopi gen. et sp. nov. (from the Letná and Vinice formations, see below) is described herein as Thoralicarpus cf. prokopi gen. et sp. nov. (see below).

In Barrande's time, Praha-Šárka (Fig. 22.1) was a cumulative name for several fossiliferous sites (mostly open fields) located immediately to the northwest of Prague city. All these sites are now built up and no longer accessible. The most exploited one was Šárka (or Vokovice) brickyard (Bouček 1927), where the shales with siliceous nodules yielded a particularly abundant and diverse assemblage of marine invertebrates typical of the Euorthisina-
Placoparia soft-bottom community (Havlíček & Vaněk 1990; Polechová 2013). In Praha-Šárka area, assemblages are dominated by trilobites (Asaphellus desideratus, Colpocoryphe bohemica, Ectillaenus katleri, Ormathops atavus, Placoparia cambriensis, Pricyclopyge binodosa, Trinucleoides reussi), along with bivalves (Praenucula spp., Pseudocyrtodonta spp., Redonia deshayesi), brachiopods (Eodalmanella socialis, Euorthisina moesta), gastropods (Cyrtodiscus nitidus, Tropidodiscus pusillus), ostracods (Conchoprimitia osekensis), phyllocarids (Caryocaris spp.) and stylophoran echinoderms (Lagynocystis pyramidalis, Mitrocystites mitra). In this area, other relatively common faunal elements include asterozoans (Archeogaster pentagonus, Eophiura bohemica, Palaeura neglecta), brachiopods (Paterula incognita, Wosekella debilis), cephalopods (Bactroceras sandbergeri, Bathmoceras complexum), conulariids, gastropods (e.g. Barrandicella ovata, Lesueurilla prima, Ptychonema desiderata, Pygmaeoconus porrectus, Sinuities sowerbyi), graptolites (e.g. Corymbogruptus retroflexus, Didymogruptus sp.), hyolithids (e.g. Bactrotheca teres, Elegantilites euglyphus, Gompholites cinctus, Nephrotheca sarkaensis, Pauxillites pauxillus), kirkocystid mitrates (Anatifopsis barrandei, Balanocystites primus), machaeridiants (Plumulites spp.), ostracods (e.g. Brephocharieis ctiradi), rostroconchs (Ribeiria apusoides) and numerous trilobites (Bohemopyge discreta, Ectillaenus sarkaensis, Eoharpes primus, Nerudaspis aliena, Plasiaspis bohemica, Prionocheilus vokovicensis). Finally, some taxa are particularly rare in Praha-Šárka area, as for example the bivalve Babinka prima, the crinoid Ramseyocrinus primus, diploporites (Archeogystis desiderata, Pyrocyctites pirum), the mitrocystitid mitrate Promitrocystites barrandei and some trilobites (Areiaspis barrandei, Bohemolichas incola, Caudillaenus advena, Chatkalagnostus frici, Geragnostella tullbergi, Microparia spp., Pliomeros senilis, Sarkia bohemica, Selenopeltis macrophthalma, Uralichas avus).
The Praha-Šárka fauna, which includes abundant and diverse blind (or with reduced eyes) trilobites (e.g. *Colpocoryphe bohemica*, *Ormathops microptalmus*) along with large-eyed, probably mesopelagic taxa (e.g. *Pricyclopyge binodosa*) matches closely the definition of atheloptic assemblages (sensu Fortey & Owens 1987), which are generally considered as associated to relatively deep environmental conditions (Henry *et al.* 1997). This interpretation is in good accordance with the occurrence of abundant specimens of the mitrate *Lagynocystis pyramidalis* (Lefebvre 2007a; Lefebvre *et al.* 2010b), and the taphonomic features of most invertebrate taxa, which are suggestive of the relatively long exposure of *in situ* decaying carcasses (e.g. often articulated but collapsed skeletons) in a calm, offshore setting. In the Šárka Formation, the single known specimen of scotiaecystid cornute found in a concretion from Praha-Šárka area is a partly disarticulated, incomplete theca and a portion of proximal aulacophore (taphonomic grade 3 sensu Martin *et al.* 2015).

**Dobrotivá Formation.** The lithology and facies of the Dobrotivá Formation (upper Darriwilian to lowermost Sandbian) are very similar to those of the underlying Šárka Formation. In the Prague Basin, the Dobrotivá Formation varies in thickness from 100 to 450 m. The progressive deepening of the Prague Basin (black shale sedimentation) was accompanied by the rise of adjacent dry lands. From these elevated blocks, sandy deposits accumulated along steep slopes, on both sides of the basin (Havlíček 1998). These sandy deposits are very poor in faunal remains, but they contain abundant ichnofossils. In black shales, well-preserved fossils can be found – mainly the shelly fauna and trilobites. Other fossil material usually originates from originally carbon-rich, secondarily silicified concretions. Benthic and nectobenthic assemblages of the Šárka and Dobrotivá formations are much similar to each other, whereas their pelagic elements are rather different (Havlíček 1998; Marek 1999; Manda 2008). As far as echinoderms are concerned, the Dobrotivá
Formation yielded a relatively diverse assemblage comprising asterozoans (*Hypophiura*), crinoids (*Ramseyocrinus?*, undescribed taxa), diploporites (*Calix*), rhombiferans, and stylophorans with rare cornutes (*Arauricystis, Bohemiaecystis, Galliaecystis, Hanusia, Prokopicystis*) and more abundant mitrates (*Anatifopsis, Diamphidiocystis, Lagynocystis, Mitrocystella, Mitrocystites*) (Barrande 1872, 1887; Chauvel 1941; Ubaghs 1968; Jefferies 1968, 1973; Prokop 1985; Cripps 1989a, b; Parsley 2000; Prokop & Petr 1999; Lefebvre *et al.* this volume). The four specimens of non-hanusiid cornutes known so far from the Dobrotivá Formation (*Arauricystis clariondi* sp. nov. and *Bohemiaecystis bouceki*) were found in four distinct localities.

The first locality, Praha-Šárka (Fig. 22.1), is the type locality of *Bohemiaecystis bouceki*. However, as this is also the case for the underlying Šárka Formation (see above), the name of this locality does not refer to one precise fossiliferous site, but to a set of fields and outcrops located northwest of Prague city in Barrande's time and no longer accessible. In Praha-Šárka area, the Dobrotivá Formation yielded a relatively low diversity invertebrate assemblage comparable to those occurring in Malé Přílepy (see below) and other recent temporary excavations in Vokovice area. This assemblage is dominated by some trilobites (*Degamella princeps, Ornathops novaki, Placoparia zippezi, Zeliszkella oriens*), associated to relatively common phyllocarids (*Caryocaris* sp.), and some less frequent trilobite taxa (*Ectillaenus benignensis, Parabarrandia crassa*) (see Budil 1999; Peršín & Budil 2009; David & Budil 2015).

The paratype of *Bohemiaecystis bouceki* (NMP.L32304) was found in a second locality (Šárka field near Hammernikova villa; Fig. 22.2), which was a field yielding siliceous concretions, in the surroundings of Prague city in Barrande's time. The precise location of this former field is nowadays probably close to the primary school in the part of Prague called Vokovice (Nad Lávkou street) (Peršín, personal communication 2020). Based on historical
collections, the Dobrotivian assemblage collected in this locality is comparable to the one found in Praha-Šárka (see above).

The third specimen of *B. bouceki* (CMC.IP.50176) was collected in Malé Přílepy, which is a well-known locality situated about 18 km SW of Praha-Šárka (Fig. 22.3). This site yielded probably the most diverse assemblage (e.g. over 30 trilobite taxa) observed in the Dobrotivá Formation. However, it is likely that this unusually high diversity results from the mixing of several distinct fossiliferous, concretion-bearing horizons. Fossils occur in loose concretions collected at the surface of ploughed fields. Most echinoderms and trilobites are found as fully articulated specimens. The Malé Přílepy assemblage is dominated by some trilobites (*Degamella princeps*, *Ormathops novaki*, *Placoparia zippei*, *Pricyclopyge longicephala*), the brachiopod *Benignites primulus* and phyllocarids (*Caryocaris* sp.). Other relatively common members of the assemblage include the brachiopod *Rafanoglossa impar*, conulariids, hyolithids, kirkocystid mitrates (*Anatifopsis* sp.), machaeridians (*Plumulites* sp.), several molluscs (*Barrandicella* sp., cephalopods, *Cyrtodiscus nitidus*, *Praenucula* sp., *Ptychonema desiderata*), ostracods and some trilobites (*Cyclopyge bohemica, Ectillaenus benignensis, Eoharpes benignensis*). More occasional faunal elements of the Malé Přílepy assemblage comprise the bivalve *Pseudocyrtodonta ala*, the brachiopod *Paterula circina*, chelicerate arthropods (*Archeolimulus hanusi*), the gastropod *Sarkanella vokovicensis*, graptolites, palaeoscolecid worms (*Gamascolex herodes*), sponge spicules and some trilobite taxa (e.g. *Bergamia agricola*, *Bohemilla* sp., *Corrugatagnostus morea*, *Dindymene plasi*, *Dionide jubata*, *Microparia* sp., *Nobiliasaphus repulsus*, *Parabarrandia crassa*, *Petrbokia longicauda*, *Selenopeltis macrophthalma*, *Zeliszkella oriens*). This assemblage has also yielded rare specimens of cheirocrinid rhombiferans, cornute (*Bohemiaecystis bouceki, Hanusia prilepensis*) and mitrate stylophorans (*Diamphidiocystis* sp., *Lagynocystis pyramidalis, Mitrocystella incipiens, Mitrocystites mitra*).
The name of the last locality, Zbiroh, is reported on the label of a single specimen of cothurnocystid cornute (described below as *Arauricystis clariondi* sp. nov.) belonging to the Barrande collection in the National Museum, Prague (NMP.L13230). Its stratigraphic position is uncertain, with only 'Dd1' mentioned on the label. In Barrande's original concept, this stratigraphic interval embraces all units from the Třenice to the Dobrotivá formations (i.e. Lower–Middle Ordovician) (see e.g. Chlupáč *et al.* 1998). However, the lithology (micaceous black shales) of the slab containing the fossil suggests that it was found either in the Šárka Formation or, more likely, in the Dobrotivá Formation (P. Budil, pers. comm. April 2018). This putative age is compatible with locality details. The city of Zbiroh, which is located about 18 km NE of Rokycany in the southwestern part of the Prague basin, lies well outside of Ordovician outcrops. However, old mines located about 5 km south of Zbiroh, near the villages of Kařez and Kařízek, were exploited in Barrande's time for iron ores deposits within the Dobrotivá Formation. This area, south of Zbiroh thus represents the most probable candidate for this specimen locality (Fig. 22.4). Although the Dobrotivá Formation is mapped around the villages of Kařez and Kařízek, no surface outcrops are any longer available. However, faunal elements typical of the Dobrotivá Formation were known from mine dumps around the former 'Veronika mine' (Klouček 1913). This iron ore faunule is dominated by conulariids (especially *Metaconularia imperialis*) associated to common lingulid brachiopods (*Paterula cercina*, *Rafanoglossa impar*) and rare trilobites (*Dindymene plasi*, *Eoharpes benignensis*, *Zbirovia arata*). Nearby temporary excavations in the shales also yielded some remains of brachiopods (*Paterula cercina*) and trilobites (*Ormathops inflatus*, *Zeliszkella oriens*).

All three specimens of *Bohemiaecystis bouceki* are preserved in concretions and consist of fully articulated thecae (including the minute digital in contact with M'4), sometimes with the proximal aulacophore and stylocone (holotype) attached. Similarly, the single specimen of
Arauricystis clariondi sp. nov. corresponds to an almost complete, fully articulated theca (in upper aspect), with proximal rings, stylocone and associated cover plates in open position on both sides of it. In the cothurnocystid specimen, the preservation of minute skeletal elements (e.g. supracentral spines collapsed on the upper thecal surface, cover plates along the stylocone) suggests very quiet environmental conditions and the in situ decay of carcasses exposed on a soft sea bottom, very likely in a distal setting, well below storm wave base. The absence of the aulacophore in most specimens of Bohemiaecystis bouceki is possibly original, but it can also result from the small size of the concretions in which they are preserved, and which matches very closely their thecal outlines.

Letná Formation. No cornute remains have been reported so far from the Libeň Formation. The overlying Letná Formation (Sandbian) is characterised by the alternation of coarse and fine siliciclastic sediments generally in centimeter to decimeter thick, strongly bioturbated beds (Kukal 1958, 1998; Havlíček 1998; Mikuláš 1998a, b, 1999). Dominant lithologies consist of fine-grained sandstones and sub-greywackes, sandy siltstones, clayey siltstones and clayey sandstones, while clayey shales are rare (Kukal 1958, 1998). The thickness of the formation is very variable, ranging from 40 m to 650 m (Havlíček 1998). Dalmanitids (Dalmanitina socialis) and trinucleids (Deanaspis goldfussi) dominate among trilobites (with many other genera present and locally common; see Fatka et al. 2013). Notably diverse are non-trilobite arthropods (Chlupáč 1965, 1999a, b; Rak et al. 2009, 2013; Ortega-Hernandez et al. 2010; Van Roy et al. 2021). Bivalves belong to the Modiolopsis community (see Kříž & Steinová 2009; Polechová 2019). Other molluscs such as gastropods and orthocone cephalopods are relatively rare. Conulariids are diverse. Two distinct brachiopod-dominated communities have been described in the lower-middle part (Drabovia redux community) and the upper part of the formation (Bicuspina community) (Havlíček 1982, 1998; Havlíček &
Vaněk 1990). Echinoderms are mostly present in the uppermost part of the Letná Formation, near the boundary with the overlying Vinice formation. Echinoderm faunas are extremely diverse with asterozoans (asteroids and ophiuroids), coronates (*Mespliocystites*), crinoids (*Caleidocrinus*), diploporites (*Aristocystites*), edrioasteroids (*Agelacrinites*, *Argodiscus*, *Hemicystites*), eocrinoids (*Ascocystites*), paracrinoids (*Letenocrinus*), rhombiferans (*Echinospheraeites*, *Macroclystella*, *Rhombifera*), solutans (*Dendrocystites*), stylophorans (*Anatifopsis*, *Aspidocarpus*, *Barrandeocarpus*, new *Enoploura*-like anomalocystitid, new *Eumitrocystella*-like paranacystid, *Thoralicarpus* gen. nov.) (see Barrande 1872, 1887; Ubaghs 1979; Prokop & Petr 1990, 1999; Noailles *et al.* 2014). Scotiaecystid cornutes have been found in two distinct localities.

The first one corresponds to three temporary excavations (2008–2010) made for the basement of new buildings in the village of Zahofany, at the extremity of Borová Street and along the slope of Děd Hill (Fig. 22.5). Material could not be collected directly from the exposures, but from scree extracted from the three excavations, which were stratigraphically spanning the boundary between the Letná and Vinice formations. The stratigraphically lower excavation yielded an assemblage typical of the upper part of the Letná Formation; in the second excavation, fossils from the Letná and Vinice formations were occurring together; and the third, stratigraphically upper site, yielded exclusively faunal elements typical of the lower part of the Vinice Formation. The clayey shales of Borová Street outcrop yielded a relatively diverse assemblage comprising bivalves, conulariids (*Archaeoconularia fecunda*), hyolithids, machaeridians (*Plumulites fraternus*), rostroconchs (*Ribeiria* sp.) and trilobites (e.g. *Dalmanitina proaeva elfrida*, *Deanaspis senftenbergi*, *Zeliszkella deshayesi*). These levels also yielded abundant echinoderm remains, consisting mostly of solutans (*Dendrocystites barrandei*) and stylophorans (e.g. *Anatifopsis* sp., *Aspidocarpus bohemicus*, *Diamphidiocystis* sp., *Barrandeocarpus jaekeli*, scotiaecystid cornutes). In Borová Street, three relatively
complete specimens of *Thoralicarpus* gen. nov. (theca, proximal aulacophore, with
sometimes stylocone and first next ossicles; taphonomic grades 2–3 sensu Martin *et al.* 2015)
were found in the lowermost excavation, i.e. in the upper part of the Letná Formation (Fig.
23c).

The second locality (Chrustenice, Fig. 22.6) is situated about 11.5 km NE of Zahofany
(Borová Street) and about 2 km E of Malé Přílepy (see above) and comprises of a series of
natural and artificial outcrops. In Chrustenice, over twenty specimens of scotiaecystid
cornutes were found in grey to yellow, thinly laminated sandstones with few massive
intercalated quartz sandstone beds. These stylophorans were collected just below iron ore
deposits at the base of the overlying Vinice Formation, i.e. in layers possibly slightly younger
than the lower fossiliferous excavation in Borová Street. In Chrustenice, most layers are
dominated by echinoderms, and the associated fauna is significantly rarer and less diverse
than in most other levels of the Letná Formation (e.g. non-trilobite arthropods are absent).
Some beds correspond to almost monospecific mass occurrences of fully articulated
individuals of the solutan *Dendrocystites barrandei*. Some other layers are characterised by
abundant ophiuroids, often associated with *D. barrandei* and other echinoderms. These
asterozoan/solutan dense beds also yielded relatively common specimens of bryozoans,
conulariids, coronates (*Mespilocystites bohemicus*), edrioasteroids, kirkocystid mitrates
(*Anatifopsis* sp.), machaeridians (*Plumulites* sp.), rhombiferans (*Echinosphaerites infaustus*),
diploporites (*Aristocystites*), rhynchonelliform brachiopods, as well as articulated trilobites
(*Cekovia transfuga*, *Prionocheilus mendax*), some of them with possibly exceptionally
preserved soft parts (gut). More occasional members of the Chrustenice assemblage include
crinoids (*Caleidocrinus multiramus*), the enigmatic echinoderm *Hexedriocystis* sp., rare
molluscs (cephalopods, *Nonorios pater*), various rhombiferans (*Homocystites cf. alter,*
*Macrocystella bohemica, Rhombifera bohemica*), tentaculites (*Conchicolites* sp.), and some
trilobites (*Dalmanitina socialis*, *Deanaspis goldfussi*, *Eccoptochile clavigera*, *Eccoptochiloides tumescens*).

This locality yielded over twenty specimens of the scotiaecystid *Thoralicarpus prokopi* gen. et sp. nov. (see below). Most individuals are complete, fully articulated (theca and aulacophore), with closed to slightly ajar cover plates still articulated to underlying ossicles (taphonomic grade 1 sensu Martin *et al.* 2015). However, minute details of skeletal morphology (e.g. number of supracentrals, aspect of lamellipores) are often obscured by the coarse grain size of the associated sandstone (Fig. 23a–b). These taphonomic features are, in many respects, very comparable to those observed in Bou Nemrou, Morocco (Izegguirene Formation, lowermost Sandbian; see above) and some other echinoderm Lagerstätten. As in Bou Nemrou, it is very likely that Chrustenice echinoderm dense beds correspond to original live assemblages, suddenly buried by obrution (storm) deposits (Nohejlová *et al.* 2018). This interpretation is supported by the preservation of echinoderms (e.g. fully articulated individuals, cornute cover plates closed or ajar), the occurrence of various growth stages (e.g. in ophiuroids and scotiaecystids), the associated lithology, and storm-generated associated sedimentary structures (Nohejlová *et al.* 2018). Moreover, as this is also frequently the case in echinoderm dense beds, the associated fauna is relatively rare and not very diverse (see Lefebvre 2007a). Similarly to the situation in Bou Nemrou, the preservation of trilobite guts in Chrustenice suggests that this locality also represents a new Late Ordovician Konservat-Lagerstätte.

**Vinice Formation.** The Vinice Formation (uppermost Sandbian to Katian) is characterised by a marine transgression over the stable segments bounding the Prague Basin (see Havlíček 1998). Dark grey to black shales are the dominant lithofacies. The thickness of the formation varies from about 20 m up to 450 m at the deepest part of the basin. At most localities, the
Benthic fauna is typically monotonous, not very diverse, adapted to soft substrates and poorly oxygenated environmental conditions. Ichnofossil diversity is much lower than in the underlying Letná Formation. Vinice assemblages are generally dominated by molluscs (bivalves, gastropods) and hyolithids, along with a limited number of trilobite taxa (mostly *Dalmanitina proaeva elfrida* and *Deanaspis senftenbergi*; see Havlíček & Vaněk 1966). Other faunal elements include rare graptolites, trilobites of the cyclopygid biofacies, and brachiopods typical of the *Paterula* community. In the lowermost part of the formation, oolitic iron ores (Zdice-Nučice ore horizon) yielded distinct and more diverse assemblages (Havlíček 1998). Echinoderms are much less common and diverse than in the underlying Letná Formation (Barrande 1872, 1887; Havlíček 1982, 1998; Havlíček & Fatka 1992; Prokop & Petr 1999; Noailles et al. 2014; Paul 2018). They can be assigned to two distinct communities. The first one is restricted to the iron ore horizon at the base of the formation and comprises coronates (*Mespilocystites*), diploporites (e.g. *Aristocystites*, *Fungocystites*, *Orocystites*, *Prokopius*) and rhombiferans (e.g. *Echinosphaerites*, *Rhombifera*). The second echinoderm assemblage occurs exclusively within the micaceous shales of the Vinice Formation and is dominated by kirkocystid mitrates (*Anatifopsis*). Other taxa are rare and include mostly solutans (*Dendrocystites*), along with scotiaecystid cornutes and mitrocystitid mitrates (*Aspidocarpus*, *Barrandeocarpus*, *Diamphidiocystis* and a possible new *Eumitrocystella*-like paranacystid).

Ten specimens of scotiaecystids were found at a single locality, which is in the stratigraphically uppermost excavation in the village of Zahořany (Borová Street, see above; Fig. 22.5). This exposure yielded an assemblage typical of the lower part of the Vinice Formation. All cornutes found in this horizon are here assigned to *Thoralicarpus prokopi* gen. et sp. nov. (see below). In one specimen (CGS.LK.14), some elements of the proximal aulacophore are still partly connected to a complete, almost fully articulated theca.
(taphonomic grade 3 sensu Martin et al. 2015). Most other individuals correspond to more or less strongly disarticulated thecae (appendage entirely missing; taphonomic grade 4). One isolated portion of distal aulacophore (about 10 ossicles still articulated to each other) is preserved near the theca of one specimen (CGS.L.K.7). These taphonomic features are suggestive of a relatively long post-mortem exposure in very quiet environmental conditions, probably well-below storm wave base.

Zahořany Formation. The Zahořany Formation (Katian) is composed mainly of a monotonous sequence of siltstones with rare intercalations of shales and silty sandstones. This unit varies in thickness from 70 m to 400 m across the Prague Basin (Havlíček 1998). In the shallowest settings of the Zahořany Formation, storm-generated sediments with hummocky cross-stratification are common, and bioturbation is frequent (Mikuláš 1998a). Assemblages are particularly diverse in such environmental conditions, with abundant brachiopods (Drabovia, Aegiromena) associated with bivalves, conulariids, echinoderms, gastropods, hyolithids and trilobites (Dalmanitina proaeva proaeva, Marrolithus, Vysocania, Selenopeltis, Prionocheilus). In deeper settings, brachiopods are less common and occurring within low-diversity benthic faunas (Havlíček 1998). Echinoderms are relatively diverse in the Zahořany Formation, with asterozoans (Bohemura, Siluraster), coronates (Mespiilocystis), crinoids (Polycrinus), diploporites (Aristocystites, Calix, Codiacystis, Fungocystites), edrioasteroids (Agelacrinites), eocrinoids (Cardiocystites), rhombiferans (Echinosphaerites, Homocystites, Rhombifera), solutans (Dendrocystites), and both cornute (Destombesicarpus, Domfrontia) and mitrate stylophorans (Anatifopsis, Barrandeocarpus, Diamphidiocystis) (Barrande 1872, 1887; Prokop 1984; Petr 1989a; Parsley 1990, 1998; Prokop & Petr 1999; Noailles et al. 2014; Lefebvre et al. this volume).
In Levín (SW of the small city of Králův Dvůr; Fig. 22.7), cross-bedded micaceous siltstones with occasional sequences of thinner and finer intercalations yielded recently a relatively diverse assemblage of well-preserved, articulated echinoderms, including the first two cornute taxa reported so far from the Zahořany Formation: *Destombesicarpus budili* gen. et sp. nov. and *Domfrontia aff. milnerorum*. The Levín assemblage is dominated by bivalves, the two brachiopods *Aegiromena aquila* and *Rafinesquina pseudoloricata*, diploporites (Aristocystites bohemicus, Codiacystis bohemica), hyolithids (*Elegantilites* sp.), and the trilobite *Dalmanitina proaeva*. Other common members of this assemblage include cephalopods, the cornute *Domfrontia aff. milnerorum*, graptolites, machaeridians (*Plumulites* sp.), mitrates (*Anatifopsis* sp., *Barrandeocarpus* sp.), the rhombiferan *Echinosphaerites infaustus*, rostroconchs (*Ribeiria apusoides*, *Technophorus sharpei*), tentaculites (*Conchicolites* sp.) and several trilobites (*Cekovia salteri*, *Eccoptochile perlata*, *Flexicalymene incerta*, *Prionocheilus pulcher*, *Selenopeltis inermis*). The Levín assemblage also yielded rare to occasional specimens of some brachiopods (e.g. *Petrocrania inexpectata*, *Rostricellula ambigena*), encrusting bryozoans, the cornute *Destombesicarpus budili* gen. et sp. nov., edrioasteroids, gastropods (*Grandostoma bohemicum*, *Sinuitopsis neglecta*), the glyptocystitid rhombiferan *Homocystites alter*, the mitrate *Diamphidiocystis regnaulti*, *solutans* (*Dendrocystites sedgwicki*) and some trilobites (*Actinopeltis* sp., *Chlustinia keyserlingi*, *Nobiliasaphus nobilis*, *Vysocania panderi*). Ten individuals of *Domfrontia* (Fig. 21f–g) and one of *Destombesicarpus* (Fig. 21d) were collected in Levín. At this locality, cornutes show a relatively wide range of preservation from slightly disarticulated thecae with no appendage (taphonomic grade 4 *sensu* Martin et al. 2015) to complete, fully articulated thecae with both proximal and distal aulacophore preserved (taphonomic grades 1–2). In the holotype of *Destombesicarpus budili* (CGS.OZ.152), the appendage is missing, but most of the delicate marginal spines are still
articulated along the theca (Fig. 21d). In spite of their very small size (less than 5 mm),
cornutes of the Leýn assemblage are particularly well-preserved, with minute morphological
details (e.g. stereom microstructure of thecal plates) captured by the very fine grain of the
rock (micaceous siltstones) in which they are preserved.

Bohdalec Formation. In the Prague Basin, the thickness of the Bohdalec Formation
(Katian) varies from 20 to 500 m, but it usually ranges from 100 to 200 m. The base of the
formation is marked by a discontinuous horizon of oolitic rocks (the Karlík horizon), which
contains mostly brachiopod-dominated faunas. Two main lithofacies have been described in
the Bohdalec Formation: a claystone sequence dominated by dark grey thinly bedded clayey
shales, and the Polyteichus facies, characterised by alternations of shales, siltstones and fine
grained sandstones (Havlíček 1998). The proximal (shallower) Polyteichus facies is limited to
a narrow strip in the eastern part of Prague, while most of the Bohdalec Formation between
Prague and Zdice is represented by dark grey siltstones and shales. Trilobite faunas are very
similar to those of the underlying Zahořany Formation, but echinoderms are much scarcer and
less diverse (Barrande 1887; Petr 1989b; Parsley 1990; Mikuláš et al. 1995; Prokop & Petr
1999; Noailles et al. 2014). They include asterozoans (e.g. Klarasterina, Taeniaster), crinoids
(Caleidocrinus), diploporites (Aristocystites), rhombiferans (Echinosphaerites), solutans
(Dendrocystites) and both cornute (Domfrontia) and mitrate stylophorans (Anatifopsis,
Aspidocarpus, Barrandeocarpus, Diamphidiocystis). In siltstones of the Bohdalec Formation,
echinoderms almost exclusively consist of diploporites (Aristocystites). These levels have also
yielded some crinoid remains (mostly columnals and stem fragments; complete cups are very
rare), as well as some rare specimens of Dendrocystites and mitrates (Aspidocarpus). In both
siltstones and the Polyteichus facies, some ophiuroid dense beds have been described in
storm-generated lenses. They probably result from the sudden burial of (para-) autochthonous
communities by obrution deposits (Petr 1989b; Mikuláš et al. 1995). Dark shales of the Bohdalc Formation have yielded different invertebrate faunas, probably associated to deeper and less oxic environments. These more distal assemblages are characterised by the trilobite *Onnia*, associated with bivalves, brachiopods, cephalopods, conulariids, gastropods, hyolithids, and rare stylophorans (mostly anomalocystitids and kirkocystids).

In 2018, an excavation made within the small city of Zdice (about 2.5 km SW of Levín; Fig. 22.9) temporarily exposed fine shales of the upper part of Bohdalc Formation, which yielded a single specimen of the cornute *Domfrontia aff. milnerorum*, associated with a low diversity fauna. The Zdice assemblage is dominated by two brachiopod taxa (*Aegiromena* and *Paterula*). Other relatively common faunal elements comprise bivalves, isolated echinoderm columnals, hyolithids, machaeridians (*Plumulites*), ostracods, and the trilobites *Arthrorhachis* and *Onnia*. Rare members of the Zdice assemblage include conulariids, rostroconchs, mitrate stylophorans (*Anatifopsis*, anomalocystitids) and some trilobites (*Cyclopyge*, *Eudolatites*, *Sokhretia*?). The cornute from Zdice corresponds to a small, complete though disarticulated theca, with no aulacophore remains (taphonomic grade 4 sensu Martin et al. 2015). Minute morphological details (e.g. stereom microstructure) are perfectly preserved. Skeletal disarticulation probably results from the in situ decay of the cornute, in an otherwise quiet and distal setting, well below storm wave base.

**Králův Dvůr Formation.** The Králův Dvůr Formation (late Katian–early Hirnantian) is only exposed in the middle part of the Prague Basin. This 25 to 200 m thick unit corresponds to a monotonous, often intensively bioturbated, succession of grey to greyish-green silty shales with a low content (up to 0.3%) in organic matter (Havlíček 1998). A prominent change in sedimentation, correlated across the whole 'Mediterranean Province' (Havlíček 1989), can be observed at the base of this formation, where the black shale lithofacies of the underlying
Bohdalec Formation is replaced by greyish to greenish shales with micritic carbonate nodules. A major faunal turnover also occurs at this level: the *Aegiomena-Drabovia* brachiopod fauna of underlying units is replaced by low-diversity associations assigned to the relatively deep-water and soft-bottom *Foliomena* fauna (Kraft et al. 2015; Colmenar et al. 2017). The Podolí iron ore horizon, which is locally developed at the base of the Králův Dvůr Formation, yielded a remarkable and unusual echinoderm assemblage with *Haplosphaeronis, Heliocrinites* and *Mespilocystites* (Mikuláš & Prokop 2003). A low-diversity echinoderm assemblage occurs in the overlying shale facies, with rare crinoids (*Polycrinus*) and stylophorans (*Anatifopsis, Barrandeocarpus, Destombesicarpus, Diamphidiocystis, Lagynocystis*) (Barrande 1887; Prokop & Petr 1999). A second very fossiliferous interval is located in the uppermost part of the Králův Dvůr Formation: a pelocarbonate horizon, which is often designated as the 'Perník Bed' (i.e. gingerbread bed), yielded a distinct echinoderm assemblage including coronates (*Mespilocystites*), diploporites (*Eucystis*) and rhombiferans (*Echinosphaerites, Heliocrinites*).

The biostratigraphy of the Králův Dvůr Formation was recently revised by Kraft et al. (2015). They identified three distinct graptolite zones: two of them (*Anticostia teres* and *Styracograptus lobatus* interval Zone, and *Dicellograptus laticeps* Zone) are stratigraphically below the Perník Bed, and a third one (*Metabolograptus ojsuensis* Zone) several metres above it. The *M. ojsuensis* is correlated with the *M. extraordinarius* Zone of other regions and thus, with the base of the Hirnantian (Kraft et al. 2015; see discussion in Gutiérrez-Marco et al. 2017). Fossils of the Králův Dvůr Formation are particularly diverse, with a dominance of benthic taxa. Taxonomic diversity is higher than in most other Ordovician units of the Prague Basin (Havlíček & Vaněk 1966). Trilobites and brachiopods are among the most common groups. Stratigraphic and lateral variations in the composition of their assemblages were used to identify several fossil associations (or communities), defined either on brachiopods or on...

One specimen of Domfrontia (Fig. 21e) was found in Nová Vráž - Černošice (about 17 km S of Praha-Šárka and 11 km SE of Chrustenice; Fig. 22.8). In this locality, soft grey to greenish silty shales with occasional nodules yielded a late Katian fauna typical of the Dicellograptus laticeps Zone (as defined by Kraft et al. 2015). The Nová Vráž - Černošice assemblage is dominated by the gastropod Grandostoma grande and the two trilobites Amphitryon radians and Zetillaenus wahlenbergianus, associated with abundant bivalves, crinoid columnals, and ostracods. Relatively common members of this fauna include brachiopods (Anx jejunoides, Dedzetina macrostomoides, Rafanoglossella leiskowiensis), cephalopods, hyolithids, machaeridians and the trilobite Kloucekia ruderalis. Occasional to rare elements of the Nová Vráž - Černošice assemblage comprise stylophoran echinoderms (Diamphidiocystis, Domfrontia) and some trilobite taxa (Cyclopyge marginata, Dionide speciosa, Lonchodomas portlocki, Microparia speciosa). Most invertebrate taxa are found as disarticulated specimens. The single specimen of Domfrontia collected at this locality corresponds to a complete, collapsed (slightly disarticulated) theca and a partly disarticulated aulacophore (taphonomic grade 2 sensu Martin et al. 2015), both preserved with delicate morphological details (e.g. stereom microstructure).

A single specimen of chauvelicystid cornute tentatively assigned here to Destombesicarpus budili gen. et sp. nov. was found in Barrande's classical locality Lejškov (Fig. 22.10), where an almost complete sequence of the Králův Dvůr Formation is accessible in a small ravine. The cornute was found in the lower part of the succession, associated with relatively common and sometimes articulated trilobites (Onnia ultima, Flexicalymene declinata, Kloucekia pachypa, Amphitryon radians), along with some less common faunal elements, such as
bivalves, brachiopods, columnals of *Polycrinus kosoviensis*, kirkocystid mitrates (*Anatifopsis* sp.), ostracods and the trilobite *Dionide speciosa*.

**Iberian Massif, Spain**

Ordovician rocks crop out extensively in the different structural and palaeogeographic zones of the Iberian Massif (Fig. 24c), involving terrigenous shelf sedimentation in a passive margin stage before the onset of the early convergent events leading to the Variscan Orogeny. The only known occurrences of Ordovician cornutes are so far limited to single localities in the Central Iberian and Ossa Morena zones. These two areas respectively represent the shallow inshore and deeper offshore settings of the same peri-Gondwanan platform, previously interpreted as different faunal domains (Robardet & Gutiérrez-Maroo, 1990, 2004). In Variscan times, the Ossa Morena Zone was tectonically juxtaposed to the Central Iberian Zone by the Puente Génave-Castelo de Vide shear zone (Martín Parra et al., 2006).

**Cantera Shale.** This argillaceous unit shows important variations in thickness (from 15 to more than 80 m) within the southwestern part of the Central Iberian Zone, where a microconglomeratic and ferruginous horizon with phosphatic pebbles and iron oolites, located towards its lower or middle third, marks a widespread hiatus which can be correlated at a regional scale with other Upper Ordovician sequences in Ibero-Armorica, Bohemia and Sardinia. In the small Viso del Marqués syncline, the formation is especially thick and fossiliferous, having yielded at the La Palomera site, 3 km west of the town of Viso del Marqués (province of Ciudad Real: VM in Fig. 24), a particularly diverse echinoderm assemblage, partly described by Gil Cid et al. (1996a, b, c, d, 1999), which comes from at least two different horizons. A recent biostratigraphic review by Gutiérrez-Maroo et al. (2018)
established a Sandbian 2–Katian 1 age for all fossiliferous beds located above the ferruginous and microconglomeratic horizon, and which yielded ten different trilobite taxa (Actinopeltis tejoensis, Colpocoryphe grandis, Dalmanitina cf. philippoti, Deanaspis cf. goldfussi, Iberocoryphe sp., ‘Panderia’ beaumonti, Phacopidina? armoricana, Prionocheilus verneuili, Radnoria guyi, Vysocania cf. iberica), eleven brachiopod taxa (Aegiromena aquila, Dactylogonia cf. blyskavensis, Drabovia sp., Gelidorthis sp., Reuschella sp., Rostricellula sp., Svobodaina armoricana, Triplesia sp. and some Harknessellidae, Strophomenidae and Rafinesquininae indet.), thirteen echinoderm taxa (Anatifopsis sp., Aristocystites? sp., Dendrocystites sp., Haplosphaeronites sp., ‘Orocystites' helmhackeri, hemicosmitids indet., Homocystites geyeri, Macrocystella pauli, Mespilocystites lemenni, Ortsaecrinus cocae, Rhombifera bohemia, Ristnacrinus? sp., and Thoralicarpus jefferiesi), as well as some bryozoans, cephalopods, cnidarians (Sphenothallus) and gastropods.

Float siltstone blocks on the trackside (ca. 38°31’27"N, 03°35’16"W) yielded skeletal remains of scotiaecystid cornutes, which were originally described as Bohemiaecystis jefferiesi by Gil Cid et al. (1996d). The original type material of B. jefferiesi consists of six individuals, two of which correspond to almost complete, more or less disarticulated thecae with associated proximal aulacophore and stylocone (taphonomic grade 3 sensu Martin et al. 2015), two others correspond to partially preserved, disarticulated thecae (taphonomic grade 4), and the last two are only isolated thecal plates (taphonomic grade 5). Consequently, the Viso del Marqués scotiaecystids exhibit a wide array of decay stages, suggesting a prolonged exposure of carcasses on the sea-floor, in relatively quiet environmental conditions. In this study, the detailed reexamination of the original type material -and only known specimens- of these cornutes confirmed the necessity to place them in a new genus (Thoralicarpus), morphologically intermediate between Bohemiaecystis and Scotiaecystis (see discussion below). Moreover, the reevaluation of T. jefferiesi also shows that some aspects of its
morphology remain poorly known (e.g. the precise shape and extent of the spinal blade cannot be documented based on available material).

Valle syncline, Ossa Morena Zone. The Ordovician sequence in this part of the Ossa Morena Zone (locality CS in Fig. 24) shows marked differences with the remaining areas of the Iberian Massif (e.g. absence of the Armorican Quartzite). The occurrence of both latest Katian carbonates and Hirnantian glaciomarine diamictites are features shared with other areas of the Iberian peninsula, but they more likely reflect large-scale events affecting the entire peri-Gondwanan areas of SW Europe. Formal lithostratigraphic units are not yet defined, but the studied material (the cornute *Domfrontia*? sp.) comes from siliceous nodules within an unnamed formation of dark mudstones, 15–20 m thick, which lies above a thick succession (>200 m) of grey-green shales and siltstones yielding Floian graptolites and trilobites. The fossiliferous nodules are middle Darriwilian in age (Dw2) and are located in the upper 3–5 m of the dark mudstone formation, occurring directly below a discontinuous ooidal ironstone bed that constitutes the base of the third Ordovician formation. The latter is composed of 60–80 m of sandstones containing brachiopods and trilobites of probable latest Darriwilian age (Robardet & Gutiérrez-Marco 2004, with references therein).

An Ordovician locality with fossiliferous nodules lies approximately 9.5 km west-northwest of the town of Cazalla de la Sierra (province of Seville), south of the km 8.5 of the local road SE-179 from Cazalla de la Sierra to El Real de la Jara, and very close to the main entrance to Las Cañas farm (geogr. coord. 37°57′40″N, 5°51′17″W). The fossil assemblage recorded from the nodules consists of diverse invertebrate taxa, which exhibits strong similarities with middle Darriwilian faunas from the Šárka Formation of Bohemia (Czech Republic) and the Ancenis Unit of the southern Armorican Massif of France (Robardet & Gutiérrez-Marco 2004). The provisional list of taxa includes bivalves (*Redonia deshayesi*),
brachiopods (Euorthisina minor), echinoderms (Domfrontia? sp., Lagynocystis pyramidalis, rhenopyrgid edrioasteroids), gastropods (Sinuites), hexactinellid sponge spicules, hyolithids (Cavernolites, Leolites, Pauillites), machaeridians (Plumulites), orthocone nautiloids, ostracods, rostroconchs (Tolmachovia), and trilobites (Ectillaenus sp., Kodymaspis puer, Nerudaspis cf. aliena, Salterocoryphe, Selenopeltis aff. buchi).

In this locality, cornute remains are particularly rare. The two known specimens consist of incomplete, strongly disarticulated thecae (taphonomic grade 4 sensu Martin et al. 2015), suggesting relatively advanced decay stages in quiet sea bottom conditions. The stylophoran assemblage is largely dominated by the mitrate Lagynocystis pyramidalis, thus suggesting rather deep and/or poorly oxygenated environments (see e.g. Henry et al. 1997; Lefebvre 2007a; Lefebvre et al. 2010b).

**Material and methods**

**Material and institutional abbreviations**

All known specimens of Middle and Late Ordovician cornutes from the Czech Republic, France, Morocco and Spain deposited in public collections were examined or re-examined. This material includes all original specimens previously described and/or figured by Chauvel (1971, 1986), Chauvel & Nion (1977), Cripps & Daley (1994), Gil Cid et al. (1996d), Ruta (1999a), Lefebvre (2000a), and Lefebvre et al. (2008, 2010a). However, a large part of the study material is new and has never been previously described or figured (coll. Auvray, Courville, Gutiérrez-Marcia, Kašička, Lefebvre, Reboul, Zicha). Additional specimens also had to be (re)examined for comparison purposes, including the type material of Lyricocarpus courtessolei, Nanocarpus dolambii, Procothurnocystis courtessolei, and P. owensi (Ubaghs
Methods

All studied specimens are preserved as empty 'negative' moulds in the rock (Figs 18, 21, 23). Consequently, they were cast with latex, so as to reconstruct their original 'positive' aspect. Latex peels were coated with ammonium chloride (NH₄Cl), either for drawing purposes with a camera-lucida apparatus mounted on a Zeiss SteREO Discovery.V8 stereomicroscope binocular, or for photographs, made with a Canon 5DSR camera equipped with a MP-E 65 or 100 mm macro lens. When necessary, limited preparation of the material was made, using needles, under the binocular, so as to remove small portions of rock hiding morphological details.
Measurements were made with the software AxioVision 4.8.2 working with the Zeiss AxioCam MRc5 digital camera mounted on the same stereomicroscope binocular used for the observation of specimens. Thecal width (TW) corresponds to the largest width of the theca, measured more-or-less perpendicular to the main axis (Figs 25–26). Thecal length (TL) was estimated perpendicular to TW, along the main axis (Figs 25–26).

Systematic Palaeontology

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)

Class Stylophora Gill & Caster, 1960

Order Cornuta Jaekel, 1901

Remarks. The order Cornuta is retained here as an informal, paraphyletic taxonomic entity comprising all non-mitrato stylophorans (see discussion above; Table 1). Future phylogenetic analyses taking into account plate patterns of yet undescribed Furongian–Tremadocian taxa will probably clarify if 'Cornuta' can be maintained as a monophyletic order, grouping at least some of the seven clades of non-mitrato stylophorans (Amygdalothecidae, Ceratocystidae, Chauvelicystidae, Cothurnocystidae, Hanusiidae, Phyllocystidae, Scotiaecystidae).

Genus Milonicystis Chauvel, 1986

Type species. Milonicystis kerfornei Chauvel, 1986

Diagnosis. A genus of cornute stylophorans with an asymmetric cordiform theca made of 11 marginals delimited by an external peripheral flange; lower thecal surface unornamented, with
two longitudinally elongate infracentral areas; right infracentral area made of few, large elements, surrounded by M1, M1, M2, Mc, M3, M4 and Z; no spinal on M3; Z in central position, posteriorly in contact with M4; left infracentral area made of relatively large plates, delimited by M1, M2, M3, M4, D, G, M4 and Z; G and D incorporated into marginal frame, in close contact with each other or sutured; MS and M3 absent (lost); upper thecal surface comprising two adorals, numerous supracentrals, no pore structures; lower side of ossicles smooth to slightly keeled.

Remarks. Milonicystis was originally described as a mitrocystitid mitrate (Chauvel 1986), before being correctly re-evaluated as a cornute by Cripps & Daley (1994). Within cornutes, most phylogenetic analyses suggested amygdalothecid affinities, with Milonicystis closely related to Amygdalotheca and/or Nanocarpus (Cripps 1991; Daley 1992; Cripps & Daley 1994; Parsley 1997, 1998b; Ruta 1999b, 2003; Lefebvre 2005). This phylogenetic position was mostly supported by relatively similar thecal outlines, the possession of a posterior zygal plate in central position, and a comparable ornamentation (‘mushroom-like' spikes) on the supracentrals of A. griffei (see Ubaghs 1970) and M. kerfornei (see Cripps & Daley 1994).

The identification of skeletal homologies in stylophorans suggests that similar-looking cordiform, bilaterally symmetrical thecal morphologies were acquired convergently in various cornute lineages (Amygdalothecidae, Chauvelicystidae, Hanusiidae, and Phyllocystidae), probably in response to relatively comparable modes of life (see Lefebvre & Vizcaíno 1999; Lefebvre 2001, 2003a; Lefebvre et al. 2006; Noailles 2016). Within stylophorans, the central position of Z is not unique to amygdalothecids: this character also occurs, for example, in hanusiids, mitrates, 'Phyllocystis' jingxiensis, and the Tizagzaouine cornute (see above). However, in all amygdalothecids, mitrates and 'P.' jingxiensis, Z is posteriorly in contact with both M3 and G, because of the expansion and joining of these two marginals, posteriorly to
the zygal plate (Fig. 16c; Lefebvre & Ausich 2021). The situation is different in Milonicystis: Z is in contact with a single marginal (M₄), which is absent (lost) in both amygdalothecids and mitrates. Moreover, mushroom-like spikes on supracentrals are not unique to A. griffei and M. kerfornei, as they also occur in other cornutes, such as chauvelicystids (e.g. Sokkaejaecystis; see Lee et al. 2005). Milonicystis was also sometimes tentatively assigned to chauvelicystid cornutes, because of the presence of a Mc marginal, the absence of ornamentation on the lower thecal surface (protuberances, spikes), and the posterior opening of its marginal frame (see Lefebvre & Vizcaïno 1999; Lefebvre 2000a, 2001; Lee et al. 2005).

However, all these characters are widely distributed among stylophorans, and they cannot be used to support any close relationship with chauvelicystids. All chauvelicystids have spines articulated to the thecal frame, and a posterior zygal plate in marginal position (see below).

Future phylogenetic analyses of stylophorans will clarify the systematic position of Milonicystis. This taxon shares with hanusiids (Fig. 14) and the Tizagzaouine cornute (Fig. 15c) the possession of a zygal plate Z in central position and posteriorly in contact with M₄. Putative hanusiid affinities can be rejected, because of the absence of the M₄-M'₄ bar (main apomorphy of Hanusiidae) on the upper thecal surface of Milonicystis (see above; Lefebvre & Vizcaïno 1999). Milonicystis is morphologically closer to the yet undescribed Tizagzaouine cornute from the late Tremadocian of Morocco (see Ware & Lefebvre 2007; Lefebvre et al. 2016a), with which it shares a relatively unique plate pattern with Z in central position, D and G integrated into the marginal frame, and both M₄ and Mc on the right lower thecal side.

However, the two taxa are different: the Tizagzaouine cornute is more boot-shaped, it has a proto-lamellate organ on its upper surface, and its zygal plate is posteriorly in contact with both G and M₄. Consequently, Milonicystis is not assigned here to any stylophoran family. This genus probably derives from a Tizagzaouine cornute-like ancestor, and they could both form a small clade possibly related to hanusiids.
Two taxa are here assigned to *Milonicystis*: the type-species, *M. kerfornei* Chauvel, 1986 (late Darriwilian, France) and *M. reboulorum* sp. nov. (early Sandbian, Morocco). An earlier occurrence of *Milonicystis* (mid-late Floian) was reported by Lefebvre *et al.* (2016a), based on a single specimen (part and counterpart; ML20-269310) collected at Taichoute, in the upper part of the Fezouata Formation. Although incompletely preserved (partly disarticulated theca, proximal rings and associated stylocone), this specimen can be assigned to *Milonicystis*. This identification relies on the possession of a zygal plate Z in central position and posteriorly in contact with a single marginal, the morphology of marginals (wide skeletal elements, with a narrow peripheral flange) and ossicles (strongly notched abaxial flanks, elevated longitudinal median groove), the absence of ornamentation on the lower thecal side (knobs, protuberances, ...), the occurrence of mushroom-like spikes on supracentrals, and the absence of any pore-structures in the right anterior corner of the upper thecal surface.

*Milonicystis kerfornei* Chauvel, 1986

Figures 21a, 25a, 27–28, 29a–g

1986 *Milonicystis kerfornei* Chauvel, p. 79, figs. 1–2

1991 *Milonicystis kerfornei* Chauvel – Cripps, p. 347, figs 14, 15, 17, table 4

1992 *Milonicystis kerfornei* Chauvel – Daley, p. 144, fig. 15, table 2

1994 *Milonicystis kerfornei* Chauvel – Cripps & Daley, p. 113, figs 7–9, 10f, 16, pl. 3–4

1996d *Milonicystis kerfornei* Chauvel – Gil Cid *et al.*, p. 315, fig. 2.20

1997 *Milonicystis* sp. – Parsley, p. 230, fig. 6, appendix 2


1998b *Milonicystis* sp. – Parsley, p. 115

1999 *Milonicystis kerfornei* Chauvel – Lefebvre & Vizcaïno, p. 442
Holotype. IGR.PAL.15774.1 (coll. Chauvel & Nion): part and counterpart of an almost complete individual consisting of a fully articulated theca, proximal aulacophore, and posterior part of distal region (stylocone and two proximal-most ossicles; cover plates not preserved; Figs. 28c–d, 29a–b). Comparison of Chauvel’s original drawing of the lower thecal surface (Chauvel 1986, fig. 2A) with later photographs of latex casts of the same surface (see Cripps & Daley 1994, pl. 3 fig. 2) suggests that it is probably a reconstruction combining elements observed on the two opposite thecal surfaces. The same concretion has yielded a second well-preserved individual (IGR.PAL.15774.2), next to the holotype (Figs 28a, 29c). This additional individual also consists of a fully articulated theca, proximal rings, stylocone, and the next two ossicles (no cover plates).

Paratype. IGR.PAL.15167 (coll. Chauvel & Nion; Figs 28b, 29f–g): part and counterpart of a fully articulated theca (left anterior region not visible in upper aspect), with disrupted
proximal aulacophore, and partly disarticulated proximal portion of distal region (slightly
displaced stylocone and 5–6 next ossicles preserved in various orientations; no cover plates).

Other material. Two more specimens are available since the original description of *M.
kerfornei* (Chauvel, 1986) and its reevaluation by Cripps & Daley (1994). The first one,
IGR.PAL.15640 (coll. Chauvel; Figs 21a, 28e, 29d), was originally erroneously identified by
J. Chauvel as a poorly preserved individual of the mitrate *Mitrocystella incipiens miloni*. It
corresponds with a complete, slightly disarticulated theca and associated proximal
aulacophore, both in upper aspect (no counterpart). The second specimen, UCBL-FSL 170939
(coll. Guillou) contains two individuals side-by-side (part and counterpart). One is relatively
poorly preserved (UCBL-FSL 170939.2), but the other one consists of fully articulated
proximal rings inserted into a complete theca (UCBL-FSL 170939.1; Figs 28f, 29e).

Horizon and locality. All specimens were collected in the upper part of the Traveusot
Formation (Dw3, late Darriwilian), about 3 km E of Guichen, Ille-et-Vilaine, Brittany,
France. The holotype, the paratype and specimen IGR.PAL.15640 are from Traveusot (Fig.
20.4), whereas the fourth specimen (UCBL-FSL 170 939) was collected in the nearby locality
of le Domaine (Fig. 20.2).

Diagnosis. A species of *Milonicystis* with a relatively wide peripheral flange around regularly
curved marginal frame and thin, delicate lateral thecal walls; marginals, zygal plate and most
infracentrals particularly large; D and G in close contact and possibly sutured to each other;
supracentirals small and numerous, each ornamented with mushroom-like spike; proximal
aulacophore narrow, consisting of 5 to 6 rings.
Description. Heart-shaped, sub-triangular, moderately asymmetrical theca, with strongly
convex, almost rounded posterior extremity and antero-abaxial corners (Fig. 27). Right
antero-abaxial corner extending slightly more anteriorly than left one. Almost straight anterior
thecal margin, with short and shallow notch at aulacophore insertion. Left thecal side
relatively short, gently curved to almost straight. Right margin longer and more convex.
Lateral thecal walls low, thin, decreasing in height posteriorly, more or less parallel to thecal
outlines and borne on upper surface of particularly wide marginals. Lateral walls dividing
each marginal into two subequal fields: a flat to slightly downward recurved, relatively wide
external flange, and a flat internal region forming part of the floor of intrathecal cavity. Lower
thecal surface almost flat, without any ornamentation. All observed thecae about of the same
size (9.5 < TL < 12 mm; Fig. 25a), but with significant differences in outlines (Fig. 28), from
relatively broad (TL/TW ~ 1.1; e.g. IGR.PAL.15774.2, UCBL-FSL 170939.1) to more
elongate (TL/TW ~ 1.5: e.g. IGR.PAL.15167, IGR.PAL.15774.1).
Anterior marginals strongly unequal in size, with M₁ much smaller than M’₁. M₁ almost
pentagonal, with straight to slightly sinuous anterior margin, more or less parallel lateral and
subequal lateral sides, and two posteriorly converging distal edges protruding within right
infracentral area (Figs 28a–c, 29a, c, f). M’₁, wide, sub-hexagonal skeletal element forming
the anterior portion of zygal strut (Figs 28, 29a–g). In upper aspect, anterior portion of M₁
bearing thin right aulacophore apophysis, and abaxially to it, shelf for articulation with
overlying adoral (A₁). Abaxial shelf well-preserved in IGR.PAL.15640 (Fig. 28e, 29d), with
deep, drop-like infundibulum, and adaxially to it, funnel-shaped anterior transverse groove
(posteriorly) and deep, narrow anterior oblique groove (anteriorly). Anterior margin of M’₁
straight to slightly convex, with shallow adaxial notch at aulacophore insertion. M’₁ antero-
adaxially in contact with M₁ along gently curved, concave suture, and antero-abaxially with
M’₂. Postero-adaxial and postero-abaxial edges of M’₁ gently curved, in contact with right and
left infracentral areas, respectively. Posteriorly, long transverse contact between M'\textsubscript{1} and Z. In upper aspect, anterior portion of M'\textsubscript{1} bearing left aulacophore apophysis, and posteriorly to it, anterior portion of zygal crest. Zygal crest forming well-defined longitudinal ridge, increasing in height posteriorly (Figs 28f, 29e).

M\textsubscript{2}, wide skeletal element, forming rounded right antero-abaxial thecal corner, in contact with both M'\textsubscript{1} and Mc along two relatively short sutures, almost perpendicular to each other (Figs 28, 29a–g). Outer margin of M\textsubscript{2} strongly convex and much longer than opposite edge, along right infracentral area. Next two right marginals, Mc and M\textsubscript{3}, almost similar in shape and size, relatively elongate, with long and convex outer (abaxial) and inner (adaxial) edges, and much shorter, straight transverse sutures with other marginals (Figs 28, 29a–g). M\textsubscript{4}, hexagonal skeletal element, anteriorly in contact with M\textsubscript{3}, the right infracentral area and Z along relatively short, straight to gently curved sutures (Figs 28, 29a–g). Abaxial margin of M\textsubscript{4} straight, long, though slightly shorter than in Mc and M\textsubscript{3}. Postero-adaxial edge of M\textsubscript{4} long, strongly concave along left infracentral area. M\textsubscript{4} posteriorly in contact with glossal, along very short, straight suture. Inner (upper) surface of M\textsubscript{4} bearing a thin, low triradiate ridge, resulting from the confluence of lateral thecal wall and, almost perpendicularly to it, posterior part of zygal crest. Glossal, small, elongate, almost quadrangular marginal at posterior extremity of theca, abaxially sutured to M\textsubscript{4}, and adaxially in contact with digital along very short suture (Figs 28a–b, d–f, 29b–g). Anterior and posterior edges of G straight to gently curved.

M'\textsubscript{2} slightly wider than opposite marginal (M\textsubscript{2}), forming rounded left anterior corner of thecal frame (Figs 28, 29a–g). Adaxially, M'\textsubscript{2} largely in contact with M'\textsubscript{1}, and posteriorly, with left infracentral area. Anterior margin of M'\textsubscript{2} long and strongly convex. M'\textsubscript{2} posteriorly in contact with M'\textsubscript{3} along short, straight suture. Next two marginals, M'\textsubscript{3} and M'\textsubscript{4}, morphologically similar elongate elements, with straight to gently curved outer margins, and
more sinuous adaxial edges along contact with large infracentrals (Figs 28, 29a–g). M'_4 posteriorly sutured to narrow, elongate, gently arched digital forming posterior extremity of thecal frame with G. In most specimens, D slightly longer and more curved than G. Zygal plate in central position, particularly wide and elongate (Figs 28a–c, 29a, c, f). Z anteriorly in contact with M'_1 and posteriorly with M'_4, along relatively short and straight sutures. Lateral edges of Z strongly convex along left and right infracentral areas. Internal (upper) surface of Z bearing (most of) posterior part of zygal crest.

Right infracentral area narrow, longitudinally elongate, consisting of few, particularly large, polygonal, tessellate skeletal elements. In best preserved specimen (IGR.PAL.15774.2), right infracentral area consisting of five plates (Figs 28a, 29c). Number of right infracentrals possibly identical in holotype (Figs 28c, 29a). Two most posterior right infracentrals displaying similar sizes, morphologies, and contacts with surrounding thecal plates in three distinct individuals (IGR.PAL.15167, IGR.PAL.15774.1–2). Left infracentral area slightly more extensive, though narrow and longitudinally elongate. In IGR.PAL.15774.2 (Figs 28a, 29c), left infracentral area consisting of about 20 wide polygonal elements, some of them as large as right infracentrals, but most of them smaller.

Adorals not preserved, except in holotype (IGR.PAL.15774.1) with transversely elongate, quadrangular A_1 collapsed over anterior portion of underlying marginal M_1 (Figs 28d, 29b). Right (abaxial) edge of A_1 apparently bearing a small notch (right adoral orifice?) surrounded by a low ridge.

Supracentrals extremely numerous, small, polygonal and tessellate, most of them bearing a high central spike. Supracentral spikes 'mushroom-like' or 'bobin-shaped', consisting of a narrow 'stem' and a larger 'head' bearing one or several small spikes (Figs 28d, 29b, d–e, g). No pore-structures in right anterior corner of supracentral area. Periproct poorly preserved,
consisting of a small, cone-shaped pyramid located at posterior extremity of upper thecal surface, close to D-G suture (Figs 28d, 29b).

Proximal aulacophore short (~1.25 mm wide, and ~2 mm long), poorly preserved in most specimens, consisting of at least five (Fig. 29c), more likely six telescopic rings (Fig 29a–b).

Few small, quadrangular tectals preserved in holotype (Fig. 29a–b). Strongly recurved, transversely elongate inferolaterals forming lower and lateral walls of proximal rings (Figs 28f, 29a–b, e). Pair of anterior-most inferolaterals well-preserved in holotype (Fig. 29a–b), each with slightly raised distal margin, largely overlapping wide, proximal portion of long, funnel-shaped stylocone. Lower surface of stylocone and ossicles smooth, hemi-cylindrical (Fig. 29a), though faint, low longitudinal ridge possibly present (Fig. 29c). Upper surface of ossicles bearing deep longitudinal median groove, delimited abaxially by two high longitudinal ridges (Fig. 29b, d, g). Interossicular articulations flat, well-visible on disarticulated distal aulacophore of IGR.PAL. 15167 (Fig. 29f–g). Two opposite wing-like processes for cover plate insertion on lateral sides of each ossicle. Anterior portion of distal appendage poorly known, with only two (Fig. 29a, c) and up to five, possibly six ossicles (Fig. 29f–g). No cover plates preserved.

Remarks. The morphology of *M. kerfornei* was reevaluated here based on six individuals. Its revised reconstruction (Fig. 27) is largely congruent with previous ones produced by Chauvel (1986) and Cripps & Daley (1994), relying on one and three individuals respectively. However, reexamination of the original type material does not confirm some aspects of previous reconstructions. For example, Cripps & Daley (1994) suggested that four adorals were present in *Milonicystis*. If true this feature would have been unique in all styllophorans. However, their conclusion largely relies on the erroneous identification of the two small, slightly displaced, proximal-most tectals, interpreted as a pair of central adorals (‘y1’ and ‘y2’)
in the holotype (see Cripps & Daley 1994, p. 116). Although it was certainly present in *Milonicystis*, no evidence of the left adoral (A' 1) could be observed in all available specimens.

*Milonicystis reboulorum* sp. nov.

Figures 25b, 29h, 30

2008 *Milonicystis* sp. – Lefebvre et al., p. 11

2010a *Milonicystis*? sp. – Lefebvre et al., p. 8

Derivation of name. The species honors Véronique and Roland Reboul, who collected the holotype and unique specimen of *M. reboulorum*, as well as many other stylophorans in the Ordovician of Morocco.

Holotype. MHNM.15690.77 (coll. Reboul; Figs 29h, 30a): a complete, fully articulated individual in upper aspect (no counterpart) consisting of a theca, proximal aulacophore and relatively long portion of distal part, with closed cover plates articulated to underlying ossicles. Because of preservation in relatively coarse sandstones, fine details and delicate structures are not visible.

Horizon and locality. Single known specimen collected in the Izegguirene Formation (Sa1, lower Sandbian) at Bou Nemrou (ECR-F4), Jbel Tijarfaïouine Massif, about 30 km SW of Erfoud, eastern Anti-Atlas, Morocco (see above; Fig. 17.5).

Diagnosis. A species of *Milonicystis* with a relatively narrow peripheral flange and thick lateral thecal walls; gently curved marginal frame with slightly concave right posterior
margin; marginals and zygyal plate moderately wide; D and G in close contact but not sutured
to each other; proximal aulacophore large, consisting of seven rings.

Description. Asymmetrical, elongate, cordiform to slightly boot-shaped theca (TL = 14.5 mm,
TW = 10 mm), with relatively straight to gently curved left margin, much shorter than
opposite, right thecal side (Figs 25b, 30b). No evidence of ornamentation (e.g. knobs, spikes,
spinal blade) on lower surface of marginals. Anterior thecal outlines possibly straight to
gently concave, with right anterior corner extending more anteriorly than opposite, left
anterior corner. Posterior extremity of marginal frame rounded and almost closed (digital and
glossal adjoining but, apparently, not sutured to each other). Right thecal margin with shallow
re-entrant along M₄, separating long, strongly convex anterior part (along right infracentral
area) and much shorter, straight posterior portion (along left infracentral area). Marginal
frame surrounded by narrow peripheral flange, strongly decreasing in width posteriorly.
Lateral walls of theca particularly tall close to aulacophore insertion, decreasing in height
posteriorly, formed by thick, upright outer edges of marginals. Lower thecal surface divided
into two unequal, longitudinally elongate infracentral areas by narrow, slightly oblique, gently
curved strut.

Outlines and boundaries of marginals often difficult to identify precisely, because of coarse
preservation and absence of counterpart showing lower aspect of theca. Marginals apparently
stout, but relatively narrow. Anterior marginal M₁ largely hidden by overlying right adoral
(A₁), but apparently restricted to anterior thecal margin, along particularly wide aulacophore
insertion. M₂ poorly preserved, relatively short, narrow, forming rounded right anterior thecal
corner, and in contact with both M₁ and M₃ along short, straight sutures. Next two right
marginals, M₃ and M₄, narrow, of comparable size, both longer than M₂. M₃ convex and M₄
almost straight. M₃ posteriorly in contact with M₄ along short, straight suture. M₄ Y-shaped
marginal, with two short anterior branches in contact with Z (adaxially) and M₃ (abaxially)
and a longer posterior portion, distally sutured to the glossal. Posterior portion of zygal crest
borne on upper (internal) side of antero-adaxial branch of M₄. Glossal short, with blunt distal
tip, apparently not in contact with D.
M', relatively large, T-shaped, with anterior part at aulacophore insertion, and short, broad
posterior branch forming proximal portion of strut. Zygal branch of M'₁ with two unequal
lateral margins: left one long, mostly straight along right infracentral area, and right one
shorter, concave, along left infracentral area. Upper (internal) surface of M'₁ bearing low
anterior part of zygal crest. M'₁ posteriorly in contact with Z along short, straight suture. Left
thecal margin apparently made of four plates. M'₂, M'₃ and M'₄ relatively narrow, elongate,
more or less of the same size, although precise boundaries uncertain. M'₂ gently curved,
forming rounded left anterior corner of thecal frame. M'₃ almost straight. M'₄ bowed, with
short anterior part aligned with M'₃, and oblique, longer distal portion along posterior
extremity of left infracentral area. Digital short, narrow, elongate, with pointed distal tip,
almost in contact with G. Zygal plate Z in central position in contact with M'₁ (anteriorly) and
M₄ (posteriorly) along short, straight sutures. Precise morphology of Z on lower surface not
known, but apparently relatively elongate, narrow, sub-quadrangular. Internal (upper) surface
of Z bearing low zygal crest, slightly increasing in height posteriorly.
Two subequal, slightly depressed adorals (A'₁ and A₁) collapsed posteriorly to relatively
high aulacophore apophyses and anterior thecal walls, at aulacophore insertion. Small notch
(right adoral orifice?) apparently present on antero-abaxial edge of A₁.
Number and morphology of infracentral plates unknown. Left infracentral area wide,
longitudinally elongate, more or less crescent-shaped, with relatively narrow anterior and
posterior extremities, and maximum width at junction between distal branch of strut and
marginal frame. Abaxial border of left infracentral area regularly curved and convex from M'₁
(anteriorly) to D (posteriorly). Adaxial margin of left infracentral area gently curved and concave along zygal bar (anteriorly), and almost straight along G and distal branch of M₄ (posteriorly). Right infracentral area wide, longitudinally elongate, rhomb-shaped. Anterior sides of right infracentral area diverging posteriorly along M₂, M₁ and M'₁ (on the left) and M₂ and Mc (on the right), and posterior sides converging distally along M'₁, Z and M₄ (adaxially) and Mc, M₃ and M₄ (abaxially).

Large, discontinuous patches of poorly preserved supracentral area forming thin, reticulate membrane lying over upper (internal) surface of lower thecal side. Number and morphology of supracentrals unknown due to coarse grain of rock. No evidence of pore-structures in right anterior corner of upper thecal surface. Small cone-shaped, poorly preserved anal pyramid occurring at distal-most extremity of supracentral area, in between digital and glossal. Pyramid possibly consisting of few (5–10) platelets.

Proximal aulacophore unusually wide (~3.5 mm) and long (~5 mm) compared to thecal dimensions, and consisting of seven imbricate tetramerous rings. Each proximal ring made of two strongly arched inferolaterals forming its lower and lateral walls, and a pair of overlying small, quadrangular tectals. Each ring with raised oblique anterior lip, and depressed proximal 'neck', largely overlapped by next, more posterior ring. 'Spiny aspect' of proximal aulacophore resulting from raised anterior margins of successive rings. Stylocone funnel-shaped, elongate (~3 mm long), largely overlapped proximally by distal-most ring of proximal region. Lower aspect of ossicles unknown. Particularly long portion of fully articulated distal aulacophore preserved (~14.5 mm), consisting of stylocone and over 25 ossicles. Upper surface of ossicles hidden by almost complete, fully articulated left and right series of closed to slightly ajar ambulacral cover plates. Two pairs of opposite cover plates attached to stylocone, a single pair to each next ossicle. Cover plates poorly preserved, imperfectly fitting along upper mid-line. Within a same series, distal portion of each cover plate clearly overlapping proximal part
of next, more anterior element. No trace of putative ornamentation visible on cover plates.

Short portions of longitudinal median groove sometimes visible on upper surface of ossicles, where some cover plates are missing or displaced, e.g. at anterior-most, slightly recurved extremity of distal aulacophore.

Remarks. Although some aspects of its morphology are not documented, MHNM.15690.77 can be relatively unambiguously assigned to Milonicystis. This identification relies on the occurrence of similar plate patterns in the Moroccan specimen (Figs 29h, 30) and M. kerfornei (Fig. 27). In particular, they both share the possession of a zygal plate Z in central position, posteriorly sutured to a single marginal (M4). As in M. kerfornei: (1) the left infracentral area is delimited by M'1, M'2, M'3, M'4, D, G, M4 and Z; (2) the right infracentral area is surrounded by M'1, M1, M2, Mc, M3, M4 and Z; (3) M5 and M'5 are absent (lost); (4) M'4 and M4 are not forming a transverse strut on the upper thecal surface; and (5) pore-structures are absent.

Although M. kerfornei and M. reboulorum are morphologically close and about of the same size (TL ~10 mm), they also display some differences, which justify their identification as two distinct taxa. For example, in M. kerfornei, marginals are wide, lateral thecal walls are thin and delicate, and the proximal aulacophore is short and narrow (Fig. 27). In contrast, M. reboulorum is characterised by narrower, stouter marginals forming thick lateral thecal walls, and by a particularly wide and elongate proximal aulacophore (Fig. 30). It cannot be entirely excluded that these two contrasted morphologies represent ecophenotypes associated to different environmental conditions. M. reboulorum with its more robust theca and much larger proximal aulacophore (probably housing more powerful muscles) was living in more proximal settings and on coarser substrates than M. kerfornei. In contrast, the more delicate theca and small-sized proximal aulacophore of M. kerfornei possibly represent adaptations for life on fine-grained sediments, in more distal settings. The late Floian specimen of
Milonicystis sp. from Taichoute, Morocco (see above; Lefebvre et al. 2016a) is morphologically closer to *M. kerfornei* than to *M. reboulorum*.

**Family Amygdalothecidae** Ubaghs, 1970

*Diagnosis.* A family of cornute stylophorans with a posteriorly open, almost bilaterally symmetrical thecal frame; lower thecal surface unornamented, with two longitudinally elongate, unequal infracentral areas; right infracentral area delimited by *M'*1, *M*1, *M*2, *Mc*, *M*3 and *Z*; no spinal on *M*3; *Z* in central position, posteriorly in contact with *M*3 and *G*, or only with *M*3; left infracentral area in contact with *D*, *M'*4, *M'*3, *M'*2, *M'*1, *Z*, *G*, and sometimes with *M*3; *G* and *D* incorporated into marginal frame; *M*4, *M*5 and *M'*5 absent (lost); upper thecal surface comprising two adorals and no pore structures; strong downward-directed spike on lower side of proximal-most ossicles.

*Remarks.* As originally defined by Ubaghs (1970), the family Amygdalothecidae included all cornutes with a zygal plate *Z* in central position, a posteriorly open marginal frame (loss of *M*5 and *M*5'), and no pore structures on the upper thecal surface (e.g. *Amygdalotheca, Galliaecystis, Reticulocarpos*; see also Jefferies & Prokop 1972; Chauvel & Nion 1977; Ubaghs 1983, 1991; Derstler 1979; Martí Mus 2002). The same characters and the putative absence of *Mc* were used by Lefebvre & Vizcaíno (1999) to define the suborder Amygdalothecida, in which they identified two main subdivisions: Amygdalothecidae (with no *M'*4-*M*4 bar on the upper thecal surface: *Amygdalotheca, Beryllia, Domfrontia, Nanocarpus*), and Hanusiidae (with a *M'*4-*M*4 posterior bar: *Galliaecystis, Hanusia, Prokopicystis, Reticulocarpos*) (see also e.g. Lefebvre 2000a, 2001). In the last 20 years, the description of Furongian cornutes with previously unrecorded plate patterns confirmed the
probable monophyly of these two families (see above). However, the morphology of
Drepanocarpos suggests that early hanusiids possessed a Mc marginal (see above; Fig. 14a–
b). The plate pattern of 'Phyllocystis' jingxiensis (Fig. 16a) indicates that the cothurnocystid
marginal Mc was also present in both amygdalothecids and mitrates (Lefebvre & Ausich
2021). Moreover, the morphology of 'P.' jingxiensis also suggests that the central position of
Z is homoplastic in both Amygdalothecidae and Hanusiidae (see above). Consequently, these
two families are probably not closely related to each other, and the suborder Amygdalothecida
is not retained here as a valid taxonomic group.

Most phylogenetic analyses have suggested that Amygdalotheca and Nanocarpus were
closely related to Milonicystis, the three forming a well-defined clade: 'unnamed taxon 1'
(Cripps 1991; Daley 1992) or Amygdalothecinae (Cripps & Daley 1994; see also Ruta 2003;
Lefebvre 2005). As argued above, Amygdalotheca griffei, Milonicystis kerfornei and
Nanocarpus dolambii share three features (i.e. heart-shaped thecal outlines, loss of pore
structures, Z in central position). However, all these characters are widely distributed in
stylophorans, and thus, cannot be considered apomorphies uniting these three taxa in a clade
(see above). Plate homologies suggest that Z is posteriorly sutured to M₄ in Milonicystis (Figs
27, 30), but to both M₃ and G in Amygdalotheca (Fig. 16c). Pending a global phylogenetic
analysis of stylophorans taking into account the plate patterns of Furongian taxa, available
evidence suggests that Milonicystis is probably more closely related to the undescribed
Tizagzaouine cornute (see above) than to amygdalothecids.

Three genera are assigned here to the family Amygdalothecidae: Amygdalotheca Ubaghs,
1970, Domfrontia Cripps & Daley, 1994 and Nanocarpus Ubaghs, 1991. Amygdalotheca (Fig.
3b) is the earliest representative of the family. This monospecific genus is known from the
late Tremadocian of France (Montagne Noire; Ubaghs 1970; Vizcaíno & Lefebvre 1999) and
Morocco (Anti-Atlas; Lefebvre et al. 2016a). A. griffei is the only amygdalothecid retaining a
zygal plate Z posteriorly in contact with both M and G (plesiomorphic condition, as in 'P. jingxiensis' and mitrates; see Lefebvre & Ausich 2021). The possession of serial homologues of D and G on both sides of the anal opening probably represents an autapomorphy of Amygdalotheca (Fig. 16c).

*Nanocarpus* (Figs 31–32, 33a) is known in the late Floian of the Montagne Noire, France (*N. dolambii*; Ubaghs 1991; Vizcaíno & Lefebvre 1999) and possibly also in the late Tremadocian of the Anti-Atlas, Morocco (*N. cf. dolambii*; Lefebvre et al. 2016a). This genus was also reported in the Furongian of Guangxi, South China (*N. guoleensis*; Han et al. 2000; Chen et al. 2008). This identification largely relied on the occurrence of a posteriorly open marginal frame, strong spines on ossicles, and a zygal plate Z in central position. However, reexamination of original specimens of this Furongian stylophoran indicates that 'N. guoleensis' is characterised by particularly wide adorals (Lefebvre & Ausich 2021). Moreover, the frequent preservation of its distal aulacophore in flexed position over the theca implies the presence of relatively complex interossicular articulations in 'N. guoleensis' (Lefebvre & Ausich 2021). Consequently, these two characters strongly support the view that 'N. guoleensis' more likely represents an early mitrate rather than an amygdalothecid cornute (*Zamora et al. 2013b; Lefebvre et al. 2016b; Zhu et al. 2016*). The morphology of 'N. guoleensis' also suggests that amygdalothecids and mitrates both probably derive from a common, 'P. jingxiensis'-like ancestor (Lefebvre & Ausich 2021). Although mitrates were long considered as deriving from amygdalothecids (see e.g. Cripps 1988; Parsley 1991, 1997, 1998b; Ubaghs 1991; Ruta 1999a, b, 2003), it is more likely that these two clades are sister-groups (Lefebvre & Ausich 2021).

The late Katian cornute from Morocco initially reported by Chauvel (1971) as 'AVII' was formally described as *Juliaecarpus milnerorum* by Ruta (1999a), who pointed out strong morphological similarities between this taxon and the three amygdalothecid genera *Beryllia,*
Domfrontia and Nanocarpus. Ruta (1999a, p. 77) was also the first to question the accuracy of the reconstructions proposed by Cripps & Daley (1994) for Beryllia and Domfrontia. Juliaecarpus was later considered as a junior synonym of Nanocarpus by Lefebvre (2001), because J. milnerorum and N. dolambii display similar thecal plate patterns (see also Lefebvre 2003a, 2007a; Lefebvre et al. 2007; Noailles 2016). So as to clarify the systematic position of Juliaecarpus within amygdalothecids, the morphologies of Beryllia, Domfrontia, and Nanocarpus were all reevaluated here.

In his original description of N. dolambii, Ubaghs (1991) provided accurate camera-lucida drawings of the holotype (UCBL-FSL 712529) and photographs of three specimens (including the holotype), but no reconstruction. Although exquisitely preserved in the shales of the Landeyran Formation, the original material examined by Ubaghs (1991) is semi-articulated, with some thecal plates slightly displaced or collapsed (taphonomic grade 1 sensu Martin et al. 2015). A reconstruction of Nanocarpus dolambii is proposed herein (Fig. 31), based on the original type material (now deposited in Lyon under UCBL-FSL registration numbers) and numerous additional specimens collected in the last 30 years (coll. Lefebvre, Vizcaïno; Figs 32, 33a). The resulting morphology is an elongate, sub-quadrangular, almost bilaterally symmetrical theca, with a relatively straight right margin, and a posteriorly recurved left side. The central position of the zygal plate Z is confirmed, as well as its contact with both M'1 (anteriorly) and M3 (posteriorly; no suture with G). The main difference with previous figures of N. dolambii (e.g. Ubaghs 1991; Parsley 1997; Lefebvre & Vizcaïno 1999; Ruta 1999a, b; Lefebvre 2001; Martí Mus 2002) concerns the posterior extremity of the theca, which is much wider than in the slightly disarticulated holotype. As pointed out by Ubaghs (1991), all integumentary areas of Nanocarpus consist of a thin reticulate membrane, possibly made of several large, polygonal, tessellate skeletal elements with indistinct boundaries.
In this study, the reexamination of the original type material of *Beryllia miranda* Cripps & Daley, 1994 and *Domfrontia pissotensis* (Chauvel & Nion, 1977) not only confirmed Ruta's (1999a) doubts about the validity of their reconstructions by Cripps & Daley (1994), but it also suggested that these two taxa, which occur in the same locality and within the same strata, are very likely conspecific. Cripps & Daley (1994, p. 102, 108) acknowledged that skeletal remains of *B. miranda* and *D. pissotensis* were often difficult to assign precisely to one of these two taxa. Reexamination of the original type material indicates that most of the morphological differences between *Beryllia* and *Domfrontia* pointed out by Cripps & Daley (1994) are taphonomic. Best preserved individuals were generally identified as *Beryllia* (e.g. BMNHUK.E.63496.1–2, IGR.PAL.15701; see Cripps & Daley 1994, pl. 2 figs 1–6), whereas more disarticulated ones were assigned to *Domfrontia* (e.g. IGR.PAL.15702; see Cripps & Daley 1994, pl. 1 figs 5–6). Consequently, *Beryllia* is considered a junior synonym of *Domfrontia*. The morphology of *D. pissotensis* was reevaluated and a new reconstruction is proposed (see below).

The reevaluation of the thecal patterns of *Domfrontia* and *Nanocarpus* indicates that they are both composed of homologous 13 major skeletal elements (M'_1, M'_2, M'_3, M'_4, D, Z, M_1, M_2, M_c, M_3, G, A'_1 and A_1), which display identical contacts (e.g. Z sutured only with M'_1 and M_3). Consequently, *Domfrontia* Cripps & Daley, 1994 can be considered as a junior synonym of *Nanocarpus* Ubaghs, 1991. However, a generic distinction between these two taxa is tentatively maintained here, based on differences in the plating of integumentary areas. In *Nanocarpus* (Fig. 31–32, 33a), both infracentral and supracentral surfaces are thin, flexible, retiform membranes without any obvious plate boundaries (see above). In *Domfrontia* (Figs 33b–c, 34–42), integumentary areas consist of several, relatively large polygonal elements, one of them being particularly wide and closely associated to the anal opening. Ruta (1999a, p. 75) was probably the first to correctly identify such an anal plate in *D. pissotensis*. 
However, he considered that this skeletal element was of supracentral origin and was thus a 'suranal plate' (see Ruta 1999a). This identification is not confirmed by the reexamination of the original material of Domfrontia, which rather suggests that an anal plate is present, but at the posterior extremity of the lower thecal surface (see e.g. specimen BMNHUK.E.63499; Cripps & Daley 1994, pl. 2 fig. 3). This large skeletal element is thus more likely of infracentral origin, and should be more properly designated as a 'subanal plate'. Similar subanal plates formed by elements of the left infracentral area have been acquired, independently, in other stylophoran lineages: e.g. in kirkocystid (Anatifopsis, Balanocystites; see Jefferies 1986; Lefebvre 2001, 2003a) and early mitrocystitid mitrates (Chinianocarpos; Ubaghs 1970; Jefferies 1986; Lefebvre 2000c, 2001).

Ruta (1999a, p. 76) questioned the possible occurrence of a similar anal plate in Nanocarpus dolambii, based on the presence of a 'posterior pouch' between D and G in the holotype (see Ubaghs 1991, figs 2, 3a–b). Reexamination of the abundant available material of N. dolambii provided no definitive evidence supporting the presence of an anal plate in this cornute. In the holotype of N. dolambii, the 'posterior pouch' is taphonomic and results from the slight disarticulation of distal-most marginals and the pinching of the distal extremity of integumentary areas between D and G (Figs 32a–b, 33a). In N. dolambii, the absence of clear boundaries between integumentary elements and the lack of any distinct subanal plate are probably original and not taphonomic artefacts. All specimens of Nanocarpus are preserved in fine-grained sedimentary rocks (fine siltstones and shales of the Landeyran Formation) preserving minute original anatomical details (e.g. the delicate stereom microstructure of infra- and supracentraals), as well as remains of lightly sclerotised arthropods and annelids.

Consequently, the occurrence of a subanal plate is considered here as the main morphological character supporting Domfrontia as a valid genus, distinct from the otherwise very similar and closely related cornute Nanocarpus.
In this context, the reevaluation of the abundant original material of *Juliaecarpus milnerorum* from Tizi n’Takrit (Lower Second Bani Formation) and the observation of numerous additional specimens of *J. milnerorum* from Khabt-el-Hejar (Upper Tiouririne Formation) confirm that its theca is made of the same 13 main skeletal elements as in *Nanocarpus* (see Lefebvre 2001, 2003a). However, the occurrence of integumentary areas consisting of distinct polygonal elements including a well-defined anal plate suggests that *Juliaecarpus Ruta, 1999a* is a junior synonym of *Domfrontia Cripps & Daley, 1994*. As in *D. pissotensis*, the anal plate of *D. milnerorum* corresponds to a large skeletal element occurring at the distal extremity of the left infracentral area (see Ruta 1999a, pl. 3 figs 2–3, 5, pl. 4 figs 1–2). It is thus a subanal plate. This element was previously considered as supracentral in origin, and interpreted as a suranal plate (Ruta 1999a; Lefebvre 2001, 2003a). This erroneous identification probably results from the preservation of the two delicate integumentary areas, tightly pressed against each other in the posterior part of the theca (see Ruta 1999a, p. 54). In upper aspect, the outlines of the subanal plate are thus frequently clearly visible through the thin and flexible overlying supracentral elements (see Ruta 1999a, pl. 2 fig. 4, pl. 5 fig. 2).

However, in several specimens, the occurrence of supracentrals above the anal plate demonstrates that it is of infracentral origin (e.g. BMNHUK.EE.3119; see Ruta 1999a, figs 4C, pl. 1 fig. 5, pl. 7 fig. 4). Moreover, in some other individuals, the posterior extremity of the upper thecal surface is not disrupted and consists of several, polygonal supracentrals (e.g. BMNHUK.EE.3101; see Ruta 1999a, pl. 1 fig. 1).

Genus *Domfrontia Cripps & Daley, 1994*

*Type species.* *Reticulocarpos pissotensis* Chauvel & Nion, 1977
Diagnosis. A genus of amygdalotheccids with Z posteriorly in contact with a single marginal 
(M₃); left infracentral area in contact with D, M', M', M'₂, M', Z, M₃ and G; integumentary 
areas made of large, distinct polygonal skeletal elements; G and D particularly small, on both 
sides of wide, elliptical, posterior subanal plate.

Remarks. Domfrontia is a long-ranging genus of small-sized amygdalotheccid cornutes, 
particularly widespread in most areas of the Mediterranean Province in the Middle–Late 
Ordovician time interval. Two species were described in the Darriwilian–early Sandbian of 
the Armorican Massif, France (D. pissaotensis, see below; Chauvel & Nion 1977; Cripps & 
Daley 1994; Lefebvre 2000a) and the Katian of the Anti-Atlas, Morocco (D. milnerorum, see 
below; Ruta 1999a). Additional occurrences of Domfrontia are also reported here from the 
Darriwilian of Ossa Morena, Spain (D.? sp., see below) and the Katian of Bohemia, Czech 
Republic (D. aff. milnerorum, see below). Beryllia Cripps & Daley, 1994 and Juliaecarpus 
Ruta, 1999a are considered here as junior synonyms of Domfrontia Cripps & Daley, 1994 
(see discussion above).

*Domfrontia milnerorum* (Ruta, 1999a)

Figures 8, 18e, 25c, 33b–c, 34–37

1971 genre indéterminé AVII – Chauvel, p. 56, fig. 3f

1978 Mitrata indet. – Chauvel, p. 61, fig. 14

1999 undescribed form from the Llandeilo [sic] – Lefebvre & Vizcaíno, p. 440

*1999a* Juliaecarpus milnerorum Ruta, p. 53, figs. 1–8; pl. 1–8

2001 Nanocarpus milnerorum (Ruta) – Lefebvre, p. 612, figs. 14.1–2

2002b Juliaecarpus milnerorum Ruta – Domínguez et al., p. 51
Holotype. BMNHUK.EE.3070 (coll. Destombes-Jefferies-Savill): part and counterpart of an almost complete individual displaying partly disarticulated theca, poorly preserved proximal aulacophore, stylocone and three next ossicles in lateral aspect, without cover plates (see Ruta 1999a, pl. 3 fig. 1, pl. 7 fig. 2).

Other material. Additional study material comprises 122 numbered specimens (representing over 200 individuals) collected in two distinct localities and stratigraphic levels. Most of them (84 specimens) are from Tizi n’Takrit (Destombes locality 756, Second Bani Formation). This late Katian material includes specimen IGR.PAL.16697 (coll. Destombes), originally described and figured by Chauvel (1971, fig. 3f) as a possible kirkocystid mitrate (gen. indet. AVII). It corresponds to a single individual (part and counterpart) consisting of some disarticulated thecal plates (M₂, M’₁, M’₂, M’₃ and M’₄), disrupted proximal rings, and poorly preserved proximal-most ossicles (Figs 33b–c, 36a). All other 83 specimens from Tizi n’Takrit represent the original material used by Ruta (1999a) for the description of D. milnerorum: BMNHUK.EE.3069, 3071–75, 3079–81, 3083–86, 3088–90, 3093–95, 3098, 3101–05, 3108–09, 3111-17, 3121-25, 3127, 3129, 3131-32, 3134-41, 3143-47, 3149-50, 3152-53, 3155, 3157–58, 3160–64, 3166–71, 3173, 3175–78, 3180–81, 3183–84 (coll. Destombes-Jefferies-Savill). Although they are preserved in fine argillites, most individuals
are more or less strongly disarticulated, with thecal plates collapsed and/or displaced, proximal rings often disrupted, and more distal parts of the aulacophore generally missing (taphonomic grade 3 sensu Martin et al. 2015; see above). The other 38 specimens of D. milnerorum were collected in the coarse sandstones of Khabt-el-Hejar (Van Roy's locality E2, Upper Tiouririne Formation): AA.KEH.OS.6–36 (31 specimens, 122 individuals; coll. Lefebvre; see Fig. 19) and MHN.M.15690.126–132 (7 specimens, 9 individuals; coll. Reboul). Most individuals are complete and fully articulated (theca, proximal and distal aulacophore; taphonomic grades 1-2 sensu Martin et al. 2015; see above), but the associated coarse lithology prevents the preservation of fine morphological features.

Horizons and localities. The holotype and 84 specimens were collected about 10 m above the base of the Lower Second Bani Formation (Ka4, late Katian), at Tizi n'Takrit (Destombes locality 756), about 8 km SW of Tazarine, central Anti-Atlas, Morocco (Fig. 17.7). The other 38 specimens are from the Upper Tiouririne Formation (Ka2, early Katian), Khabt-el-Hejar section (Van Roy's locality E2), about 15 km E of Erfoud, eastern Tafilalt, Morocco (Fig. 17.6).

Diagnosis. A species of Domfrontia with weakly pronounced denticulations on lateral margins of M2 and M’2; M2 relatively elongate, slightly shorter than M’2; integumentary plates relatively large; proximal aulacophore consisting of six rings; ossicular spikes long, laterally compressed, and sharp.

Description. Theca moderately elongate (TL/TW ~1.45), with sub-elliptical, almost bilaterally symmetrical outlines (Fig. 35). Anterior thecal margin relatively wide, straight to slightly concave, with shallow median notch at aulacophore insertion. Posterior margin much
shorter, almost straight to slightly convex. Antero-abaxial thecal corners rounded, with left one extending more anteriorly than right one. Lateral margins regularly convex, gently curved with right one slightly more arched than left one. Maximum thecal width (TW) across Mc and $M_3'$ (Fig. 25c). Thecal walls slightly higher anteriorly, regularly decreasing in height distally. Lower thecal side almost flat to very slightly concave, without any ornamentation, except a series of low, regular knobs along abaxial margins of $M_2$ and $M_2$, best preserved in Tizi n'Takrit specimens (e.g. BMNHUK.EE.3069, 3072, 3129). Upper thecal surface flat to gently convex (e.g. AA.KEH.OS.14b, 20, 27, 32r). Specimens from Tizi n'Takrit larger ($7 < TL < 10$ mm; mean value $\sim 8.5$ mm) than those from Khabt-el-Hejar ($2 < TL < 9$ mm; mean value $\sim5.2$ mm). No significant morphological difference within each assemblage (no obvious allometries), as well as between the two assemblages.

Marginal frame delicate, rigid, posteriorly closed by wide subanal plate of infracentral origin, at distal extremity of lower thecal surface (Fig. 35). Marginals 10 (5 on the left, 5 on the right), relatively narrow, elongate, made of porous, reticulate stereom. Anterior thecal margin almost entirely made by $M_1$ and $M'_1$. Lower surface of anterior marginals almost flat, except low, downward recurved transverse lip, posteriorly to aulacophore insertion (e.g. BMNHUK.EE.3129). Each anterior marginal bearing relatively high, cup-shaped, anteriorly concave apophysis, adaxially and posteriorly to aulacophore insertion (e.g. BMNHUK.EE.3072, 3077, 3101, 3144). Abaxially to apophyses, anterior edges of both $M_1$ and $M'_1$ forming high shelves for insertion of adorals. $M_1$ short, broad, quadrangular, moderately elongate transversely (Fig. 36d), with internal structures (infundibulum, anterior oblique and transverse grooves) on upper surface of anterior abaxial shelf (e.g. AA.KEH.OS.24a). Anterior and posterior edges of $M_1$ sinuous to gently convex. $M_1$ laterally in contact with $M'_1$ (adaxially) and $M_2$ (abaxially) along short, straight sutures. $M_2$ longer and more elongate than $M_1$, forming rounded right anterior thecal corner (Figs 34, 36–37). Lateral
edge of M₂ bearing several (4–5), regularly spaced, downward directed low tubercles (e.g. BMNHUK.EE.3072, 3129, 3144). Next two right marginals, Mc and M₃, almost of the same length, and both longer than M₂ (Figs 34, 36b–f, 37). Lateral edges of Mc and M₃ sharp, without any knob. Mc sub-quadrangular, elongate, gently arched, with a slightly convex abaxial margin. M₃ with similar morphology, but with more sinuous left (adaxial) and posterior margins, along sutures with Z, subanal plate and G (e.g. AA.KEH.OS.20, BMNHUK.EE.3178). Glossal very small, short, sub-triangular elongate distal process with a blunt distal end, closely associated to M₃ and subanal plate (e.g. BMNHUK.EE.3178).

Anterior portion of M'₁ contributing equally as M₁ to anterior portion of marginal frame. M'₁ also forming long and relatively large anterior part of zygal bar on lower thecal surface (Figs 33b, 34b, d–i, 36a, d–f, 37a, c–f). Internally, M'₁ bearing anteriorly left portion of anterior transverse groove (posteriorly to left apophysis) and, posteriorly, anterior portion of zygal crest (e.g. AA.KEH.OS.24a, BMNHUK.EE.3101, 3143). On internal (upper) surface of M'₁, zygal crest very low anteriorly, regularly increasing in height distally (e.g. BMNHUK.EE.3101, 3143). M'₁ particularly elongate, with straight to slightly concave margin along right infracentral area, and longer, more sinuous edge along left infracentral area. M'₁ in contact with M₁ (adaxially), Z (posteriorly), and M'₂ (abaxially) along short, straight sutures. M'₂ elongate, strongly arched, forming rounded left antero-abaxial thecal corner (Figs 34, 36–37). M'₂ slightly longer than opposite marginal M₂, but similarly ornamentated with a series of low knobs on its abaxial edge (e.g. BMNHUK.EE.3069, 3072).

Next left marginal (M'₃) about as long as M'₂, but sub-quadrangular, elongate, almost straight to weakly curved, with a gently convex abaxial margin (Figs 36, 37a–b, e–f). M'₄ similarly shaped as M'₃, but slightly longer than both M'₂ and M'₃ (Figs 36b–f, 37a–c, e–f). M'₄ posteriorly in contact with both D and subanal plate (e.g. BMNHUK.EE.3101). Digital
particularly small, sub-triangular, with blunt distal extremity, inserted in between large subanal plate and posterior margin of M'_4 (e.g. BMNHUK.EE.3101).

Lower thecal surface divided into two unequal fields by oblique zygal strut made of two plates (M'_1 and Z). Z elongate, sub-pentagonal, in central position, forming posterior part of zygal bar (Figs 34, 36c–f, 37a, c–e). Anterior part of Z slightly narrower, proximally in contact with M'_1, and with two elongate, slightly concave lateral edges along left and right infracentral areas. Distal part of Z larger, in contact with both M_3 and subanal plate. Internal (upper) surface of Z bearing posterior portion of relatively high zygal crest (e.g. AA.KEH.OS.15f, BMNHUK.EE.3072, 3178). Left and right infracentral areas relatively large, longitudinally elongate, with left one more extensive than right one. Both integumentary areas paved with relatively large, thin, polygonal plates made of retiform, porous stereom, forming tessellate, unorganised surfaces (Fig. 34a, c). No obvious difference in size between left and right infracentrals. Particularly wide, sub-elliptical subanal plate at posterior extremity of left infracentral area, in contact with Z, M_3, G, D, and M'_4 (Figs 34, 36b–f, 37a–b, e–f). Lower surface of subanal plate almost flat to slightly concave, with delicate radiating fringe along its long, gently curved posterior margin (e.g. BMNHUK.EE.3178).

Adorals (A'_1 and A_1) thin, elongate, forming low arch above aulacophore insertion. Left adoral slightly longer than right one (Fig. 36e–f, 37a–b, d, f). Right adoral orifice (hydropore) in antero-abaxial corner of A_1, above infundibulum borne on underlying anterior shelf of M_1 (Figs 34b, 36f). Supracentral area forming thin, flexible polyplated membrane showing oblique course of underlying zygal crest (Figs 34b, d–i, 36b–c, e–f, 37a, c–f). Supracentrals fewer and larger than infracentrals, tessellate, unorganised, with particularly porous, retiform microstructure. Supracentrals apparently decreasing in size antero-posteriorly (e.g. BMNH.EE.3072, 3119, 3144). No pore structures on upper thecal surface. Anal opening
probably slit-like, at distal extremity of supracentral area, along and immediately above posterior margin of subanal plate.

Proximal aulacophore relatively broad, slightly longer than wide, consisting of four telescopic rings in smallest observed individuals (e.g. AA.KEH.OS.10a, TL=2.6 mm). In larger specimens, proximal appendage consistently made of six imbricate rings (Figs 34a–f, 36d–e, 37b–d). Each proximal ring consisting of four plates: two symmetrical, arched inferolaters forming its lower and lateral walls, and above them, two smaller, almost quadrangular tectals. Distal aulacophore comprising stylocone and at least three ossicles (Fig. 34f), but probably more, as suggested by long, poorly preserved distal portions of appendage (e.g. 5 or 6 ossicles in AA.KEH.OS.18b). Cover plates absent in Tizi n'Takrit specimens, possibly preserved in Khabit-el-Hejar material, but too poorly preserved for description.

Stylocone funnel-shaped, moderately elongate, with long, straight, laterally compressed median spike at anterior extremity of its lower surface (e.g. BMNHUK.EE.3101, 3121, 3146). Similarly-shaped, though slightly shorter spikes on lower surface of, at least, next three ossicles (e.g. BMNHUK.EE.3101, 3175). Well-defined, deep longitudinal median groove, with no obvious transverse channels, on upper surface of stylocone and ossicles (Fig. 37a–d).

Remarks. Almost all specimens from Tizi n'Takrit are more or less strongly disarticulated (see above; Chauvel, 1971; Ruta 1999a): marginals are displaced, supracentrals are collapsed over internal side of lower surface, proximal rings are disrupted, and distal aulacophore is often absent. However, preservation of this material in fine argillites made it possible to capture minute morphological details (e.g. knobs on M₂ and M'₂, porous stereom microstructure of skeletal elements, ossicular spikes). In contrast, most specimens from Khabit-el-Hejar are fully articulated, but their occurrence in coarse sandstones hampers the preservation of fine morphological details. Although their taphonomy is different and they occur in distinct
stratigraphic levels, the two assemblages of small amygdalothecids from Khabt-el-Hejar (Upper Tiouririne Formation, early Katian) and Tizi n’Takrit (Lower Second Bani Formation, latest Katian) are here assigned to the same species, *D. milnerorum*. This identification relies on the strong morphological similarities between individuals of the two localities: identical thecal platings (same major skeletal elements with equivalent morphologies, contacts, and relative proportions) and similarly-built aulacophore (six proximal rings, same ornamentation on distal ossicles).

The main morphological difference between the two assemblages is the mean size of individuals: specimens from Tizi n’Takrit (7 < TL < 10 mm; mean ~8.5 mm) are significantly larger than those from Khabt-el-Hejar (2 < TL < 9 mm; mean ~5.2 mm). This difference possibly results from a sampling bias. For example, the comparison of the mean size of individuals of *D. milnerorum* belonging to the Marrakesh (AA.KEH.OS) and Marseille (MHNM) collections are different, although they were all sampled in the same locality and same levels (Fig. 19). The mean size of Marseille specimens (TL ~7.5 mm) is significantly larger than that of Marrakesh specimens (TL ~4.8 mm). This discrepancy can be explained by different sampling strategies, with the Marseille collection biased towards the largest and best preserved individuals, whereas the Marrakesh one corresponds to a more exhaustive sampling. Consequently, it cannot be entirely excluded that a similar sampling bias towards larger, more eye-catchig specimens occurred with the Tizi n’Takrit material. However, the observed range of sizes in this locality (TL comprised between 7 and 10 mm) remains higher than for Marseille specimens from Khabt-el-Hejar (TL comprised between 5 and 8.5 mm).

The larger size of Tizi n’Takrit individuals is thus possibly related to an evolutionary trend towards an increase in body size through time (Cope’s rule) and/or the consequence of different environmental conditions (e.g. food and oxygen availability, temperature). Similar drastic intraspecific variations in body size have been documented in stylophorans (Lefebvre...
2007a; Lefebvre & Botting 2007; Lefebvre et al. 2016a). For example, the mitrate *Lagynocystis pyramidalis* is about twice larger in the Šárka and Dobrotivá formations (Darriwilian, Bohemia) than in the Landeyran Formation (late Floian, Montagne Noire) (Lefebvre 2007a). Similarly, specimens of the mitrate *Peltocystis cornuta* are significantly smaller in the Fezouata Formation (late Tremadocian, Morocco) than in the Saint-Chinian Formation (late Tremadocian, Montagne Noire) (Lefebvre & Botting 2007). Consequently, the observed differences in size between cornutes of the Tizi n’Takrit and Khabt-el-Hejar assemblages do not prevent them to be assigned to the same species.

The revised reconstruction of the morphology of *D. milnerorum* (Fig. 35) is largely congruent with the one originally proposed by Ruta (1999a). The main differences concern the position of the anal plate (here considered as of infracentral rather than of supracentral origin; see discussion above) and the general aspect of the theca. The more elongate thecal outlines in Ruta's (1999a) reconstruction of *D. milnerorum* (TL/TW ~1.7), probably result from the preservation of Tizi n’Takrit specimens. Almost all of them (including the holotype) are more or less disarticulated, with lateral marginals very often collapsed adaxially. The broader thecal outlines proposed here for *D. milnerorum* (TL/TW ~1.45) are based on those of the fully articulated specimens from Khabt-el-Hejar. This broader aspect is compatible with the morphology of some weakly disarticulated, better preserved individuals from Tizi n’Takrit, also characterised by a TL/TW ratio close to 1.5 (e.g. BMNHUK.EE.3144).

**Domfrontia aff. milnerorum** (Ruta, 1999a)

Figures 21e–g, 38, 39a–d

**Material.** Registered specimens include three almost complete, slightly disarticulated small amygdalothecid cornutes (coll. Zicha). CGS.OZ.123 (Figs 21e, 38a–b, 39a–b) corresponds to
a tiny, slightly collapsed theca (TL = 2.6 mm), with some nearby aulacophore fragments (part and counterpart). CGS.OZ.153 (Figs 21f, 38c, 39c) comprises an almost complete theca (TL = 5 mm) with slightly displaced marginals and part of the aulacophore (proximal rings, stylocone, first ossicle and one isolated cover plate; part and counterpart). CGS.OZ.154 (Figs 21g, 38d, 39d) displays a weakly disarticulated theca (TL = 4.7 mm) and three proximal rings, in upper view (no counterpart).

Horizons and localities. Two specimens (CGS.OZ.153, 154) were collected in the Zahořany Formation (Ka1, early Katian), at Levín (Fig. 22), Králův Dvůr, Bohemia (Czech Republic). The third one (CGS.OZ.123) was found in the Králův Dvůr Formation (Ka3–4, late Katian) at Nová Vráž - Černošice (Fig. 22), Bohemia (Czech Republic). Recently, several additional specimens of small amygdalothecids (some complete individuals, numerous isolated plates) were collected in the same two stratigraphic units in Bohemia (O. Zicha, pers. obs., late 2019–early 2020), as well as in the Bohdalec Formation (Ka2, early Katian). Preliminary observation of this additional material suggests that it very likely belongs to the same taxon as the three specimens preliminary described here as *Domfrontia aff. milnerorum*.

Description. Theca very small (2.6 < TL < 5 mm), moderately elongate, with almost bilaterally symmetrical outlines (Fig. 38). Anterior margin apparently straight, with shallow concavity at aulacophore insertion. Lateral thecal edges gently curved, moderately convex, converging posteriorly to short, straight to slightly convex distal margin. Right lateral side possibly less convex than left one. Marginal frame relatively low, decreasing in height posteriorly. All thecal plates (marginals, integumentary elements) consisting of particularly porous retiform stereom. Upper thecal surface depressed, due to collapse of supracentrals over almost flat internal (upper) side of lower thecal surface, except oblique zygal crest (Figs 38d,
On lower thecal surface, zygal bar and precise boundaries between marginals and infracentrals often difficult to distinguish (Figs 38a–c, 39a–c). No obvious ornamentation on lower thecal surface.

M₁ and M₁' contributing equally to, and forming together most of, anterior thecal margin (Figs 38a–c, 39a–c). Adjoining antero-adaxial portions of M₁ and M₁' recurred upwards into cup-shaped, proximally concave apophyses at and posteriorly to aulacophore insertion (Figs 38d, 39d). Antero-abaxial edges of M₁ and M₁' forming two opposite, symmetrical high shelves, laterally to apophyses, for insertion of adorals (Figs 38d, 39d). Anterior margins of both M₁ and M₁' gently convex. M₁ relatively short, broad, sub-quadrangular, with sinuous to concave posterior margin, along right infracentral area (Figs 38a–c, 39a–c). M₁ laterally in contact with M₁' (adaxially) and M₂ (abaxially) along sinuous sutures (Figs 38a–c, 39a–c). M₂ forming rounded right anterior thecal corner, slightly shorter than next two right marginals (Mc and M₃). No evidence of serrations on lateral edges of M₂. Mc straight to gently curved, possibly as long as M₃. Precise morphology of M₃ and putative contacts with nearby skeletal elements (Z, G, subanal plate) not clearly visible on available specimens. Glossal possibly preserved, apparently short, sub-triangular, with convex posterior margin and blunt distal tip (Figs 38c, 39c).

M₁' forming long, slightly arched, distally tapering, anterior part of zygal bar, with relatively short, slightly concave right border (along right infracentral area) and longer, more sinuous left margin (along left infracentral area) (Figs 38c, 39c). Zygal plate Z poorly preserved, bearing on its upper (internal) surface short, straight posterior portion of zygal crest stopping close to M₃ (Figs 38d, 39d). M₂' elongate, gently curved, forming rounded left anterior corner of theca, about of the same size and morphology as both M₃' and M₄'. No obvious ornamentation (e.g. knobs) on lateral edges of M₂'. M₄' slightly straighter than M₂'.
and $M'_3$ (Figs 38d, 39d). Digital poorly preserved, possibly corresponding to small sub-triangular posterior skeletal element, close to subanal plate (Figs 38a, 39a).

Right adoral ($A_1$) sub-quadrangular, moderately elongate transversely, partly roofing aulacophore insertion above right apophysis, with right adoral orifice possibly present along abaxial suture with underlying marginal $M_1$ (Figs 38d, 39d). Left adoral ($A'_1$) not observed.

Supracentral area indistinct retiform porous membrane in smallest specimen (Figs 38b, 39b), but consisting of numerous, small, polygonal, tessellate skeletal elements in larger individuals (Figs 38d, 39d). Subanal plate poorly preserved, sub-elliptical, transversely elongate, relatively wide, at posterior extremity of left infracentral area (Figs 38a, c, 39a, c). Delicate radiating fringe on posterior, gently curved, convex margin of subanal plate (Figs 38c, 39c).

Proximal aulacophore poorly preserved in all available specimens, consisting of at least three telescopic rings (Figs 38c–d, 39c–d). Anterior edge of lower surface of stylocone bearing long, wide, downward recurved median spike with fibrillar ornamentation along laterally flattened flanks (Figs 38c, 39c). Long, similarly ornamented median spike on lower surface of next ossicle (Figs 38c, 39c). More distal parts of aulacophore not observed or too poorly preserved (Figs 39a–b). Upper (internal) aspect of stylocone and first ossicle not observed. In CGS.OZ.153 (Figs 38c, 39c), single isolated displaced cover plate occurring next to stylocone spike. Cover plate large, fan-shaped, with radiating fibrillar ornamentation.

Remarks. Although they occur in distinct stratigraphic units within the Katian of Bohemia, all three above described specimens are here considered as conspecific. This interpretation relies on their very similar morphologies: their thecae are made of the same number of plates, with comparable relative proportions, the same retiform, porous texture, and identical contacts with surrounding elements. This material can be confidently assigned to *Domfrontia*, based on the occurrence of two adorals, ten marginals, a posterior zygal plate in central position, two
infracentral areas, with the left one posteriorly closed by a wide subanal plate inserted between two small distal marginals (D and G). This identification is further supported by the recent discovery of several additional, morphologically similar specimens in the Zahořany, Bohdalc and Králův Dvůr formations. In CGS.OZ.154, the occurrence of numerous small, polygonal supracentrals at the posterior extremity of the upper thecal surface confirms that, in *Domfrontia*, the anal plate occurs in distal position, on the underlying left infracentral area (see discussion above).

Comparison with the two other described species of *Domfrontia* suggests that Bohemian specimens differ from *D. pissotensis* (see below; Figs 40–42) in (1) the ornamentation on the lower surface of their stylocone and ossicles (spikes are much smaller in *D. pissotensis*); (2) the relative proportions of their right marginals (in *D. pissotensis*, M₂ is shorter and Mc, longer); and (3) the plating of their supracentral area (numerous small elements, instead of few, very large ones in *D. pissotensis*). Conversely, the small Katian cornutes from Bohemia are morphologically closer to coeval amygdalothecids from Morocco. With *D. milnerorum* (Fig. 35), they share the possession of a similar strong ornamentation on the lower surface of stylocone and ossicles, as well as comparable relative proportions of right thecal marginals (M₂, Mc, M₃). However, several aspects of the morphology of Bohemian amygdalothecids are still unknown (e.g. precise number of proximal rings, morphology of Z, occurrence of lateral knobs on M₂ and M’₂, aspect and number of infracentrals). Moreover, other features of the Czech *Domfrontia* are possibly different from those occurring in *D. milnerorum*, as for example the plating of the supracentral area. This integumentary surface is made of few, relatively large plates in *D. milnerorum*, but of numerous, small elements in Bohemian specimens. Consequently, the three available individuals of Czech amygdalothecids are here temporarily identified as *D. aff. milnerorum*, pending more abundant and better preserved specimens are collected and described.
Domfrontia pissotensis (Chauvel & Nion, 1977)

Figures 21c, 25d, 40–42

*1977  Reticulocarpos pissotensis Chauvel & Nion, p. 37, fig. 2; pl. 1 figs 1–3, pl. 2 figs 1–2

1981  Reticulocarpos pissotensis Chauvel & Nion – Chauvel, p. 87

1983  Reticulocarpos pissotensis Chauvel & Nion – Ubaghs, p. 46

1986  Reticulocarpos pissotensis Chauvel & Nion – Jefferies, p. 238, figs 7.36, 9.6

1987  Reticulocarpos pissotensis Chauvel & Nion – Jefferies, p. 287

1987  Reticulocarpos pissotensis Chauvel & Nion – Jefferies et al., p. 471, fig. 26

1988  Reticulocarpos pissotensis Chauvel & Nion – Cripps, p. 1068, figs. 16–17, table 2

1989a  Reticulocarpos pissotensis Chauvel & Nion – Cripps, p. 58, figs. 9, 23

1989b  Reticulocarpos pissotensis Chauvel & Nion – Cripps, p. 236, fig. 25

1991  Beryllia miranda Cripps & Daley – Cripps, p. 347, figs 13A, 14, 15, 17, table 4

1991  Domfrontia pissotensis (Chauvel & Nion) – Cripps, p. 348, figs 14, 15, 17, table 4

1991  Reticulocarpos pissotensis Chauvel & Nion – Ubaghs, p. 160

1992  Domfront cornute – Daley, p. 144, fig. 15, table 2

1992  Reticulocarpos pissotensis Chauvel & Nion – Daley, p. 144, fig. 15, table 2

1992  Domfrontia pissotensis (Chauvel & Nion) – Woods & Jefferies, p. 20, fig. 12

1994  Reticulocarpos pissotensis Chauvel & Nion – Ubaghs, p. 119

1994  Domfrontia pissotensis (Chauvel & Nion) – Cripps & Daley, p. 101, figs 2, 12, pl. 1

   figs 5–8

1994  Beryllia miranda Cripps & Daley, p. 107, figs. 4–6, 12, pl. 1 figs 1–4; pl. 2 fig. 1–6

1996d  Beryllia miranda Cripps & Daley – Gil Cid et al., p. 315, fig. 2.34

1996d  Domfrontia pissotensis (Chauvel & Nion) – Gil Cid et al., p. 315, fig. 2.35
1996 *Domfrontia* sp. – Gee, p. 277, fig. 4.21

1997 *Beryllia* sp. – Parsley, p. 230, fig. 6, appendix 2

1997 *Domfrontia*? sp. – Parsley, p. 230

1998b *Beryllia* sp. – Parsley, p. 116

1999 *Beryllia* sp. – Lefebvre & Vizcaïno, p. 440

1999 *Domfrontia pissetotensis* (Chauvel & Nion) – Lefebvre & Vizcaïno, p. 440

1999a *Beryllia miranda* Cripps & Daley – Ruta, p. 51, fig. 10

1999a *Domfrontia pissetotensis* (Chauvel & Nion) – Ruta, p. 74, fig. 11

1999b *Beryllia miranda* Cripps & Daley – Ruta, p. 127, fig. 4B

1999b *Domfrontia pissetotensis* (Chauvel & Nion) – Ruta, p. 132, fig. 11C

2000a *Domfrontia pissetotensis* (Chauvel & Nion) – Lefebvre, p. 109, fig. 3.1

2000a *Beryllia miranda* Cripps & Daley – Lefebvre, p. 109, fig. 3.2

2001 *Domfrontia* sp. – Lefebvre, p. 608

2001 *Beryllia miranda* Cripps & Daley – Lefebvre, p. 617, fig. 19.2

2002b *Beryllia miranda* Cripps & Daley – Domínguez *et al.*, p. 50

2002b *Domfrontia pissetotensis* (Chauvel & Nion) – Domínguez *et al.*, p. 51

2002 *Beryllia miranda* Cripps & Daley – Martí Mus, p. 108

2002 *Domfrontia pissetotensis* (Chauvel & Nion) – Martí Mus, p. 108

2003a *Beryllia* sp. – Lefebvre, p. 521

2003a *Domfrontia* sp. – Lefebvre, p. 521

2003 *Beryllia* sp. – Lefebvre & Fatka, p. 90

2003 *Domfrontia* sp. – Lefebvre & Fatka, p. 90

2003 *Beryllia miranda* Cripps & Daley – Ruta, p. 563, fig. 2

2003 *Domfrontia pissetotensis* (Chauvel & Nion) – Ruta, p. 563, fig. 2

2005 *Beryllia miranda* Cripps & Daley – Lefebvre, p. 481, figs 2, 3
2005  *Domfrontia pissotensis* (Chauvel & Nion) – Lefebvre, p. 482, figs 2, 3

2006  *Beryllia miranda* Cripps & Daley – Lefebvre *et al*., appendix

2006  *Domfrontia pissotensis* (Chauvel & Nion) – Lefebvre *et al*., appendix


2009  *Domfrontia pissotensis* (Chauvel & Nion) – Rahman *et al*., 2009, p. 427, table 2

2015a  *Beryllia miranda* Cripps & Daley – Lefebvre *et al*., p. 306

2015a  *Domfrontia pissotensis* (Chauvel & Nion) – Lefebvre *et al*., p. 306

Holotype. IGR.PAL.15702.1 (coll. Robardet): part and counterpart of an almost complete individual, comprising partly disarticulated theca (e.g. lateral marginals collapsed adaxially onto upper thecal surface), proximal aulacophore, and distal part of appendage with stylocone, next two ossicles, and associated cover plates (Figs 41a, 42a; see also Chauvel & Nion 1977, fig. 2a,c,e–f, pl. 1 figs 1a–c, 2a–b; Cripps & Daley 1994, fig. 2A–D, pl. 1 figs 5–8). The lower surface of the holotype was severely damaged during ultrasonic cleaning, while on loan at the NHM, London (R.P.S. Jefferies, *in litt*. 13 Dec. 1979). Comparison with original photographs of its lower surface (see Chauvel & Nion 1977; Cripps & Daley 1994) indicates that the right part of the theca (M<sub>1</sub>, M<sub>2</sub>, Mc, M<sub>3</sub>, right infracentral area) and most of the aulacophore are now missing. The counterpart, showing the holotype in upper aspect, is intact. Next to the holotype, a second, relatively well-preserved individual (IGR.PAL.15702.2) occurs on the same slab. It consists of a fully articulated, posteriorly incomplete theca and a partly disrupted proximal aulacophore (Fig. 41b).

Other material. Additional material comprises 29 other specimens. Five of them were used in the original description of *D. pissotensis* (see Chauvel & Nion, 1977; Cripps & Daley, 1994): IGR.PAL.15701, 15703–5 (coll. Robardet) and IGR.PAL.15706 (coll. Nion). IGR.PAL.15701
corresponds to a well-preserved individual, with almost complete, fully articulated theca (including subanal plate), proximal aulacophore and posterior part of distal appendage (see Chauvel & Nion 1977, fig. 2b, pl. 1 fig. 3a–b). All four other specimens are isolated thecal and/or aulacophore plates. Examined material also includes the 23 original specimens used by Cripps & Daley (1994) to reevaluate the morphology of small Armorican amygdalothecids and define the two genera *Beryllia* and *Domfrontia*: BMNHUK.EE.63486–508 (coll. Cripps & Jefferies). BMNHUK.EE.63496 contains three well-preserved individuals. One of them (BMNHUK.EE.63496.1; Figs 41d–e, 42c–d) was originally designated as holotype of *Beryllia miranda* Cripps & Daley, 1994 (part and counterpart). It consists of a fully articulated, almost complete theca (posterior part missing), with associated proximal rings, stylocone and first ossicle (see Cripps & Daley 1994, pl. 1 figs 1–4, pl. 2 figs 1–2). The two individuals occurring on the same slab are similarly oriented as the holotype (none is upside down). BMNHUK.EE.63496.2 consists of an almost complete, fully articulated theca, with proximal aulacophore and stylocone (part and counterpart; see Cripps & Daley 1994, pl. 2 figs 4–5). BMNHUK.EE.63496.3 corresponds to a less well-preserved theca, with some remains of the appendage extending on the upper surface of BMNHUK.EE.63496.2. With the exception of BMNHUK.EE.63499, which displays a complete, fully articulated theca in lower aspect (no counterpart; Figs 41f, 42b), most other specimens of *Domfrontia* registered at the NHM, London correspond to isolated thecal and/or aulacophore plates (B. Lefebvre, pers. obs., Dec. 2008). Study material also includes a new specimen collected in the 2000s (GR/PC.1795; coll. Courville). It corresponds to a relatively large slab of shales (no counterpart) containing crinoid fragments and two tectonically slightly distorted individuals of *D. pissotensis* (Figs 21c, 41c, 42f). One of them (GR/PC.1795.1) consists of an almost complete theca and associated proximal aulacophore in lower aspect. The second one
(GR/PC.1795.2) is more poorly preserved and its distal appendage is extending obliquely across the theca of the other individual.

Horizons and localities. All specimens but one (GR/PC.1795) were collected in the Le Pissot Formation (Dw3, late Darriwilian), at Le Pissot, Domfront, Orne, France (see above; Fig. 20.6). GR/PC.1795 was found in the uppermost part of the Traveusot Formation (Sa1, early Sandbian), at Beauséjour, Bain-de-Bretagne, Ille-et-Vilaine, France (see above; Fig. 20.5).

Diagnosis. A species of Domfrontia with no denticulations along lateral margins of M₂ and M'₂; M₂ small, much shorter than M'₂; integumentary plates particularly large; proximal aulacophore made of five rings; ossicular spikes short, stout, and blunt.

Description. Theca small (4.5 < TL < 9 mm), relatively elongate (TL/TW ~1.3), sub-elliptical, with almost bilaterally symmetrical outlines (Figs 25d, 40). All thecal plates porous, made of reticulate stereom. Boundaries between major skeletal elements (adorals, marginals, zygal) and integumentary plates relatively distinct. Anterior thecal margin almost straight to slightly concave, with shallow notch at aulacophore insertion. Antero-abaxial thecal corners rounded, with left one extending possibly slightly more anteriorly than right one. Lateral thecal edges regularly curved, gently convex, with left one possibly slightly shorter and straighter than opposite one. Maximum thecal width across Mc and M'₂-M'₃ boundary. Lateral thecal margins converging distally into relatively short, straight to slightly convex posterior margin. Thecal walls regularly decreasing in height towards posterior extremity. Lower thecal surface almost flat, without any obvious ornamentation. Oblique internal ridge (zygal crest) on upper side of M'₁ and Z, clearly distinct underneath collapsed supracentrals (Fig. 42d–e).
Marginal frame made of 10 relatively narrow, elongate elements (five on the left and five on the right), and posteriorly closed by large subanal plate inserted between D and G on lower thecal surface. M₁ and M’₁ contributing equally to anterior thecal margin and forming most of it. Anterior adaxial parts of both M₁ and M’₁ forming together cup-shaped, proximally concave apophyses at, and posteriorly to, aulacophore insertion (e.g. IGR.PAL.15702.1). M₁ sub-quadrangular, moderately elongate transversely, with slightly convex to sinuous anterior and posterior edges, and shorter, almost straight lateral sutures along M’₁ (on the left) and M₂ (on the right) (Figs 41b, d, f, 42b–c). M₂ particularly short, smaller than M’₁, and forming rounded right anterior corner of theca. No obvious ornamentation on abaxial edges of M₂.

Next two right marginals gently curved, abaxially convex, unequal in size, with Mc longer than M₃ (Figs 41b–c, f, 42b, e–f). M₃ in contact with Mc (anteriorly), G (posteriorly), and both Z and G (adaxially) (Figs 41b, f, 42b). Glossal very short, sub-triangular, with blunt distal tip, and inserted between M₃ and subanal plate (Figs 41b, f, 42b).

Zygal branch of M’₁ elongate, almost straight, relatively large, not significantly tapering distally, with right margin (along right infracentral area) much shorter than left one (along left infracentral area) (Figs 41b–c, f, 42b–c). Internal (upper) side of M’₁ bearing anterior part of zygal crest. Anterior margin of M’₁ sinuous to gently convex. M’₁ in contact with M₁ (adaxially), Z (posteriorly), and M’₂ (abaxially) along short, straight sutures. M’₂ strongly arched, elongate, forming rounded left anterior thecal corner. No ornamentation observed on abaxial edge of M’₂. M’₂ and next two left marginals (M’₃ and M’₄) about of the same length. M’₃ and M’₄ almost similar in shape, elongate, gently curved, with slightly convex abaxial margin. M’₄ posteriorly in contact with both D and subanal plate (Figs 41c, f, 42b, f). Digital short, sub-triangular, in between M’₄ and subanal plate (Figs 41f, 42b). Zygal plate Z in central position, relatively short, moderately elongate, with narrower anterior region forming posterior part of zygal strut, and slightly larger posterior area in contact with M₃ and subanal
plate. Lateral margins of Z slightly concave, unequal in length, with right one (along right infracentral area) longer. Posterior part of zygal crest on internal (upper) side of Z.

Lower thecal surface divided into two unequal fields by oblique strut formed by M'_1 and Z. (Figs. 41b–c, f, 42b–c). Integumentary areas relatively large, longitudinally elongate, unequal in size, both consisting of few, large, polygonal elements. No obvious difference in size between left and right infracentrals, but in each integumentary area, some skeletal elements significantly larger than neighbouring ones. Right infracentral area sub-triangular in shape, with short, concave anterior border along M'_1, M_1 and M_2), almost straight adaxial margin (along zygal bar) converging posteriorly with slightly longer, gently curved, convex abaxial edge (along M_2, Mc and M_3). Left infracentral area narrower anteriorly than posteriorly, with long sinuous to slightly concave right border (along zygal bar), and gently curved, convex left edge (along M'_2, M'_3 and M'_4). Large subanal plate at distal extremity of left infracentral area (Figs 41c, f, 42b). Subanal plate quadrangular to pentagonal in shape, slightly more elongate transversely, with relatively convex anterior and posterior margins. Delicate radiating fibrillar fringe along distal border of subanal plate.

On anterior edge of upper thecal surface, aulacophore insertion roofed by two relatively broad subequal adorals (Figs 41a, e, 42a, d). A'_1 antero-abaxially sutured to underlying M'_1. Right adoral orifice present along suture between M_1 and right-anterior extremity of A_1 (Figs 41a, 42a). Supracentrals particularly porous, wide, polygonal and tessellate, some of them particularly large (Figs 41a, e, 42a, d). No pore structures in right anterior corner of supracentral area.

Proximal aulacophore relatively broad and elongate, consisting of five telescopic rings (Figs 41a, e, 42a, d). Inferolaterals clearly distinct, paired, bilaterally symmetrical, with narrow proximal neck and wider distal edge overlapping next appendage element. Organization of upper part of proximal rings less distinct, generally poorly preserved (Figs
41a, e, 42a, d–e), possibly consisting of small, paired, symmetrical, markedly retiform tectals (Figs 41a, 42a). Stylocone relatively broad, wide, with low, laterally compressed, anterior median spike on lower side. Similarly-shaped spike on lower surface of next two ossicles. Upper surface of stylocone and ossicles with longitudinal median groove, and apparently, transverse channels (IGR.PAL.15704). Cover plates paired, wing to fan-shaped, with narrower articulatory facet made of denser stereom, and more porous, fibrillar, wide outer margin. Each cover plate overlapping next, more distal element of the same series (Figs 41a, 42a). In most specimens, anterior portion of distal aulacophore absent beyond second ossicle (Figs 41d–e, 42b–d). In some individuals, longer portions of distal appendages present, but too poorly preserved to show any details (Fig. 42e–f).

Remarks. Domfrontia pissotensis was initially described by Chauvel & Nion (1977) based on a handful of specimens. Although the individual they designated as holotype (IGR.PAL.15702.1) is mostly complete, its lateral thecal margins and proximal aulacophore are disarticulated and/or collapsed, and the posterior zygal plate is not clearly distinct. Based on several, better preserved specimens collected in the same level and the same locality, Cripps & Daley (1994) described a new cornute, Beryllia miranda. In their reevaluation of the original material of Chauvel & Nion (1977), Cripps & Daley (1994) assigned all disarticulated, poorly preserved specimens to D. pissotensis (e.g. IGR.PAL.15702), and fully articulated, better preserved ones to B. miranda (e.g. BMNHUK.EE.63496, 63499, IGR.PAL.15701). Cripps & Daley (1994, p. 102, 108) nevertheless acknowledged that, in many cases, it was almost impossible to assign some specimens to one or the other taxon. In the reconstructions provided by Cripps & Daley (1994), the morphologies of D. pissotensis and B. miranda appear clearly distinct. Domfrontia is characterised by a sub-quadrangular, very flat theca, with two large adorals, five proximal rings, and a zygal bar made of two plates
(with the posterior one in central position, but not reaching the marginal frame). In contrast, the theca of *Beryllia* is broad, almost rounded, inflated, with three small adorals, five proximal rings, and a zygal bar made of three small plates (M'_1, and two posterior central elements, not in contact with the marginal frame).

Based on the reexamination of the original material of *B. miranda* and *D. pissotensis* deposited at the NHM London, Ruta (1999a, p. 76) was the first to point out that the thecal plate patterns of *Beryllia* and *Domfrontia* were very similar to each other and, in particular, that the relative proportions of their thecal plates were identical (see also Cripps & Daley 1994, p. 108). Ruta (1999a, p. 77) also questioned the validity of some aspects of the reconstructions proposed by Cripps & Daley (1994) and, in particular, the morphology of the zygal bar. He also pointed out the occurrence of a relatively wide anal plate with a posterior fringe in most specimens (Ruta 1999a, p. 75). In this study, the examination of all original specimens of Chauvel & Nion (1977) and Cripps & Daley (1994) coupled with the observation of new individuals (GR/PC.1795) not only confirms the observations made by Ruta (1999a), but also demonstrates that *Beryllia miranda* and *Domfrontia pissotensis* are conspecific.

The more elongate, sub-quadrangular aspect of the holotype of *Domfrontia* (IGR.PAL.15702.1; Figs 41a, 42a) is taphonomic and results from the adaxial collapse of lateral marginals. Similar elongate morphologies are widespread in slightly disarticulated specimens of *Domfrontia* and *Nanocarpus*, and in particular in the Tizi n’Takrit material of *D. milnerorum* (see above). Thecal outlines of fully articulated individuals of *D. pissotensis* are very similar to those of similarly well-preserved specimens of *D. milnerorum* from Khabt-el-Hejar (see above). The reexamination of Armorican amygdalothecids also demonstrates that their zygal bar is made of two plates (M'_1 and Z), with the posterior one (Z) in central position, but distally sutured to the marginal frame (M_3). The incomplete, polyplated struts
reconstructed by Cripps & Daley (1994) for *Beryllia* and *Domfrontia* are based on broken anterior marginals M'₁. As pointed out by Ruta (1999a), a wide anal plate is clearly distinct in most observed individuals (e.g. BMNHUK.EE.63496.1–2, 63499, GR/PC.1795.1, IGR.PAL.15701; Figs 41c, f, 42b, e–f). However, this plate occurs at the distal extremity of the left infracentral area, and not at the posterior end of the supracentral area: it is thus a subanal plate. Reexamination of the original material of *Beryllia* does not confirm the presence of three small adorals, but indicates that two relatively broad elements (A₁ and A'₁) were roofing the aulacophore insertion on the upper thecal surface. In the holotype (IGR.PAL.15702.1; Figs 41a, 42a), Chauvel & Nion (1977, p. 39, fig. 2a) reported the occurrence of an unusual ornamentation on the largest, anterior supracentral (low ridge radiating from a central umbo). Such a ridge is actually present, but it corresponds to the imprint of the underlying zygal crest. Consequently, a reevaluated reconstruction of *D. pissotensis* is proposed herein (Fig. 40), based on all specimens previously assigned to both *Beryllia* and *Domfrontia*.

*Domfrontia milnerorum* and *D. pissotensis* are morphologically very similar to each other (e.g. small size, comparable thecal outlines, polyplated integumentary areas made of large elements, large subanal plate, same major skeletal elements displaying almost identical contacts). However, they also display some morphological differences, which justify their assignment to two distinct taxa. The main difference concerns the ornamentation on the lower surface of the stylocone and proximal-most ossicles: spikes are short and blunt in *D. pissotensis*, whereas they are long and sharp in *D. milnerorum* (see above). Another difference involves antero-lateral marginals M₂ and M'₂: in *D. pissotensis*, M₂ is very short, much smaller than M'₂, and both plates are unornamented; in *D. milnerorum*, M₂ and M'₂ are almost of the same size (M₂ is only slightly shorter than M'₂), and both bear a distinctive serrated ornamentation on their abaxial margins (see above). Finally, the proximal
aulacophore is made of five rings in D. pissotensis, but of six ones in D. milnerorum (see above).

3354 Domfrontia? sp.

3355 Figures 39e–f, 43

3357 1977 Reticulocarpos sp. – Chauvel & Nion, p. 40, fig. 3, pl. 2 fig. 3

3358 1981 Reticulocarpos sp. – Chauvel, p. 87

3359 1986 Reticulocarpos sp. – Chauvel, p. 79

3360 2003 cornute indet. – Lefebvre & Fatka, p. 91

3361 2007 Reticulocarpos? sp. – Lefebvre & Gutiérrez-Marco, p. 15

3363 Material. Within the six specimens tentatively identified here as Domfrontia? sp., four were originally described as Reticulocarpos sp. by Chauvel & Nion (1977, fig. 3a–b, pl. 2 fig. 3a–c): IGR.PAL.15707–15710 (coll. Nion). This material comprises some isolated thecal elements (large, thin, reticulate integumentary plates, gently curved narrow marginals) and disarticulated portions of distal aulacophore (stylocone, ossicles, cover plates). The two other specimens (MGM-6444O, 6445O; coll. Gutiérrez-Marco) correspond to two incomplete, partly disarticulated thecae (part and counterpart), comprising some marginals and integumentary plates (Figs 39e–f, 43)

3372 Horizons and localities. The four specimens yielding isolated cornute plates were collected in the lower part of the Traveusot Formation (Dw2, middle Darriwilian) at locality 'côte 85', Laillé, Ille-et-Vilaine, France (see above; Fig. 20.1). The two incomplete thecae are from the
upper 3–5 m of a yet unnamed formation of dark mudstones (Dw2, middle Darriwilian), Cazalla de la Sierra, Valle Syncline, Ossa Morena, Spain (see above; CS on Fig. 24b–c).

*Description.* Thecae of Iberian cornutes incomplete, more or less disarticulated, moderately elongate, almost bilaterally symmetrical (not boot-shaped), small sized (less than 10 mm long) with straight to gently curved lateral margins (Figs 39e, 43a–b). Both specimens too poorly preserved to estimate TL and TW (however, TL probably less than 10 mm). Marginals porous, reticulate, thick and narrow, without marginal flange and/or any obvious ornamentation on lower surface or along abaxial edges. M₁ missing in both individuals. M₂ and M₃ incompletely preserved, apparently narrow and elongate. M₃ similarly shaped, with gently curved, convex abaxial margin. Posterior part of M₃ adaxially in contact with Z (Figs 39e, 43a). Glossal and digital not preserved. Aulacophore insertion and proximal margin of M'₁ not visible. M'₁ forming straight, elongate, relatively wide anterior part of zygal strut. Posterior zygal plate (Z) in central position, almost straight, slightly shorter than zygal part of M'₁, distally sutured to M₃. Internal (upper) surface of both M'₁ and Z bearing strong zygal crest. M'₂ strongly arched, forming rounded left anterior corner of theca (Fig. 43c). M'₃ and M'₄ similarly shaped, rod-like, straight to slightly curved, almost of the same length (Figs 39e, 43a–b). Adorals not observed. Left and right infracentral areas relatively wide, both longitudinally elongate, consisting of relatively large, thin skeletal elements with porous, reticulate texture. Posterior extremity of left infracentral area poorly preserved, possibly with larger subanal(?) plate (Figs 39e, 43a). Supracentraals wide, reticulate, polygonal, forming thin, porous, isotropic, tessellate pavement. No evidence of transverse M₄-M'₄ posterior bar on upper thecal surface (Fig. 43b). Occurrence of putative pore structures impossible to document (right anterior part of supracentraal area not preserved). Thecae of Armorican
specimens consisting of few isolated skeletal elements: fragments of reticulate integumentary
surfaces, and small, elongate, narrow, gently curved marginals.

No aulacophore remains observed in Iberian specimens. Armorican material yielding
several well-preserved, isolated elements of distal appendage. Stylocone straight, with parallel
abaxial margins, small proximal cavity, and long, posteriorly recurved, laterally compressed
median spike at anterior edge of lower surface (IGR.PAL.15709). Similarly-shaped spike on
lower side of isolated ossicles. Lateral flanks of spikes with radiating, fibrillar ornamentation
(IGR.PAL.15709). Upper surface of stylocone and ossicles bearing median longitudinal
median groove and transverse channels (IGR.PAL.15707). Isolated cover plates fan-shaped,
with thicker base made of denser stereom, and more delicate, wing-like outer portion with
fibrillar, radiating ornamentation.

Remarks. The two incomplete stylophorans from Ossa Morena can be assigned to cornutes,
because of their narrow marginal frame, but mainly because they are lacking large adorals on
their upper thecal surface. Although poorly preserved, their marginal frame was not boot-
shaped and posteriorly open, thus excluding putative hanusiid (no M₄-M'₄ bar at distal end of
upper thecal surface), cothurnocystid, phyllocystid and scotiaecystid (absence of both M₅ and
M'₅ at posterior extremity of left infracentral area). Chauvelicystid affinities can be also
rejected, because of the central position of the posterior zygal plate. The two cornute
specimens from Ossa Morena share with Milonicystis a similarly shaped, bilaterally
symmetrical theca and the central position of Z. However, the contact of Z with M₃, the
morphology of supracentrals (large, reticulate) and marginals (narrow and porous), and the
possible occurrence of a subanal(?) plate rather suggest affinities with amygdalothecids and,
more precisely, with Domfrontia. The left anterior marginal of Spanish cornutes is
morphologically similar to M'₂ in both D. milnerorum and D. pissotensis. However, Ossa
Morena specimens differ from the two described species of *Domfrontia* by their unusually long posterior zygal plate. Consequently, pending the discovery of additional, better preserved and more complete material, the two cornute specimens from the Valle syncline are tentatively identified herein as *Domfrontia?* sp.

Although they occur in the same lithostratigraphic unit as some specimens of *Domfrontia pissotensis* (Traveusot Formation), the skeletal remains found at the 'côte 85' locality are stratigraphically older (middle Darriwilian instead of early Sandbian) and morphologically distinct. The main difference concerns the aspect of distal appendage spikes: they are short and blunt in *D. pissotensis*, whereas they are long, sharp and recurved in the 'côte 85' material. Their morphology is more similar to the spikes occurring in *D. milnerorum*, but also in *Nanocarpus*, as well as in some hanusiids (e.g. *Prokopicystis, Reticulocarpos*; see Jefferies & Prokop 1972; Cripps 1989a; Chauvel & Nion 1977). Transverse channels are absent in *D. milnerorum*, but they occur on the upper surface of the stylocone and ossicles in *D. pissotensis, Nanocarpus dolambii, Reticulocarpos hanusi*, and *Prokopicystis mergli* (see Jefferies & Prokop 1972; Chauvel & Nion 1977; Cripps 1989a; Ubaghs 1991). The retiform, porous aspect of associated thecal plates is also compatible with both amygdalothecid and hanusiid affinities. Consequently, isolated skeletal elements from the lower part of the Traveusot Formation are very tentatively identified here as *Domfrontia?* sp., pending more and better preserved material is collected.

Family **Chauvelicystidae** Daley, 1992

*Diagnosis.* A family of cornute stylophorans with spines articulated at least to left side of a posteriorly open thecal frame (M₅ and M'₅ lost); lower thecal surface unornamented; Z in marginal position; lower side of proximal-most ossicles smooth to weakly ornamented.
Remarks. The subfamily Chauvelicystinae was originally defined by Daley (1992) for the small clade uniting the two genera *Chauvelicystis* and *Prochauvelicystis*, both characterised by spines articulated to the left thecal side ('unnamed clade 2b' in Cripps 1991; see also Cripps & Daley 1994). This concept was later emended by Lefebvre & Vizcaíno (1999) so as to include both spiny (e.g. *Ampelocarpus*, *Chauvelicystis*, *Prochauvelicystis*) and spineless cornutes (e.g. *Lyricocarpus*, *Milonicystis*) with a Mc marginal and a posteriorly open marginal frame (see also Lefebvre 2000a, 2001; Lee et al. 2005). In this context, the *Chauvelicystis*-like spineless cornute *Flabellicarpus* was considered either as the sister-group of the Chauvelicystinae (Martí Mus 2002) or as a member of this subfamily (Lee et al. 2005; Lefebvre 2005). In the last 15 years, the discovery of several new spiny and spineless cornutes in the Furongian of South China, the Lower Ordovician of Morocco and the Upper Ordovician of Bohemia, along with the herein revision of previously described key taxa (genus AVIII, *Lyricocarpus*, *Milonicystis*) both contributed to clarify the diagnosis of the stylophoran clade comprising *Chauvelicystis* and *Prochauvelicystis*, which is here elevated to family level (Chauvelicystidae).

For example, the long suspected relationship between *Flabellicarpus* and chauvelicystids (Martí Mus in Lefebvre & Vizcaíno 1999; Martí Mus 2002; Ruta 2003; Lee et al. 2005; Lefebvre 2005) was recently challenged by the discovery of *Phyllocystis* jingxiensis (Fig. 16a) in the Furongian of South China (Han & Chen 2008). Although still pending revision, the morphology of this cornute suggests close affinities with both *Flabellicarpus* (Fig. 15d), amygdalotheccids and early mitrates (Lefebvre & Ausich 2021). In particular, *P.* jingxiensis shares with *Flabellicarpus* the possession of a posteriorly narrowly open marginal frame (loss of M5 and M') in between almost adjoining digital and gossal, widely expanded posterior blades (spinal and gossal), large external flanges along marginals, and a similar particularly
long proximal aulacophore (10–12 rings). In both *Flabellicarpus* and 'P.' *jingxiensis*, the presence of a small M₄ above Z is uncertain (Martí Mus 2002; Han & Chen 2008). M₄ is clearly lost in both amygdalothecids and early mitrates (Lefebvre & Ausich 2021), but it is still present in basal chauvelicystids (e.g. *Chauvelicystis*, *Prochauvelicystis*). 'P.' *jingxiensis* mainly differs from *Flabellicarpus* in the wider expansion of its spinal and glossal blades, which are posteriorly in contact and sutured to each other. Consequently, it is very likely that *Flabellicarpus* represents either the sister-group of both chauvelicystids and the clade uniting amygdalothecids and mitrates, or alternatively, occupies a very basal position within the (Amygdalothecidae + Mitrata) clade.

Similarly, possible affinities of the spineless cornute *Milonicystis* (Figs 27, 30) with chauvelicystids were suggested by Lefebvre & Vizcaïno (1999), based mostly on the occurrence of similarly open marginal frames (loss of M₅ and M’₅) and the absence of ornamentation on the lower thecal surface (see also Lefebvre 2000a, 2001; Lee et al. 2005). *Milonicystis* also shares with some chauvelicystids (e.g. *Sokkaejaecystis*) the possession of bobin-shaped supracentrals (Lee et al. 2005). However, these features are widespread within stylophorans and do not represent apomorphies uniting *Milonicystis* and chauvelicystids (see above). The two posterior marginals M₅ and M’₅ are also absent (lost) e.g. in amygdalothecids, *Flabellicarpus*, hanusiids, mitrates, 'P.' *jingxiensis* and the Tizagzaouine cornute (see above; Lefebvre & Ausich 2021). Protuberances are absent not only in *Milonicystis* and chauvelicystids, but also in amygdalothecids, *Flabellicarpus*, mitrates and 'P.' *jingxiensis*. Finally, bobin-shaped supracentrals are also present in some amygdalothecids (e.g. *Amygdalotheca griffei*; Ubachs 1970). The reevaluation of the morphology and plate pattern of *Milonicystis* does not support any close relationship with chauvelicystids, but rather suggests affinities with the yet undescribed Tizagzaouine cornute (see above; Fig. 15c). This conclusion is further supported by the absence of two key features of chauvelicystids:
**Milonicystis** lacks spines articulated to the left thecal margin and its posterior zygal plate is not in marginal position.

The systematic position of *Lyricocarpus* (late Floian, Montagne Noire, France) also long remained controversial within stylophorans (Ubaghs 1994; Parsley 1997; Lefebvre & Vizcaíno 1999; Ruta 1999b, 2003; Lefebvre 2001, 2005; Martí Mus 2002; Lee *et al.* 2005). Affinities with amygdalothecids and/or early mitrates (e.g. *Chinianocarpos*, *Peltocystis*) were originally suggested by Ubaghs (1994), based on the symmetrical thecal outlines, the wide expansion of M'1 and Z, the occurrence of a small spike on the lower surface of the stylocone, and the absence of the right infracentral area in *Lyricocarpus* (see also Parsley 1997; Ruta 1999b, 2003). In contrast, Lefebvre & Vizcaíno (1999) considered that *Lyricocarpus* was a highly derived, spineless member of the subfamily Chauvelicystinae (see also Lefebvre 2001, 2005; Lee *et al.*, 2005). This identification relied mostly on the strong similarities between the plate patterns of *Lyricocarpus* and morphologically close, spiny chauvelicystines (e.g. *Ampelocarpus*). The reexamination of the original type material of *Lyricocarpus courtessolei* (coll. Vizcaíno, now deposited in Lyon) made it possible to prove the occurrence of several spines articulated to the left thecal margin in both the holotype (UCBL-FSL 712546; Figs 44d–e, 45a) and the paratype (UCBL-FSL 712550; Figs 44a–b, 45b–c). Although they had never been reported so far in *Lyricocarpus*, some of these spines were indeed already visible on Ubaghs’ (1994) original photographic plates. The occurrence of undisputable spines along its second left marginal (M2 or M3) definitively supports the assignment of *Lyricocarpus* to chauvelicystid cornutes.

Comparison with similarly shaped chauvelicystids (e.g. *Ampelocarpus*, *Destombesicarpus* gen. nov.) suggests that spines were very likely originally more extensively distributed along the left thecal side of *Lyricocarpus* and probably also present on the opposite (right) margin (Fig. 46a–b). Since the original description of *L. courtessolei* by Ubaghs (1994), five
additional individuals have been found in the same stratigraphic unit (Landeyran Formation) of the Montagne Noire, France (coll. Lefebvre: UCBL-FSL 711692–93; coll. Lacombe: UCBL-FSL 711697; and coll. Vizcaïno: UCBL-FSL 712633, 712699). In all available specimens, the rarity of spines probably results from the collapse and disarticulation of the theca. Spines are similarly seldom preserved in *Ampelocarpus landeyranensis* (Figs 3e, 4e), which is found in slightly older levels in the same formation (see Lefebvre & Vizcaïno 1999). The abundant skeletal remains of the small-sized scotiaecystid cornute *Bohemiaecystis ubaghsi* co-occurring with *Ampelocarpus* are also consistently disarticulated and incomplete (see Ubaghs 1983; Lefebvre & Vizcaïno 1999). Although the precise taphonomic conditions prevailing in the Landeyran Formation still remain to be elucidated, it is very likely that most cornute remains found in this unit correspond to already decayed and collapsed carcasses, probably disarticulated *in situ* by weak bottom currents and/or organic activity. Their preservation in quiet and relatively deep environmental conditions probably results from their smothering by occasional, thin distal storm deposits (see Lefebvre 2007a).

The possession of articulated spines is a relatively widespread character within cornutes. Such spines can be inserted along the lateral walls of the proximal aulacophore in both amygdalothecids (*Amygdalotheca*; Ubaghs 1970) and chauvelicystids (e.g. *Sokkaejaecystis*; Lee *et al.* 2005). Similarly, small spines articulated to the right margin of the theca do not occur only in several chauvelicystids (e.g. *Ampelocarpus, Chauvelicystis*; see Chauvel 1966; Ubaghs 1970, 1983; Lefebvre & Vizcaïno 1999) but also in some scotiaecystids (e.g. along M3, Ms and Z in *Bohemiaecystis griffei*; see Ubaghs 1970). Consequently, the presence of articulated spines cannot be considered as an autapomorphy of chauvelicystids. However, as this was originally pointed out by Daley (1992), the occurrence of articulated spines along the left thecal margin is unique to chauvelicystids. In this clade, spines are often also present along the opposite (right) thecal margin (e.g. *Ampelocarpus, Chauvelicystis*) and, when they
are absent (e.g. Prochauvelicystis, Sokkaejaecystis), the right marginals are then modified into a series of large spike-shaped elements.

As they are defined herein (i.e. cornutes with spines articulated to the left margin of a posteriorly open thecal frame), chauvelicystids form a relatively diverse clade of Ordovician stylophorans (Tremadocian–Katian) comprising the six genera Ampelocarpus, Chauvelicystis, Destombesicarpus gen. nov., Lyricocarpus, Prochauvelicystis and Sokkaejaecystis, as well as two yet undescribed taxa from the Lower Ordovician of Morocco (Fezouata Formation; Lefebvre et al. 2016a). The family Chauvelicystidae is characterised by a well-defined evolutionary trend from asymmetrical, boot-shaped thecae to almost bilaterally symmetrical, bottle-shaped outlines, which is achieved through a progressive reduction of the number of marginals and the resorption of the right infracentral area (Lefebvre 2001). This trend is also accompanied by a drastic reduction of thecal size, possibly related to heterochronic (paedomorphic?) processes.

Within this clade, the morphology of Chauvelicystis (Fig. 16d; Tremadocian–Floian) is probably the most plesiomorphic (Lefebvre & Vizcaïno 1999; Lefebvre 2001; but see Daley 1992). Its markedly boot-shaped theca is made of 12 marginals (D, G, M'1–4, M1–4, Mc, Z), three adorals (A0, A'1, A1), two large infracentral areas, and cothurnopores are present on the supracentral area. The glossal and the spinal form two particularly wide, almost adjoining posterior processes. This plate pattern is very close to that of e.g. Flabellicarpus (Fig. 15d) and Persiacarpos (see above, Fig. 13c–d; Lefebvre & Ausich 2021). This plesiomorphic morphology explains why the first skeletal remains of Chauvelicystis (C. ubaghsi; Floian, Morocco) were originally assigned to the genus Cothurnocystis (Chauvel 1966). The discovery of additional specimens of spiny 'cothurnocystids' in the late Tremadocian of the Montagne Noire (C. spinosa) prompted Ubaghs (1970) to place both C. spinosa and C. ubaghsi in a distinct genus: Chauvelicystis. Better preserved, less incomplete individuals of C.
spinoso were subsequently described by Ubaghs (1983) in the same stratigraphic unit (Saint-Chinian Formation) of the Montagne Noire. This material was assigned to a new, distinct species (C. vizcainoi) by Daley (1992). However, as pointed out by Ubaghs (1983) and Martí Mus (2006), all specimens of Chauvelicystis from the Montagne Noire are morphologically very similar and most differences result from taphonomic artefacts: e.g. the spinal blade is not missing in the holotype of C. spinosa (UCBL-FSL 168718), but simply hidden by a shell fragment. Although all arguments provided by Daley (1992) to support the identification of a second species of Chauvelicystis in the Montagne Noire have been convincingly refuted by Martí Mus (2006), the possibility that two species may have nevertheless coexisted cannot be entirely ruled out (see Lefebvre et al. 2006, 2016a; Lefebvre 2007a). In the holotype of C. spinosa and several other individuals, most supracentrals are bearing a low, wide central spike (see Ubaghs 1970 pl. 8, fig. 1a,b; Álvaro et al. 2001 pl. 13, fig. 1), whereas supracentrals are flat and smooth in the putative holotype of C. vizcainoi (UCBL-FSL 712517) and several other specimens (see Ubaghs 1983 pl. 10, fig. 1). Future investigations should help clarifying if these differences are taxonomically significant, or if they are ontogenetic (most specimens of C. vizcainoi are smaller than co-occurring ones of C. spinosa) and/or simply ecophenotypic and associated with distinct environmental conditions. The same two morphotypes have been also observed in the lower part of the Fezouata Formation (late Tremadocian) in Morocco (Lefebvre et al. 2016a).

Prochauvelicystis semispinoso (late Tremadocian, Shropshire, UK) and all other more derived chauvelicystid taxa differ from Chauvelicystis by the loss of one marginal on the left thecal side (probably M'$_2$ or M'$_3$) (see Lefebvre & Vizcaíno 1999; Lefebvre 2001; Lee et al. 2005). Prochauvelicystis (Fig. 46c–d) is a small boot-shaped cornute with a strongly reduced right infracentral area, cothurnopores on the upper thecal surface, and spike-shaped right
marginals (Daley 1992). Its marginal frame is thus made of 11 marginals (D, G, M’, M’2 or M’3, M’4, M1-4, Mc, Z) and three adorals (A0, A’1 and A1).

Sokkaejaecystis serrata (Figs 3f, 4f) from the Dongjeom Formation (Taebaeksan Basin, Korea) was originally considered as the oldest known (Furongian) member of the Chauvelicystidae (Lee et al. 2005; Lefebvre et al. 2006, 2016a; Lefebvre 2007a; Zamora et al. 2013). However, the recent reevaluation of Cambro-Ordovician stratigraphy in Korea suggests a Tremadocian age for the Dongjeom Formation (Choi 2019). This revised age is more compatible with the relatively derived morphology of Sokkaejaecystis: within chauvelicystids, this genus shares with Ampelocarpus (Figs 3e, 4e), Destombesicarpus gen. nov. (Fig. 47) and Lyricocarpus (Fig. 46a–b) the loss of two marginals (M’2 or M’3 on the left, M’4 on the right) and of the median adoral (A0). Consequently, the boot-shaped theca of Sokkaejaecystis consists of two infracentral areas, 10 marginals (D, G, M’, M’2 or M’3, M’4, M1-3, Mc, Z) and two adorals (A’1 and A1). It is very likely that the two yet undescribed cornutes mentioned by Lefebvre et al. (2016a) as ’Chauvelicystidae n. gen. n. sp. 1’ and ’Chauvelicystidae n. gen. n. sp. 2’ in the Fezouata Formation (Lower Ordovician) of the Anti-Atlas (Morocco) correspond to two distinct new species of Sokkaejaecystis. If this identification is correct, the two Moroccan species of Sokkaejaecystis differ from the Korean one by the presence of articulated spines on both thecal margins. The occurrence of spike-shaped marginals (G, M2, M3, Mc) and of spines along the proximal aulacophore both probably represent autapomorphies of S. serrata. The two Moroccan taxa mainly differ from each other by the aspect of the distal extremity of their marginal frame, which is either open, as in S. serrata (Sokkaejaecystis n. sp. 1; late Tremadocian) or closed (D and G in contact; Sokkaejaecystis n. sp. 2; late Tremadocian–middle Floian)

Ampelocarpus landeyranensis (Figs 3e, 4e) was originally described in the lower part of the Landeyran Formation (late Floian) in the Montagne Noire, France (Vizcaíno & Lefebvre...
1999; Vizcaïno et al. 2001). It is a small bottle-shaped chauvelicystid with spines articulated
to both thecal sides and a strongly reduced right infracentral area (Lefebvre & Vizcaïno 1999;
Lefebvre 2001). *Ampelocarpus* differs from *Sokkaejaecystis* (Figs 3f, 4f) in the loss of one
skeletal element (Mc or M₃) on the right thecal margin. The plate pattern of *Ampelocarpus*
thus consists of nine marginals (D, G, M₁, M₂ or M₃, M₄, M₁₋₂, Mc or M₃, Z) and two
adorals (A₁ and A₁). In the Zagora area (Morocco), the lower part of the Fezouata Formation
(late Tremadocian) yielded a single specimen (coll. Reboul, MHNM.15690.168) of a
similarly shaped, small sized, spiny chauvelicystid, which was tentatively assigned to
*Ampelocarpus* sp. (Lefebvre et al. 2016a). Rereamination of this specimen does not confirm
this idenfication and rather suggests that it more likely belongs to one of the two yet
undescribed chauvelicystid taxa occurring in these levels (chauvelicystid n. gen. n. sp. 1, see
above). On the other hand, several well-preserved specimens of a small *Ampelocarpus*-like
Floian chauvelicystid were found recently in the western part of the Ternata plain (Zagora

*Destombesicarpus* gen. nov. (Fig. 47) and *Lyricocarpus* (Fig. 46a–b) are the two most
derived members of the family Chauvelicystidae. They both correspond to small sized
cornutes with bottle-shaped outlines and spines articulated to both thecal sides. They differ
from *Ampelocarpus* (Figs 3e, 4e) in the absence of the right infracentral area and the loss of
both Mc and M₃ along the right thecal margin, so that M₂ is posteriorly sutured to Z. *Lyricocarpus*
was originally described based on material from the upper part of the Landeyran
Formation (late Floian) of Montagne Noire, France (*L. courtessolei*, see above; Ubaghs 1994;
Lefebvre & Vizcaïno 1999; Vizcaïno & Lefebvre 1999; Lefebvre 2001; Vizcaïno et al. 2001).
Two more putative specimens of *Lyricocarpus* (coll. Reboul, ML20.269.164 and
MHNT.PAL.2005.0.297) were also found at Bou Izargane (Zagora area, Morocco) in the
lower part of the Fezouata Formation (late Tremadocian) (Lefebvre et al. 2016a). However,
reexamination of this material suggests that it should rather be assigned to a distinct genus ('chauvelicystid n. gen. n. sp. 1' sensu Lefebvre et al. 2016). All younger occurrences of Lyricocarpus-like cornutes (e.g. Ubags 1994; Lefebvre & Vizcaíno 1999; Lefebvre & Fatka 2003; Gutiérrez-Marco et al. 2003; Lefebvre et al. 2007; Sumrall & Zamora 2011) are here assigned to Destombesicarpus gen. nov. (see above). The plate pattern of Lyricocarpus consists of eight marginals (D, G, M' 1, M' 2 or M' 3, M' 4, M 1-2, Z) and two adorals (A' 1 and A 1). Destombesicarpus gen. nov. (Fig. 47) differs from Lyricocarpus (Fig. 46a–b) by the loss of M' 4, so that the digital is sutured posteriorly to the second left marginal (either M' 2 or M' 3).

Destombesicarpus gen. nov. occurs both in the Izegguirene Formation (early Sandbian) of the eastern Anti-Atlas, Morocco (D. izegguirenensis gen. et sp. nov., see below; Chauvel 1971; Gutiérrez-Marco et al. 2003; Lefebvre et al. 2007) and the Zahořany Formation (early Katian) of Bohemia, Czech Republic (D. budili gen. et sp. nov.; see below).

Genus Destombesicarpus gen. nov.

Type species. Destombesicarpus izegguirenensis sp. nov.

Derivation of name. The genus is named after the late French geologist Jacques Destombes (1926–2018), who mapped the whole Ordovician succession in the Anti-Atlas area and dramatically refined its stratigraphic framework in the second half of the 20th century. The single known specimen and holotype of the type-species of Destombesicarpus was also collected by Jacques Destombes in October 1961.
Diagnosis. A genus of small-sized chauvelicystid with spines articulated to both thecal sides and no right infracentral area; bottle-shaped theca framed by seven marginals (D, M'_{2/3}, M'_1, M_1, M_2, Z and G) and two adorals (A'_1 and A_1).

Remarks. The presence of spines articulated to the left thecal margin of _Destombesicarpus_ supports its assignment to the Chauvelicystidae. Within this family, _Destombesicarpus_ is morphologically very close to _Lyricocarpus_ (e.g. similar small-sized, bottle-shaped theca with enlarged anterior marginals and no right infracentral area; see above). However, the left thecal margin of _Destombesicarpus_ is made of three plates (M'_1, M'_{2/3} and D) instead of four in _Lyricocarpus_ (loss of M'_4; see above). As defined herein, _Destombesicarpus_ comprises the two species _D. izegguirenensis_ sp. nov. (early Sandbian, Morocco) and _D. budili_ (early–late Katian, Czech Republic). In Wales, the Pontyfenni Formation (Dapingian) yielded a single specimen of a yet undescribed small sized cornute (BMNHUK.E.29928) in upper aspect (no counterpart) briefly reported as ‘_Reticulocarpos_? sp. 2’ by Jefferies (1987, fig. 148). Although it is incompletely known, its morphology strongly suggests affinities with the two chauvelicystid genera _Destombesicarpus_ and _Lyricocarpus_. If the occurrence of a single long, slightly sinuous marginal between M'_2 and D is confirmed, this specimen would then represent the oldest known occurrence of _Destombesicarpus_, and very likely, a third species morphologically distinct from both _D. budili_ and _D. izegguirenensis_.

_Destombesicarpus izegguirenensis_ sp. nov.

Figures 18d, 25e, 45d, 47–48

1971 genre indéterminé AVIII – Chauvel, p. 57, fig. 3g.

1978 Mitrata indet. – Chauvel, p. 61, fig. 14
Derivation of name. The species is named after 'Jbel Izegguirene', near Tazarine, in the central Anti-Atlas (Morocco). This hill is the type section of the Izegguirene Formation and the type-locality of Destombesicarpus izegguirenensis.

Holotype. IGR.PAL.16691 (coll. Destombes n°755c): a complete, slightly disarticulated theca in upper aspect (no counterpart) and anteriorly to it, several dissociated fragments of the distal aulacophore: the stylocone (in lower aspect) and four distinct ossicles (all in upper aspect). The holotype (Figs 45d, 48) occurs on a small slab of relatively fine, beige to grey, micaceous silststones. Delicate morphological details (e.g. stereome microstructure, thecal spines, longitudinal median groove on ossicles) are well-preserved. The holotype corresponds to the specimen originally described and figured by Chauvel (1971, fig. 3g) as 'genre indéterminé AVIII'.

Horizon and locality. Single known specimen collected in the Izegguirene Formation (Sa1, lower Sandbian) at Jbel Izegguirene (Destombes locality 755), about 15 km NW of Tazarine and 17 km SE of Nkob, central Anti-Atlas, Morocco (see above; Fig. 17.4).
Diagnosis. A species of *Destombesicarpus* with a thinly plated, bulb-shaped marginal frame, much wider anteriorly than posteriorly.

Description. Theca small, moderately elongate (TL = 5.5 mm; TW = 4 mm), bulb-shaped, with wide anterior rounded portion and narrower posterior neck (Figs 25e, 47). Thecal outlines gently curved, almost bilaterally symmetrical, with right margin longer than left one. Anterior edge of theca almost straight, with short and shallow median notch for aulacophore insertion. Lateral thecal margins regularly convex anteriorly, markedly concave and almost parallel to each other, posteriorly. Distal edge of theca straight, forming a short re-entrant laterally bounded by slightly protruding digital and glossal. Height of thecal frame decreasing only slightly posteriorly. Lateral marginals almost sub-triangular in cross section, with flat lower surface, relatively steep, slightly concave, retiform outer walls, and steeper, smooth, adaxial side. Lower thecal surface almost flat to slightly concave, partly consisting of a rigid floor (right anterior corner) formed by four adjoining, enlarged marginals (M'_1, M_1, M_2 and Z; no right infracentral area) and a thin, more flexible integumentary pavement (left infracentral area) expanding from left anterior thecal corner towards posterior neck. No evidence of any ornamentation (knobs, protuberances, spikes) on lower thecal surface. Zygal crest probably low, partly exposed under collapsed supracentral membrane.

Marginal frame posteriorly open and consisting of seven plates (three on the left, four on the right). Anterior-most marginals M'_1 and M_1 markedly unequal in size, forming together most of anterior edge of theca (Figs 45d, 48). Aulacophore insertion particularly narrow and shallow, posteriorly delimited by two small, deep and high apophyses borne by antero-adaxial margins of M_1 and M'_1. M_1 broad, almost pentagonal in shape, about half smaller than M'_1. Anterior portion of M_1 straight, except short, strongly concave antero-adaxial portion along notch for aulacophore insertion. Posterior edge of M_1 straight, almost parallel to, but shorter
than anterior margin, in contact with Z. Lateral edges of M1 sinuous, almost subequal in length, slightly diverging anteriorly. M1 abaxially sutured to M2 and adaxially to M'1. Anterior portion of M1 forming a high wall, with small, shallow, circular depression (infundibulum) along internal (abaxial) upper edge of right aulacophore apophysis. Infundibulum adaxially connected to well-marked anterior transverse groove extending downwards and running posteriorly to both aulacophore apophyses. M1 particularly wide, more or less crescent-shaped, transversely elongate. M1 adaxially sutured to both M1 (anteriorly) and Z (posteriorly). Posterior margin of M1 long and sinuous along left infracentral area. M1 abaxially in contact with M'2/3 along short and straight suture. Anterior edge of M'1 almost straight to slightly sinuous, except concave adaxial notch at aulacophore insertion. Internal surface of M'1 (and putative low anterior portion of zygal crest) largely covered by supracentrals. M2 broad, moderately elongate, sub-triangular, forming rounded right anterior corner of marginal frame (Figs 45d, 48). Abaxial margin of M2 long and regularly convex. Posterior and adaxial edges of M2 relatively sinuous, almost perpendicular to each other and unequal in size: posterior edge of M2 (in contact with Z) much shorter than left margin (sutured to M1). Z particularly elongate, forming most of right thecal margin (Figs 45d, 48). Anterior portion of Z particularly wide, largely expanding on lower thecal surface and anteriorly sutured to M2, M1 and M'1. Posterior portion of Z much narrower and distally in contact with G along short and straight suture. Outer (abaxial) edge of Z particularly long and gently convex. Along left infracentral area, adaxial margin of Z slightly shorter and gently concave. Glossal relatively short, narrow and elongate forming posterior extremity of right thecal margin (Figs 45d, 48). M'2/3 particularly long, narrow, with short, strongly curved anterior portion contributing to left anterior corner of theca, and almost perpendicular to it, much longer, straight posterior part forming most of left thecal margin (Figs 45d, 48). Digital
short, narrow, morphologically similar to glossal, with small blunt distal spike protuding posteriorly and laterally to anal cone (Figs 45d, 48).

Adorals not preserved in single known specimen. Supracentra not very numerous, tiny skeletal elements with small, wide central spike (Figs 45d, 48). Infracentra not visible (covered by supracentra). No evidence of respiratory structures (e.g. cothurnopores) in right anterior corner of upper surface. Periproct not clearly distinct, probably located at distal extremity of supracentral area, between digital and glossal. Spines numerous, articulated to both left and right thecal margins, preserved at least along G, M'/3 and Z (Figs 45d, 48). Spines narrow, elongate skeletal elements, about 0.5 mm long, made of low density stereome, with wider adradial base for articulation and blunt, opposite, abradial tip.

Proximal aulacophore not preserved, except two isolated, strongly curved, possible inferolaterals, close to appendage insertion (Figs 45d, 48). Stylocone elongate (about 1 mm long), almost cylindrical, slightly wider posteriorly (Figs 45d, 48). Lower (outer) surface of stylocone reticulate, regularly convex and unornamented (no spike). Four small isolated distal ossicles preserved, with well-marked deep longitudinal median groove between raised lateral lips, with no evidence of transverse channels (Figs 45d, 48). Lower surface of ossicles smooth and regularly convex.

Remarks. The holotype and only known individual of *D. izegguirenensis* corresponds to the original material briefly reported by Chauvel (1971) as a small, poorly preserved, heart-shaped stylophoran, possibly corresponding to a juvenile specimen of mitrate ('genre indéterminé AVIII'). Jefferies (in Ubaghs 1994, p. 119-120) was probably the first to observe the presence of spines around the theca and to correctly suggest cornute affinities (see also Lefebvre & Vizcaíno 1999; Gutiérrez-Marcot et al. 2003; Lefebvre & Fatka 2003; Lefebvre et al. 2007; Sumrall & Zamora 2011). Comparison with closely related chauvelicystids (e.g.
Ampelocarpus, Lyricocarpus) suggests that, although spines are preserved along three marginals in *D. izegguirenensis* (G, M\textsubscript{2/3}, Z), their distribution was very likely originally more extensive (i.e. also along D and M\textsubscript{2}; Fig. 47). The possibility that the holotype of *D. izegguirenensis* represents a teratological specimen of *Lyricocarpus* with one less marginal on the right thecal side cannot be entirely ruled out. However, this interpretation is considered herein as unlikely, because chauvelicystids are characterised by a regular trend towards reduction of their number of marginals (see above). The validity of the genus *Destombesicarpus* is further supported by the recent discovery of two other specimens of chauvelicystid with seven marginals in the Upper Ordovician of Bohemia (see below) and also, possibly, of a third one in the Middle Ordovician of Wales (see above; ‘Reticulocarpos? sp. 2’ in Jefferies 1987).

*Destombesicarpus* *budili* sp. nov.

Figures 21d, 45e–f, 49–50

**Derivation of name.** The species name is dedicated to the Czech palaeontologist Petr Budil, who has been actively investigating Ordovician geology and invertebrate faunas of the Prague Basin in the last 30 years.

**Holotype.** CGS.OZ.152 (coll. O. Zicha): part and counterpart of a tiny, almost complete, slightly disarticulated theca with spines articulated to its left and right margins (Figs 21d, 45e–f, 50). Aulacophore not preserved.

**Horizon and locality.** The holotype of *D. budili* was collected in Levín (Fig. 22.7), SW of Králův Dvůr, Prague Basin, Czech Republic, within the Zahořany Formation (lower Katian,
Upper Ordovician; see above). A second specimen, here tentatively assigned to the same species, was observed in the Králův Dvůr Formation (upper Katian, Upper Ordovician) at Lejškov (Fig. 22.10), Prague Basin, Czech Republic (O. Zicha, pers. obs., 2019).

**Diagnosis.** A species of *Destombesicarpus* with an almost quadrangular, thick and broad marginal frame, with almost parallel lateral sides.

**Description.** Slightly disarticulated theca of holotype extremely small (TL = 3.3 mm, TW = 1.6 mm), elongate, almost quadrangular in shape (Fig. 49). Posteriorly open, U-shaped thecal frame particularly massive, consisting of seven broad marginals (three on the left, four on the right) and two rounded adorals. All marginals strongly reticulate. Plate pattern close to bilateral symmetry. No right infracentral area. On both thecal sides, narrow and elongate integumentary surfaces (left infracentral and supracentral areas) with almost similar extension and morphology. Lower thecal surface unornamented (no knob, spike, tubercle), almost flat, except slightly recurved downwards proximal edge of the two anterior-most marginals.

Anterior margins of M₁ and M'₁ regularly convex, forming both gently curved anterior edges and rounded antero-abaxial corners of theca (Figs 45f, 50a). M₁ short, broad, in contact with M'₁ (adaxially), Z (posteriorly) and M₂ (abaxially). M₂ particularly small, inserted adaxially between M₁ and Z (Figs 45e–f, 50). External (outer) edge of M₂ strongly convex. Zygal plate Z relatively elongate, with slightly curved anterior portion in contact with M'₁, M₁ and M₂, and nearly straight posterior part forming most of right thecal margin (Figs 45e–f, 50). Glossal relatively elongate, wide, slightly protruding posteriorly to distal extremity of integumentary areas (Figs 45e–f, 50). M'₁ broad, almost pentagonal in shape, about twice larger than M₁, abaxially in contact with M'₂/₃ along a short, straight suture. M'₁ adaxially sutured to both M₁ (anteriorly) and Z (posteriorly). Distal edge of M'₁ almost parallel to
anterior thecal margin, along left infracentral area. $M_{2/3}$ relatively elongate, wide, slightly curved anteriorly, forming most of left thecal margin, with almost same shape and extension as Z on opposite (right) thecal side (Figs 45e–f, 50). Digital moderately elongate, wide element at distal extremity of left thecal margin (Figs 45e–f, 50). D comparable in size and shape to glossal, and similarly protuding posteriorly to distal extremity of integumentary areas.

Adorals paired ($A'_1$ and $A_1$), broad, relatively wide, rounded, similar to each other, roofing small and narrow aulacophore insertion (Figs 45e, 50b). Supracentral area narrow and elongate, almost quadrangular in shape, slightly larger anteriorly than posteriorly, extending to and forming distal thecal extremity in between D and G (Figs 45e, 50b). Supracentrals and infracentrals not preserved. Left infracentral area, narrow, elongate, framed by G, Z, $M_1$, $M_{2/3}$ and D. Several spines (at least 14–15) regularly articulated along outer (abradial) margins of $M_1$ and Z (on the right) and $M_{2/3}$ (on the left). Each spine with broad, reticulate articulation socket and more delicate, elongate, fibrillar abradial projection (Figs 45e–f, 50).

Periproct not observed, probably located at posterior extremity of theca. Other body openings (right adoral orifice, putative respiratory structures) not observed. No clear evidence of internal structures, except small portion of low, wide zygal crest on internal surface of $M'_1$.

Aulacophore not preserved.

Remarks. The small spiny cornute from Levín shares with *Destombesicarpus izegguirenensis* the possession of a similarly built thecal frame consisting of seven marginals, with two lateral sets of articulated spines and no right infracentral area. The comparable plate pattern of the two specimens justifies their assignment to a same genus. The very small size of the Levín chauvelicystid (about half smaller than *D. izegguirenensis*) questions the possibility that morphological differences between the two specimens from Czech Republic and Morocco are
due to growth allometries. However, their thecal outlines, plates morphology and respective proportions of skeletal elements are so markedly distinct that they are here considered as more likely belonging to two distinct species: *D. budili* and *D. izegguirenensis*. Main differences between the two taxa concern: (1) thecal outlines (bulb-shaped in *D. izegguirenensis*, nearly quadrangular in *D. budili*); (2) the almost bilaterally symmetrical plate pattern of *D. budili*, whereas *D. izegguirenensis* is more markedly asymmetrical; (3) M$_2$ is much smaller in *D. budili* and does not contribute to the right anterior thecal corner; (4) all marginals are wide in *D. budili*, whereas some of them are more delicate in *D. izegguirenensis* (e.g. D, G, M'$_{2/3}$); (5) Z and M'$_{2/3}$ are morphologically comparable in *D. budili*, whereas they are markedly different from each other in *D. izegguirenensis*.

In *D. budili*, spines are clearly present along at least three distinct marginals: M'$_{2/3}$ (on the left), M$_1$ and Z (on the right). Comparison with the situation in closely related chauvelicystids (*Ampelocarpus, Lyricocarpus*) suggests that spines were also very likely originally articulated to M$_2$, and possibly also to D, G and M'$_1$ (Fig. 49).

Family **Cothurnocystidae** Bather, 1913

*Diagnosis.* A family of cornute stylophorans with a boot-shaped theca posteriorly closed by M$_5$ and M'_5; lower thecal surface ornamented (spinal blade on M$_3$, spikes); two adorals (A$_0$ lost); D and G on both sides of posterior infracentral area; Z in marginal position; lower side of proximal-most ossicles smooth; longitudinal median groove with transverse channels.

*Remarks.* The family Cothurnocystidae was originally erected by Bather (1913) so as to separate cornutes with a rigid theca made of few larges plates (Ceratocystidae) from those with large integumentary areas delimited by a distinct, delicate marginal frame.
Cothurnocystids were also characterised by the boot-shaped outlines of their theca ('cothurnus' corresponds to a toe-spined medieval shoe) and the occurrence of a series of well-defined respiratory structures (cothurnopores, lamellipores) in the right anterior corner of their upper thecal surface (Bather 1913; Jaekel 1918). As originally defined, the family Cothurnocystidae was including the two Late Ordovician taxa *Cothurnocystis elizae* and *C. curvata*, both from the Lady Burn starfish bed of Scotland (Bather 1913, 1926; Jaekel 1918).

The diagnosis of the family was modified by Thoral (1935), so as to include taxa with a delicately framed, heart-shaped theca (*Phyllocystis*) and respiratory structures. Consequently, cothurnocystids were defined as cornutes with large integumentary areas framed by thin marginals, and with numerous respiratory structures on their upper thecal side: cothurnopores (*Cothurnocystis elizae*, *C. primaeva*, *Phyllocystis blayaci*), lamellipores (*C. curvata*) or sutural pores (*P. crassimarginata*). All boot-shaped cothurnocystids were assigned to the genus *Cothurnocystis*, and heart-shaped ones, to *Phyllocystis* (Thoral 1935; Gigout 1954; Ubaghs 1963; Chauvel 1966; Jefferies 1968).

In the late 1960s–early 1970s, the description of several new cornute genera (e.g. *Amygdalotheca, Bohemiaecystis, Chauvelicystis, Galliaecystis, Reticulocarpos, Scotiaecystis, Thoralicystis*) prompted a major revision of cornute systematics, with the identification of three distinct families based on the presence and the nature of respiratory structures: Amygdalothecidae (no openings), Cothurnocystidae (cothurnopores or sutural pores), and Scotiaecystidae (lamellipores) (Ubaghs 1968, 1970, 1983, 1994; Chauvel 1971; Ubaghs & Robison 1988; Sumrall *et al.* 1997; Sumrall & Sprinkle 1999). In this revised definition, cothurnocystids were including taxa with a delicate, well-defined marginal frame and large, thin, polyplated integumentary areas (e.g. *Cothurnocystis, Phyllocystis*) as well as cornutes with a more rigidly plated lower thecal surface made of a limited number of skeletal elements.
(e.g. *Nevadaecystis*). All boot-shaped, spineless cothurnocystids were generally assigned to the genus *Cothurnocystis* (e.g. *C.? bifida*, *C. courtessolei*, *C. fellinensis*, *C. melchiori*, *C. occitana*; Ubaghs 1970, 1983, 1994; Ubaghs & Robison 1988), and those with articulated thecal spines to *Chauvelicystis* (see above; Ubaghs 1970, 1983). In the late 1990s, three cothurnopores-bearing Cambrian taxa from Laurentia were also tentatively assigned to the Cothurnocystidae: *Acuticarpus, Archaeocothurnus* and *Ponticulocarpus* (Sumrall et al. 1997; Sumrall & Sprinkle 1999).

This classification of cornutes based on the nature of respiratory structures was not universally accepted. For example, Derstler (1979) identified three major groups of cornutes, based on the presence of respiratory openings and thecal outlines. Following Ubaghs (1970), he placed all taxa lacking respiratory structures within the family Amygdalothecidae (Derstler 1979). However, Derstler (1979) suggested to separate cornutes with respiratory openings into boot-shaped Cothurnocystidae (e.g. *Bohemiaecystis, Chauvelicystis, Cothurnocystis, Nevadaecystis, Scotiaecystis, Thoralicystis*) and more symmetrical, heart-shaped Phyllocystidae (*Phyllocystis*). Jefferies (1969) considered both Amygdalothecidae and Scotiaecystidae as well-defined taxonomic groups, but Cothurnocystidae as a paraphyletic assemblage of early stylophorans deriving from *Ceratocystis*-like forms. Consequently, he placed all cothurnocystid taxa within the family Ceratocystidae (Jefferies 1969; Jefferies & Prokop 1972).

In the late 1980s–2000s, several phylogenetic analyses of cornutes based on the detailed comparisons of skeletal patterns and the identification of putative plate homologies provided new insights into cornute systematics and prompted a deep reevaluation of the definition of the family Cothurnocystidae (Cripps 1988, 1991; Daley 1992; Parsley 1997; Lefebvre & Vizcaïno 1999; Martí Mus 2002; Ruta 2003; Lefebvre 2005). A small, well-defined clade of boot-shaped cornutes with cothurnopores and a delicate, posteriorly closed, spineless
marginal frame enclosing large, polyplated integumentary areas was almost consistently evidenced and identified either as a distinct subfamily (Cothurnocystinae; e.g. Lefebvre & Vizcaïno 1999; Lefebvre 2001) or family (Cothurnocystidae; e.g. Cripps 1988, 1991; Ware & Lefebvre 2007). Depending on the analyses, this cothurnocystid clade is including: *Cothurnocystis courtessolei*, *C. elizae* and *C. primaeva* (Cripps 1988); *C. courtessolei*, *C. elizae*, *C. fellinensis* and *Procothurnocystis owensi* (Cripps 1991; Lefebvre & Vizcaïno 1999; Lefebvre 2001); *Cothurnocystis* spp. and *P. owensi* (Parsley 1997); *C. courtessolei*, *C. elizae*, *C. fellinensis*, *C. primaeva* and *P. owensi* (Martí Mus 2002; Ruta 2003); *Arauricystis* spp., *Cothurnocystis elizae* and *Procothurnocystis* spp. (Lefebvre et al. 2017a, 2019b).

In the last twenty years, the description of several new cornute taxa in the late Cambrian–Early Ordovician time interval (e.g. *Cardiocystella*, *Persiacarpos*) provided new information on cothurnocystid plate patterns and affinities (Sumrall et al. 2009; Lefebvre et al. 2016, 2017a, 2019b; Rozhnov & Parsley 2017). Cothurnocystids, as defined here, form a small, well-defined clade of cornutes retaining plesiomorphic morphologies, relatively comparable to those of some of the earliest known stylophorans, such as *Ponticulocarpus robisoni* (Fig. 13a–b) (Spence Shale, Wuliuan; Sumrall & Sprinkle 1999) and *Archaeocothurnus bifida* (Fig. 15a–b) (Wheeler Formation, Drumian; Ubaghs & Robison 1988; Sumrall et al. 1997). The retention of numerous plesiomorphic features, even in the youngest and most derived cothurnocystids (e.g. *Cothurnocystis elizae*) makes it particularly difficult to identify apomorphies for this family.

All characters used so far to define cothurnocystids are widely distributed within early stylophorans and most other cornute lineages. For example, the possession of a lightly built theca, with large polyplated integumentary areas delimited by a delicate marginal frame (see e.g. Bather 1913; Jaekel 1918; Thoral 1935; Ubaghs 1968, 1970; Lefebvre & Vizcaïno 1999) is a widespread character within cornutes (e.g. *Amygdalotheca*, *Chauvelicystis*, *Galliaecystis*, *Glyptocystis*).
*Ponticulocarpus, Scotiaecystis* and early mitrates (e.g. *Vizcaínocarpus*). Similarly, boot-shaped thecal outlines, with a well-defined spinal blade (see e.g. Bather 1913; Jaekel 1918; Derstler 1979; Lefebvre & Vizcaíno 1999) are not unique to cothurnocystids, but also occur in all earliest stylophorans (e.g. *Ceratocystis, Ponticulocarpus*), chauvelicystids (e.g. *Chauvelicystis*), hanusiids (e.g. *Galliaecystis*) and scotiaecystids (e.g. *Bohemiaecystis*). The occurrence of cothurnopores in the right anterior corner of the supracentral area (see e.g. Bather 1913; Jaekel 1918; Thoral 1935; Ubaghs 1968, 1970; Lefebvre & Vizcaíno 1999) is not limited to cothurnocystids but occurs in many early cornutes (e.g. *Archaeocothurnus, Nevadaecystis, Ponticulocarpus*), some chauvelicystids (e.g. *Chauvelicystis*), hanusiids (e.g. *Drepanocarpos*) and phyllocystids (*Phyllocystis blayaci*). Conversely, several cothurnocystid taxa lack cothurnopores: e.g. *Arauricystis occitana* (see Ubaghs 1994) and a new form (*Procothurnocystis* n. sp. in Lefebvre et al. 2016a) from the lower part of the Fezouata Shale (late Tremadocian, Morocco). Some skeletal-based characters sometimes presented as possible cothurnocystid apomorphies also occur in other cornutes. For example, Cripps (1988) suggested that the possession of a hinged digital process, articulated to M′₄ could represent an apomorphy of the family Cothurnocystidae. However, movable digital processes, articulated to M′₄ also occurs in other cornute taxa, such as e.g. *Bohemiaecystis* and *Prosotiaecystis* (see Ubaghs 1983, 1994; Lefebvre & Vizcaíno 1999). Similarly, the occurrence of a Mc plate (Lefebvre & Vizcaíno 1999) is not unique to cothurnocystids, as this skeletal elements is also present, for example, in amygdalothecids (e.g. *Amygdalotheca*), chauvelicystids (e.g. *Chauvelicystis*) and hanusiids (*Drepanocarpos*) (see discussion above). Finally, the possession of a thecal frame posteriorly closed by a M′₅-M₅ bridge on the lower thecal surface probably represents the plesiomorphic condition in lightly built cornutes and is also documented in e.g. *Persiacarpos* and *Ponticulocarpus* (see above).
Each of the above mentioned characters is widespread within early stylophorans. However, their combined occurrence is restricted to Arauricystis, Cothurnocystis, Procothurnocystis and 'Cothurnocystis' fellinensis (Lefebvre et al. 2017a, 2019). All together these cornutes match precisely the small clade identified as Cothurnocystidae by most phylogenetic analyses (see e.g. Cripps 1991; Parsley 1997; Martí Mus 2002; Ruta 2003). Within this small group, the morphology of 'C.' fellinensis (Figs 1a–b, 10) from the Saint-Chinian Formation (late Tremadocian) of the Montagne Noire (France) appears, in many respects, as the most plesiomorphic (see e.g. Cripps 1988; Lefebvre et al. 2017a, 2019b). This interpretation is supported by the combined occurrence of three adorals (A', A0, A1), a Mc plate between M2 and M3, and a small L-shaped M4 above Z in 'C.' fellinensis (Fig. 10). This plate pattern is unique within stylophorans and strongly suggests that this cornute should be assigned to a distinct genus (see Woods & Jefferies 1992; Lefebvre et al. 2017a, 2019b). The recent description of Persiacarpos jefferiesi (Fig. 13c–d) from the Mila Formation (latest Guzhangian) of the Alborz Range (Iran) questions the possibility that 'C.' fellinensis belongs to the same genus (see above). Although the morphology of P. jefferiesi is incompletely known (see Rozhnov & Parsley 2017), this cornute nevertheless possesses a boot-shaped theca with large integumentary areas, a Mc plate in between M2 and the spinal-bearing M3, a L-shaped M4 above Z, a M5-M'5 bridge, and two small distal posterior processes (D and G). Unfortunately, a single adoral (A') is clearly preserved on the upper surface of one of the paratypes (see Rozhnov & Parsley 2017 pl. 6 fig. 2). In this specimen, a small inverted U-shaped structure, right of A', suggests that a median adoral (A0) was very likely originally present. If this point is confirmed by additional, better preserved specimens, then this would imply that 'C.' fellinensis should be assigned to the genus Persiacarpos. The Montagne Noire cornute is thus tentatively designated herein as P.? fellinensis. It differs from P. jefferiesi in thecal outlines and respective proportions of several skeletal elements (see above).
The plate pattern of *P.? fellinensis* (Fig. 10) is very similar to those of the three cothurnocystid genera *Aurauricystis, Cothurnocystis* and *Procothurnocystis* (Cripps 1988, 1991; Woods & Jefferies 1992; Lefebvre & Vizcaíno 1999; Lefebvre 2001; Martí Mus 2002; Ruta 2003; Lefebvre *et al.* 2017a, 2019b). However, *P.? fellinensis* is not considered here as a member of the family Cothurnocystidae, which is restricted to the small clade uniting *Aurauricystis, Cothurnocystis* and *Procothurnocystis*. Skeletal plate homologies suggest that several cornute taxa probably derived from a *P.? fellinensis*-like ancestor through the loss of distinct marginals: not only cothurnocystids (loss of A0), but also e.g. chauvelicystids (loss of M5 and M′5) and possibly phyllocystids (loss of D, G, M4 and M′4, see above; Ware & Lefebvre 2007). Consequently, including *P.? fellinensis* in the Cothurnocystidae would make this family paraphyletic (Cripps 1988). This option is not retained here.

The genus *Procothurnocystis* Woods & Jefferies, 1992 was defined based on a single specimen (NMW.84.176.119, part and counterpart), originally described as *Cothurnocystis* sp. in the Pontyfenni Formation (Dapingian) of Wales (Jefferies 1987). The reexamination of the holotype confirms that the original specimen is no longer complete, but was partly damaged probably during the preparation of latex casts (see Woods & Jefferies 1992, p. 2-3). The current aspect of the holotype (Fig. 1c–d) does not show any difference with previously figured casts of it (Jefferies 1987, fig. 139a-b; Woods & Jefferies 1992, pl. 1, figs 1-2), but comparison with an earlier photograph of the original specimen indicates that the left posterior extremity of the theca is now missing (see Woods & Jefferies 1992, pl. 1, fig. 3). This photograph makes it possible to infer that plates D, G, M5 and M′5 were originally present. The resulting morphology of *Procothurnocystis owensi* is very similar to that of *Persiacarpos? fellinensis*, with a marginal frame consisting of the same 14 marginals (D, G, M1–5, M′1–5, Mc and Z), cothurnopores, several elongate spine-shaped supracentrals, a proximal aulacophore made of five telescopic rings and very long, similar distal portions of...
the appendage. However, as pointed out by Woods & Jefferies (1992), *P. owensi* differs from
*Persiacarpos? fellinensis* in the possession of two adorals, instead of three (loss of the small
median adoral A0) (see also Cripps 1991; Martí Mus 2002; Lefebvre et al. 2017a, 2019b).

Reexamination of the single known specimen and holotype (MNHN.R.09421) of the
cornute originally described as *Cothurnocystis courtessolei* by Ubaghs (1970) in the Saint-
Chinian Formation (late Tremadocian) of the Montagne Noire (France) confirms that its
marginal frame consists of the same 14 marginals as in *Persiacarpos* (Fig. 13c–d) and
*Procothurnocystis owensi* (Fig. 1c–d), and very likely of only two adorals (A1 and A'1).
Consequently, this cornute is here assigned to *Procothurnocystis* (see also Lefebvre et al.
2016a, 2017a, 2019b). Ubaghs’ original reconstruction of *P. courtessolei* was based on the
camera-lucida drawing of the complete, but slightly disarticulated holotype. A new, slightly
different reconstruction of *P. courtessolei* is proposed here (Fig. 51), in which thecal plates
are replaced in their probable original, articulated position. Although its morphology is
incompletely known (e.g. most of the right part of the supracentral area is not preserved,
making it impossible to document the occurrence of putative spine-shaped platelets and
cothurnopores), *P. courtessolei* appears very similar to *P. owensi*. However, *P. courtessolei*
clearly belongs to a distinct species characterised by different thecal outlines, thinner and
more delicate marginals, a more extensive posterior infracentral area (between D, G, M5 and
M’s), and fewer proximal rings (four instead of five) in the aulacophore (Figs 52, 53c–d; see
also Ubaghs 1970).

In the Zagora area (Morocco), the Fezouata Formation (late Tremadocian) also yielded
abundant and well-preserved specimens of small, thick-framed cothurnocystids without
cothurnopores, which probably correspond to a third, yet undescribed species of
*Procothurnocystis* (Lefebvre et al. 2016a, 2019b). This new Moroccan *Procothurnocystis* is
morphologically very close to another cothurnocystid originally described in the Whipple
Cave Formation (late Furongian) of Nevada (USA) as *Cardiocystella prolixora* (Sumrall et al. 2009; Lefebvre et al. 2017a, 2019b). The type material of *C. prolixora* consists of two fully articulated specimens (holotype 1791TX13 and paratype 1791TX14) both preserved in upper aspect (Sumrall et al. 2009). In the same area, several other specimens of *C. prolixora* were recently collected in slightly younger deposits (middle Tremadocian) of the lowermost Fillmore Formation (Lefebvre et al. 2019b). This additional material comprises both articulated and disarticulated individuals, in upper and lower aspects, which provide further information on the plate pattern of *Cardiocystella* (Fig. 54a–b). Although the redescription of *C. prolixora* is beyond the scope of this study, it is worth mentioning that the new material confirms the existence of several features already suspected by Sumrall et al. (2009): occurrence of only two adorals (A\(_1\) and A'\(_1\)), a M\(_5\)-M'\(_5\) posterior bridge, and a large, extensive posterior infracentral area between D and G (as in *P. courtessolei*). New observations do not support the putative internal position of Z (no evidence that M\(_3\) and G are sutured to each other; see Sumrall et al. 2009 figs 2–3), and they suggest that a small marginal M\(_4\) is probably present above Z on the upper thecal surface. If these observations are correct, the plate pattern of *Cardiocystella* (Fig. 54a–b) would then consist of 14 marginals (D, G, M'_1-M_s, M_1-M_5, M_c and Z) and two adorals (A'\(_1\) and A\(_1\)). This would imply that *Cardiocystella* is a junior synonym of *Procothurnocystis*, and that *P. prolixora* represents the oldest known cothurnocystid (Lefebvre et al. 2017a, 2019b).

The genus *Arauricystis* Lefebvre & Vizcaíno, 1999 was originally defined for cothurnocystids possessing two or three adorals, a L-shaped M\(_4\) above Z, and no M_c plate between M\(_2\) and the spinal-bearing M\(_3\). This genus includes two taxa from the Saint-Chinian Formation (late Tremadocian) of the Montagne Noire (France): *A. occitana* (Fig. 54e–f) and *A. primaeva* (Figs 54c–d, 55b) (see Thoral 1935; Ubaghs 1970, 1994; Lefebvre & Vizcaíno 1999; Lefebvre 2001). Both taxa were originally described based on a single specimen (see...
Two more individuals, recently identified in the same stratigraphic levels of the Montagne Noire, provide some further information on the plate patterns of both *A. occitana* (UCBL-FSL 711926) and *A. primaeva* (UCBL-FSL 711698). Two adorals (A′₁ and A₁) are clearly present in the holotype of *A. occitana* (UCBL-FSL 712519; see Ubaghs 1994). Adorals are not preserved in the holotype of *A. primaeva* (UM.ACI.642; see Ubaghs 1970; Lefebvre & Vizcaïno 1999), but two adorals occur in the new specimen (loss of A₀). Consequently, the two taxa are characterised by the same plate pattern, consisting of 13 marginals (D, G, M′₁-₅, M₁-₅, Z) and two adorals (A′₁ and A₁).

Moreover, their proximal aulacophore is similarly made of five telescopic rings (Thoral 1935; Ubaghs 1970, 1994). However, significant differences in thecal outlines and ornamentation support their identification as two distinct species. Two younger occurrences of *Arauricystis* are described herein in the Izegguirene Formation (early Sandbian) of the eastern Anti-Atlas, Morocco and the Dobrotivá Formation (late Darriwilian) of Bohemia, Czech Republic (*A. clariondi* sp. nov.; see below).

Within cothurnocystids, the phylogenetic position of *Arauricystis* has long remained problematic, depending on whether Mc was secondarily lost (derived condition; Cripps 1988; Lefebvre *et al.* 2017a, 2019b) or if this plate was originally absent (plesiomorphic condition, as in e.g. *Archaeocothurnus* and *Ponticulocarpus*; see Cripps 1991; Daley 1992; Lefebvre & Vizcaïno 1999; Lefebvre 2001, 2005; Martí Mus 2002; Ruta 2003). The widespread occurrence of the Mc plate in most post-Miaolingian stylophorans (e.g. amygdalothecids, *Drepanocarpos*, chauvelicystids, mitrates, *Phyllocystis*) and its frequent loss in several taxa (e.g. most hanusiids, derived chauvelicystids) suggest that it is more likely that this skeletal element was also secondarily lost in *Arauricystis*. Moreover, the absence of the central adoral (A₀) in *Arauricystis* represents another derived character, supporting the view that its plate pattern is not plesiomorphic. Consequently, *Arauricystis* is here interpreted as a
cothurnocystid probably deriving from a *Procothurnocystis*-like ancestor by the loss of the Mc plate (Lefebvre *et al*. 2019b). Both genera are morphologically close and share the loss of A0.

The type genus of the family Cothurnocystidae, *Cothurnocystis*, was originally defined based on abundant and well-preserved material from the Lady Burn Starfish Bed (South Threave Formation, late Katian) of Scotland, UK, assigned to two distinct taxa, *C. elizae* and *C. curvata* (Bather 1913, 1926). The plate pattern of the type species, *C. elizae*, consists of 13 marginals (D, G, M'1–5, M1–3, M5, Mc and Z) and two adorals (A', A1). This plate pattern, which is considered herein as diagnostic of the genus *Cothurnocystis* (Figs 3c, 4c), is very similar though distinct from those of both *Arauricystis* (Fig. 54c–f) and *Procothurnocystis* (Figs 1c–d, 51–53). *Cothurnocystis* shares with these two taxa the loss of the median adoral A0 (apomorphy of the cothurnocystids), but it differs from them by the loss of the small, L-shaped marginal (M4) above Z. *Cothurnocystis* further differs from *Arauricystis* by the occurrence of Mc (this plate is lost in *Arauricystis*). Consequently, it seems very likely that *Cothurnocystis* derives from a *Procothurnocystis*-like ancestor by the loss of M4. The revised definition of the genus *Cothurnocystis* proposed here (i.e. a cothurnocystid with a Mc plate, but no M4) implies that most taxa originally assigned to it have been or have to be affiliated to another genus: *Arauricystis* (*A. occitana* (Ubaghs, 1994), *A. primaeva* (Thoral, 1935)), *Archaeocothurnus* (*A. bifida* (Ubaghs & Robison, 1988)), *Chauvelicystis* (*C. spinosa* (Ubaghs, 1970)), *Nevadaecystis* (*N. americana* (Ubaghs, 1963)), *Persiacarpos* (*P.? fellinensis* (Ubaghs, 1970)), *Procothurnocystis* (*P. courtessolei* (Ubaghs, 1970)), *Proscotiaecystis* (*P. melchiori* (Ubaghs, 1983)), and *Scotiaecystis* (*S. curvata* (Bather, 1913)). Consequently, the genus *Cothurnocystis* is now restricted to its type species, *C. elizae* (Lefebvre *et al*. 2017a, 2019b).
Although cothurnocystids form a small, well-defined clade deriving from a *P.? fellinensis*-like ancestor, several other cornute genera were also tentatively assigned to this family: *Acuticarpus* (Sumrall et al. 1997), *Archaeocothurnus* (Ubaghs & Robison 1988; Parsley 1997; Sumrall et al. 1997; Ruta 2003), *Ponticulocarpus* (Sumrall & Sprinkle 1999), and *Trigonocarpus* (Lefebvre & Vizcaíno 1999). The morphologies of *Acuticarpus delticus* and *A.? republicensis*, both from the Snowy Range Formation (Furongian) of Wyoming (USA) are unfortunately too incompletely known to support any precise systematic assignment within cornutes. In all available specimens, the posterior extremity of the theca is too poorly preserved to identify if it was originally open or closed either by a M5-M′5 bar (on the lower surface) or a M4-M′4 bridge (on the upper side). It is similarly unclear if Z was in central or in marginal position, and the precise number of marginals is not known (Sumrall et al. 1997).

However, the occurrence of three adorals in *A.? republicensis* represents a plesiomorphic feature, which is lost in all cothurnocystids (apomorphy of the family; see above). Moreover, the presence of a well-defined, wide peripheral flange around the theca and the correlated absence of any ornamentation on the lower surface of anterior marginals do not support any close relationship with cothurnocystids, but rather suggest affinities with cornutes such as *Flabellicarpus* (Fig. 15d), *'Phyllocystis' jingxiensis* (Fig. 16a) or *'P.' jingxiensis*-like cornutes from the Furongian of Korea (Cornuta indet. A in Lee et al. 2005) and the late Tremadocian of Morocco (cornute indet. n. gen. n. sp. 1’ in Lefebvre et al. 2016a). Consequently, *Acuticarpus* is very likely not related to cothurnocystids.

The morphologies of *Archaeocothurnus bifida* from the Miaolingian (Wheeler Formation) of Utah and *A. ghoshutensis* (Fig. 15a–b) from the Furongian (Lincoln Peak and Whipple Cave formations) of Nevada are better documented (see above; Ubaghs 1963; Ubaghs & Robison 1985; Sumrall et al. 1997). Similarities with cothurnocystids mostly result from symplesiomorphies (e.g. posterior closure of the thecal frame by a M5-M′5 bar). The presence...
of a distinct Ms element inserted along the posterior thecal margin between the spinal-bearing
M₃ (on the right) and a L-shaped M₄ (on the left) clearly supports scotiaecystid affinities (see
above; Cripps 1991; Lefebvre 2005). Similarly, the cothurnocystid-like aspect of
Ponticulocarpus (Fig. 13a–b) from the Miaolingian (Langston Formation) of Utah reflects
more symplesiomorphies (e.g. M₅-M₅' bar, L-shaped M₄ above Z) rather than close affinities.
In many respects, the morphology of cothurnocystids appears as more derived: for example,
Ponticulocarpus still possesses three adorals (plesiomorphic condition; A₀ is lost in
cothurnocystids) and lacks a Mc marginal between M₂ and M₃. It is thus likely that
Persiacarpos derives from a Ponticulocarpus-like ancestor. These two genera are not
considered here as cothurnocystids, because this would make the family paraphyletic (see
above).

Finally, putative affinities between Trigonocarpus and cothurnocystids were tentatively
suggested by Lefebvre & Vizcaíno (1999). This genus was originally described based on a
single, incomplete individual (holotype: UCBL-FSL 712531, part and counterpart) from the
Saint-Chinian Formation (late Tremadocian) of the Montagne Noire (Ubaghs 1994). In recent
years, the discovery of a second, partly preserved specimen (UM.ACI.644, part and
counterpart) confirms the occurrence of a transversely very elongate and narrow right
infracentral area, partly delimited by three spike-bearing marginals (M₂, Mc and M₃). This
specimen also adds some additional information: e.g. occurrence of a strongly curved M'₂
forming the left anterior thecal corner and bearing a strong knob on its lower surface.
However, the precise number of adorals and marginals, the putative occurrence of respiratory
structures, the precise position of the zygal plate (central or marginal), as well as the aspect of
the posterior extremity of the theca (closed or open) still remain unknown. Although
cothurnocystid affinities cannot be entirely ruled out, the very delicate morphology of
marginals, along with their strong ornamentation and the unusual transverse extension of the
right infracentral area are all features suggesting more probable affinities with the
Tizagzaouine cornute and/or early hanusiids. Pending the discovery of additional, better
preserved material of *Trigonocarpus*, this genus is thus not affiliated here to the family
Cothurnocystidae.

Genus *Arauricystis* Lefebvre & Vizcaíno, 1999

*Type species.* *Cothurnocystis primaeva* Thoral, 1935

*Diagnosis.* A genus of cothurnocystids with no Mc marginal (between M₂ and M₃), and a L-
shaped M₄ (above Z).

*Remarks.* The genus *Arauricystis* was previously known only from the late Tremadocian of
France (*A. occitana, A. primaeva*; Thoral, 1935; Ubaghs 1970, 1994; Lefebvre & Vizcaíno
1999). Its range is extended here to include two younger occurrences in the late Darriwilian of
Bohemia and the early Sandbian of Morocco (*A. clariondi* sp. nov.; see below). The two
genera *Cothurnocystis* and *Procothurnocystis* are morphologically close to *Arauricystis*, but
their number of marginals is different (*Lefebvre et al.* 2017a, 2019b). *Arauricystis* differs
from the two other cothurnocystid genera by the loss of Mc, and from *Cothurnocystis* by the
presence of M₄ (see above).

*Arauricystis clariondi* sp. nov.

Figures 25f, 55a, 56–59

2008 *Cothurnocystis* sp. – *Lefebvre et al.*, p. 11, fig. 6B
2010a *Cothurnocystis* sp. – Lefebvre et al., p. 8

2018 *Cothurnocystis* sp. – Lebrun, p. 125, fig. D

2019b *Procothurnocystis* sp. – Lefebvre et al., p. 51

**Derivation of name.** The species is named after the French geologist and stratigrapher Louis Clariond (1900–1961) for his pioneer investigations on Ordovician series in the Maïder and Tafilalt areas in the early 1930s.

**Holotype.** MHNM.15690.67 (coll. Reboul): slightly disarticulated, almost complete theca (D missing, spinal blade not preserved) in lower aspect (no counterpart) with fully articulated proximal aulacophore, stylocone, 15 proximal-most ossicles and associated cover plates (Figs 55a, 57c). Single isolated, large skeletal element near left anterior thecal corner possibly corresponding to disarticulated right adoral (A1). Infracentral pavement, precise boundaries between marginals and minute morphological details poorly preserved because of associated lithology (coarse sandstones).

**Paratypes.** MHNM.15690.4 et MHNM.15690.103 (coll. Reboul): both specimens exposed in upper aspect (no counterpart) on slabs with other echinoderm remains (*Ascocystites*, mitrates). Minute morphological details and precise plate boundaries often obscured by preservation in coarse sandstones. MHNM.15690.4 (Figs 57b, 59b) exhibiting complete, fully articulated theca with associated proximal aulacophore, stylocone, five to six proximal-most ossicles, and widely ajar, opposite sets of cover plates. MHNM.15690.103 (Figs 57a, 59c) almost complete, fully articulated theca (partly broken posteriorly during rock splitting in the field: D, M’3 and M’4 missing), with proximal rings and particularly long distal aulacophore.
Posterior half of preserved portion of distal appendage poorly preserved, but anterior (distal) part consisting of over 25 articulated ossicles and associated cover plates.

*Other material.* A single specimen, NMP.L13230 (coll. Barrande), preserved in upper aspect (no counterpart), exposing nearly complete, slightly disarticulated theca (posterior part missing: D, M', proximal aulacophore, and long portion of distal appendage (stylocone, at least eight ossicles and associated cover plates in open position) (Figs 58, 59a). Minute morphological details preserved (e.g. delicate spike-shaped supracentraals, longitudinal median groove and transverse channels on stylocone) due to fine-grained lithology.

*Horizon and locality.* Holotype and paratypes all from type-locality, Bou Nemrou (ECR-F4), Jbel Tijarfaïouine Massif, about 30 km SW of Erfoud, eastern Anti-Atlas, Morocco (see above; Fig. 17.5), Izegguirene Formation (Sa1, lower Sandbian). Fourth specimen (NMP.L13230) likely from old mines near the villages of Kařez and Kařízek, about 5 km south of Zbiroh, Rokycany area, Bohemia, Czech Republic (see above; Fig. 22.4), Dobrotivá Formation (Dw3–Sa1, upper Darriwilian to lowermost Sandbian).

*Diagnosis.* A species of *Arauricystis* with four rings in proximal aulacophore; zyal plate Y-shaped, with marginal branches much longer than central (zygal) one.

*Description.* Thecal outlines markedly boot-shaped, framed by 13 relatively broad marginals (D, G, M'1–5, M1–5 and Z) and two adorals (A'1 and A1) delimiting four distinct integumentary areas (Fig. 56). Left and right infracentral areas entirely framed by marginals. Posterior infracentral area and supracentral area connected to each other at distal extremity of theca. Lower thecal surface strongly ornamented, with elongate protuberance (M'2) and downward-
oriented spikes (M₂, M₃). Digital and glossal expressed as thin, elongate blades, posteriorly
articulated to distal extremity of marginal frame, and anteriorly largely in contact, adaxially,
with lateral edges of anal lobe. Anterior thecal margin almost straight, with low, wide median
concavity near aulacophore insertion. Left thecal margin, zygal bar and right margin of right
infracentral area almost parallel to each other and nearly perpendicular to anterior margin.
Left thecal margin almost straight. Zygal bar short, straight, narrower than marginal frame.
Right thecal margin consisting of two distinct portions: short, concave part, anteriorly
(delimited by M₂ spike and M₃ spinal), and much wider, strongly concave portion, posteriorly
(between spinal and glossal). M₅-M₅ bridge almost parallel to anterior thecal margin.
Posterior margin of right infracentral area slightly oblique to subparallel to both M₅–M₅
bridge and anterior margin. Holotype slightly smaller (TW=10.7 mm) than
MHNM.15690.103 (TW=11.5 mm), MHNM.15690.4 (TW=12 mm) and NMP.L13230
(TW=12.3 mm) (with TW estimated between M'₂–M'₃ suture, on the left, and M₂–M₃
boundary, on the right, knobs and spikes excluded; Fig. 25f). Thecal height maximal along
anterior margin (M'₁–₂, M₁–₂), regularly decreasing in distal direction, minimal along posterior
blades (digital, glossal)

Anterior edge of lower thecal surface made of four thick, broad, almost equally
contributing marginals: M'₁ and M₁ (adaxially), M'₂ and M₂ (abaxially). M₁ relatively small,
almost quadrangular, transversely elongate, with slightly concave anterior margin, straight
posterior edge (along right infracentral area) and short sutures along M'₁ (adaxially) and M₂
(abaxially). Anterior margin of M₁ forming high proximal thecal wall with, adaxially, narrow,
high cup-shaped right aulacophore apophysis, at and posteriorly to aulacophore insertion. In
specimen NMP.L13230 (Figs 58a, 59a), upper portion of M₁ bearing narrow and deep
infundibulum (abaxially to right apophysis) and well-defined anterior oblique groove (across
right upper corner of right apophysis). M'₁ relatively broad, T-shaped, with two wide and
thick anterior (marginal) branches, and more delicate posterior (zygal) portion (Figs 55a, 57c, 58a, 59a). Anterior margin of M'1 almost straight to slightly sinuous. Antero-adaxial branch of M'1 particularly short, forming high, cup-shaped vertical wall (left apophysis) along and posteriorly to aulacophore insertion. Upper (internal) aspect of left apophysis masked by articulated (Figs 57a–b, 59b–c) or slightly displaced left adoral (Figs 58a, 59a). Left anterior part of M'1 relatively short, wide, abaxially in contact with M'2. Posterior portion of M'1 short and narrow, with strongly concave lateral edges along left and right infracentral areas. Distal extremity of M'1 in contact with Z along short suture. Internal surface of posterior portion of M'1 bearing relatively high zygal crest, clearly visible in NMP.L13230 (overlying supracentra missing; Figs 58a, 50a) and more indirectly in Moroccan specimens (narrow longitudinal ridge folding the supracentral area; Figs 57a–b, 59b–c).

M'2 broad, strongly curved, T-shaped, forming right anterior thecal corner (Figs 55a, 57, 58a, 59). Antero-abaxial branch of M'2 consisting of a strong, blunt, spike-shaped protuberance directed downwards and laterally. Left (marginal) and right (spike-shaped) anterior portions of M'2 both contributing to anterior thecal margin. Posterior branch of M'2 shorter, narrower, posteriorly sutured to M'3. M'3, short, strongly curved, framing right posterior corner of right infracentral area (Figs 55a, 57, 58a, 59). Postero-abaxial extremity of M'3 carrying relatively long, blunt, downwards-directed blade-like expansion (spinal), oriented obliquely (about 45°) to main body axis. Spinal blade best preserved in MHN.M.15690.4 (Fig. 57b, 59b), though possibly incomplete distally. Marginal portions of M'3 particularly short and subequal in length. Zygal plate Y-shaped, with two wider and more elongate posterior branches in marginal position, and third (anterior) one forming distal portion of zygal bar (Figs 55a, 57c). Right posterior branch of Z particularly elongate along right infracentral area and abaxially in contact with M'3. Posterior portion of Z shorter, wider, distally sutured to both G and M'5. Anterior branch of Z particularly short, narrow, proximally in contact with M'1,
and carrying distal portion of zygal crest on its upper (internal) surface. Anterior and posterior parts of Z forming together an almost straight structure, with right branch diverging from them at acute and obtuse angles, respectively. $M_4$ elongate, narrow, slightly curved skeletal element restricted to upper thecal surface, closely associated to underlying marginal portions of Z (i.e. posterior and right branches of Z; Figs 57a–b, 58a, 59). $M_4$ also in contact with both G (posteriorly) and $M_3$ (abaxially). $M_5$, short, gently curved, transversely elongate, almost flat, pentagonal skeletal element forming with $M_5'$ (on the left) the right half of the small posterior bridge separating the left infracentral area (proximally) from the posterior infracentral area (anal lobe, distally) on the lower thecal surface (Figs 55a, 57b–c, 59b). $M_5$ sutured to G (postero-adaxially), $M_5'$ (abaxially) and Z (antero-adaxially). Anterior margin of $M_5$ gently concave along left infracentral area. Posterior margin of $M_5$ straight to slightly convex along anal lobe. Glossal elongate, narrow, slightly curved, blunt, blade-like marginal, best preserved in holotype (length: 7.3 mm; maximal width: 1.4 mm; Figs 55a, 57c). Right (adaxial) edge of G gently concave, slightly thicker than opposite (left) convex margin. Antero-abaxial extremity of G in contact with anal lobe (MHN.M.15690.103; see Figs 57a, 59c).

$M'_2$ wide, broad, strongly curved marginal forming left anterior corner of theca. In holotype, antero-abaxial portion of lower surface of $M'_2$ bearing low, elongate, downwards directed protuberance (Figs 55a, 57c). $M'_3$ wide, elongate, pentagonal skeletal element framing most of abaxial margin of left infracentral area (Figs 55a, 57b–c, 58a, 59a–b). $M'_3$ anteriorly sutured to $M'_2$, and posteriorly to both $M'_4$ (abaxially) and $M'_5$ (adaxially). $M'_4$ small, elongate, almost quadrangular element forming left posterior extremity of marginal frame (Figs 55a, 57b–c, 58a, 59a–b). $M'_4$ sutured to both $M'_3$ (anteriorly) and $M'_5$ (adaxially). Digital articulated to distal, slightly protruding extremity of $M'_4$. Precise morphology of D preserved only in specimen MHN.M.15690.4 (Figs 57b, 59b). Digital apparently narrower and
shorter than glossal, but precise length and morphology unknown. Antero-adaxial portion of D largely in contact with anal lobe (Figs 57b, 59b). M₃ small, flat, broad marginal restricted to lower thecal surface forming (with M₅) left half of posterior bridge separating left and posterior infracentral areas (Figs 55a, 57b–c, 59b). Anterior margin of M₃ strongly concave, along left infracentral area. M₅ sutured to M₃ (antero-abaxially), M₄ (abaxially) and M₅ (adaxially).

Two adorals above aulacophore insertion, at anterior extremity of upper thecal surface. Right adoral (A₁) best preserved in NMP.L13230 (Figs 58a, 59a). A₁ almost quadrangular, transversely elongate, slightly wider adaxially than abaxially, with deep notch excavated at about mid-length of anterior edge. Notch surrounded laterally by two posteriorly converging lips forming widely open V-shaped crest (Figs 58a, 59a). Left adoral (Aʻ₁) less well preserved than A₁ in available material. Aʻ₁ gently arched, elongate skeletal element abaxially sutured to underlying Mʻ₁, and adaxially in contact with A₁ (Figs 57a–b, 58a, 59).

Infracentral areas relatively extensive, polyplated, made of numerous small, tessellate integumentary platelets. Infracentraals preserved only in holotype (Figs 55a, 57c), with large patches of more or less distinct, polygonal skeletal elements in fully articulated, almost complete left infracentral area. Left infracentral area longitudinally elongate (length: 7.8 mm; maximal width: 3.2 mm), more or less ovoid, with rounded anterior (along Mʻ₁ and Mʻ₂) and posterior extremities (along M₃ and M₅), and almost parallel adaxial (along M₁ and Z) and abaxial sides (along M₂ and M₃). In holotype (Figs 55a, 57c), right infracentral area consisting of numerous, dissociated polygonal (mostly hexgonal) small-sized elements. Right infracentral area subtrapezoidal, moderately elongate transversely (maximal length: 4.4 mm; width: 4.8 mm), delimited by five marginals (Mʻ₁, M₁, M₂, M₃ and Z). Posterior infracentral area (anal lobe) poorly preserved, corresponding to disarticulated platelets occurring posteriorly to M₃-M₅ bridge.
Supracentral area consisting of abundant, small, rounded, convex integumentary elements forming a tessellate, flexible, unorganised membrane (Figs 57a–b, 58a, 59). Although strongly dissociated, upper surface of NMP.L13230 also showing at least four collapsed, spike-shaped, elongate supracentrals (Figs 58a, 59a). In paratype MHNM.15690.103, right anterior corner of almost complete, fully articulated supracentral area showing relatively distinct evidence, in spite of poor preservation due to coarse grain size, of well-organised row of at least seven cothurnopore-like structures, each apparently made of two opposite U-shaped elements (Figs 57a, 59c). More precise morphological details of respiratory structures not preserved. In MHNM.15690.103, posterior extremity of supracentral area forming inflated, terminal structure (anal pyramid) made of distinct, elongate skeletal elements (Figs 57a, 59b).

Proximal aulacophore wide, elongate, consisting of four, particularly large imbricate rings, each made of four skeletal elements (e.g. in MHNM.15690.4, width of proximal rings [3.6 mm] corresponding to 30 percent of TW [12 mm]; Figs 57b, 59b). Each ring consisting of a pair of symmetrical, left and right inferolaterals (lower and lateral walls) roofed by two smaller, symmetrical tectals (Fig. 58b). Stylocone, moderately elongate, funnel to bobin-shaped, with straight to slightly concave lateral margins, regularly decreasing in width distally (e.g. in holotype, length: 1.9 mm; proximal width: 1.7 mm; distal width: 1.1 mm). Lower surface of stylocone entirely smooth (holotype; Figs 55a, 57c). Upper surface of stylocone best preserved in NMP.L13230 (Figs 58b, 59a), with longitudinal groove deeply encased between two lateral lips, leading to lateral depressions through paired transverse channels. Similar internal structures (longitudinal median groove, lateral lips, paired transverse channels) occurring on upper (internal) surface of more anterior elements of distal aulacophore. Particularly long, fully articulated portions of distal aulacophore preserved in several specimens: e.g. 30 mm long distal appendage in MHNM.15690.103, consisting of over 50 ossicles (25 of which are well-preserved) and associated cover plates (Figs 57a, 59c).
Each ossicle wider than long, with rounded lower surface and almost flat upper side. Two
cover plates (left and right) articulated to each underlying ossicle (Figs 57a, 59c). Cover
plates poorly preserved, apparently fan-shaped (NMP.L13230), with no obvious
ornamentation, each overlapping distally its more anterior neighbour (Figs 58b, 59a).

Remarks. In spite of their preservation in relatively coarse sandstones, the three Moroccan
specimens can be confidently assigned to the genus Arauricystis, based on their plate pattern
(absence of both A₀ and Mc, presence of M₄). The Bou Nemrou cothurnocystids differ from
the two other species of Arauricystis in their number of proximal rings (four instead of five in
both A. occitana and A. primaeva; see Thoral 1935; Ubaghs 1970, 1994). Within the genus
Arauricystis, the Moroccan specimens are morphologically closer to A. primaeva (Figs 54c–d,
55b), with which they share relatively comparable thecal outlines and a similar strong
ornamentation on marginals. However, the Bou Nemrou specimens differ from A. primaeva
in the respective proportions of some marginals (e.g. the right branch of Z is short in A.
primaeva, but particularly elongate in Moroccan specimens; in correlation, the left branch of
M₃ is much longer in A. primaeva), the straight morphology of their left thecal margin (it is
regularly curved in A. primaeva) and the shape of their spinal blade (sharp in A. primaeva,
blunt and wide in Moroccan specimens). The Bou Nemrou cothurnocystids are
morphologically more distinct from A. occitana (Fig. 54e–f): their ornamentation is stronger
(e.g. spinal blade is very reduced in A. occitana), their thecal outlines are different (e.g. the
posterior extremity of the left infracentral area is particularly wide in A. occitana) and
cothurnopores are present in the right anterior corner of the supracentral area (A. occitana
lacks respiratory structures; Ubaghs 1994). Consequently, the Bou Nemrou cothurnocystids
are here assigned to a distinct, third species of Arauricystis: A. clariondi.
Although it is preserved only in upper aspect, the single specimen of cothurnocystid from the Dobrotivá Formation (NMP.L13230; Figs 58, 59a) can be confidently identified as belonging to the genus *Arauricystis* (two adorals, no Mc marginal between M₂ and M₃, and a distinct M₄ above Z). The Bohemian cornute shares with *A. clariondi* the presence of four proximal rings (instead of five in both *A. occitana* and *A. primaeva*), similarly shaped M₃ (short, restricted to right posterior thecal corner) and Z (with long marginal branches), as well as a relatively straight left thecal margin. The putative presence of cothurnopores cannot be documented in the Czech specimen, because the right anterior region of its supracentral area is too poorly preserved (the same difficulty occurs in MHNM.15690.4 and in the two known specimens of *A. primaeva*). Several supracentrales of the Dobrotivá specimen are modified into elongate spike-like processes (Figs 58a, 59a), comparable to those already described in *Persiacarpos? fellinensis* and *Procothurnocystis owensi* (Figs 1b, d, 53b; Ubaghs 1970; Woods & Jefferies 1992). No such spike-shaped supracentrales have been observed in *A. clariondi* (see above). However, if such delicate structures were originally present in Bou Nemrou cothurnocystids, it is very likely that they would not have been preserved. In the three specimens of *A. clariondi*, minute morphological details of aulacophore elements (e.g. longitudinal median groove, transverse channels) and even precise thecal plate boundaries are largely obscured by their preservation in coarse sandstones. It is thus likely that the apparent absence of spike-shaped supracentrales in the Moroccan material is taphonomic. Consequently, in the absence of significant morphological difference between the Dobrotivá cothurnocystid and the three known specimens of *A. clariondi*, they are here interpreted as conspecific.

Family *Scotiaecystidae* Caster & Ubaghs in Ubaghs, 1968
**Diagnosis.** A family of cornute stylophorans with a boot-shaped theca posteriorly closed by

M₅ (M₃ lost); lower thecal surface ornamented (spinal blade on M₃, spikes); no Mc between

M₂ and M₃; Z in marginal position (M₄ lost); Ms between M₃ and Z; G inserted posteriorly to

M₅ and Z; two adorals (A₀ lost); periproct on upper thecal surface; lower side of proximal-
most ossicles smooth.

**Remarks.** Thoral (1935) was probably the first to identify three distinct morphotypes within

the family Cothurnocystidae, based on the nature of respiratory structures and the shape of

thecal outlines: taxa with cothurnopores and either a boot-shaped (*C. elizae, C. primaeva*) or a

heart-shaped theca (*Phyllocystis blayaci*), and those with lamellipores and a boot-shaped

theca (*C. curvata*) (see also Jefferies 1969; Derstler 1979). However, Thoral (1935) did not

assign *C. curvata* to a separate genus or a distinct family. The occurrence of lamellipores in a

new cornute from the Middle Ordovician of Bohemia prompted Ubaghs & Caster (in Ubaghs

1968) to create the family Scotiaecystidae. As defined in the *Treatise on Invertebrate

Paleontology*, the main apomorphy of this family was the possession of lamellipores (e.g.

Ubaghs 1968, 1970; Chauvel 1971; Jefferies & Prokop 1972; Sumrall *et al.* 1997; Lefebvre *et

al*. 2017b). Within scotiaecystids, two distinct monospecific genera were also created, based

primarily on the morphology of lamellipores and the number of posterior spines. *Scotiaecystis*

Caster & Ubaghs, in Ubaghs 1968 was characterised by the occurrence of a single posterior

spine (glossal) and the possession of lamellipores separated by low lamellae not protruding


*Bohemiaecystis* Caster, in Ubaghs 1968 was defined based on the absence of posterior spines

and the presence of lamellipores with relatively high lamellae, deeply extending below the

The diagnosis of the genus *Scotiaecystis* was modified by Ubaghs (1970), so as to include taxa with either one (glossal; *S. curvata*) or two (digital and glossal; *S. griffei*) posterior spines. As pointed out by Ubaghs (1970), the morphology of *S. griffei* was problematic, because its lamellipores were more similar to those of *Bohemiaecystis* (with high and deep lamellae) than to those of *S. curvata* (with low, external lamellae) (Ubaghs 1970). A solution to this difficulty was proposed by Chauvel (1971), who defined the genus *Thoralicystis* for scotiaecystids with two posterior spines and high lamellae. Thus scotiaecystids comprised three distinct genera of cornutes with lamellipores and no posterior spines (*Bohemiaecystis*), one spine (*Scotiaecystis*), or two spines (*Thoralicystis*). However, the validity of this scheme was questioned by Ubaghs & Robison (1988, fig. 11.8), who suggested that both D and G were possibly present in *Bohemiaecystis*.

The description of a new species of *Scotiaecystis* from the Upper Ordovician of northern Ireland (*S. collapsa*) provided the opportunity for Cripps (1988) to reevaluate the systematics of cornutes, based on the identification of plate homologies. This first character-based phylogenetic analysis confirmed the validity of the family Scotiaecystidae as a well-defined clade of cornutes, comprising the three genera *Bohemiaecystis, Scotiaecystis* and *Thoralicystis* (Cripps 1988, 1989a, 1991; Daley 1992; Gil Cid *et al.* 1996d; Martí Mus 2002). Following Jefferies (1986), Cripps (1988, 1989a, 1991) reinterpreted *Cothurnocystis melchiori* Ubaghs, 1983 as a scotiaecystid and, based on its plate pattern, assigned it to the genus *Thoralicystis* (see also Daley 1992; Gil Cid *et al.* 1996d; Martí Mus 2002). This late Floian cornute from the Montagne Noire (France) was originally considered as a cothurnocystid, because of the presence of numerous, distinct, though very densely packed, cothurnopore-like U-shaped plates in the right anterior corner of its supracentral area (Fig. 5b; Ubaghs 1983; Ubaghs & Robison 1988). These respiratory structures were considered by Cripps (1988, 1991) as equivalent to the lamellipores of other scotiaecystids, and forming together a lamellate organ...
Consequently, the morphological disparity of respiratory structures within Scotiaecystidae was thus wider than initially suggested (i.e. not only lamellipores with low or high lamellae, but they also included densely packed cothurnopore U-shaped plates). This implied that lamellipores s. str. could not be considered as an apomorphy of the family Scotiaecystidae. This clade was redefined based on the presence of a lamellate organ and an unique plate pattern resulting from the occurrence of an extra marginal 's' (Ms; see above) inserted between the spinal-bearing M₃ and the posterior zygal plate Z (Cripps 1988, 1989b; Daley 1992; Gil Cid et al. 1996d; Martí Mus 2002; Ruta 2003).

In a more comprehensive phylogenetic analysis of cornute stylophorans, based on more characters and taxa, Cripps (1991) suggested including the Cambrian cornute \textit{Cothurnocystis bifida} within the family Scotiaecystidae. Although \textit{C. bifida} (later assigned to the genus \textit{Archaeocothurnus} by Sumrall et al. 1997) is possessing typical cothurnopores, its placement within scotiaecystids was motivated by the occurrence of a distinct marginal Ms (Cripps 1991). This proposal of a wider scotiaecystid clade defined solely on plate homologies was not followed by most later authors, who maintained a more traditional definition for the family, based primarily on the presence of a lamellate organ (see Gil Cid et al. 1996d; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002; Ruta 2003; Ware & Lefebvre 2007; Lefebvre et al. 2017b; but see Lefebvre 2005).

Ubaghs (1994) acknowledged the placement of \textit{Cothurnocystis melchiori} within the family Scotiaecystidae (see Jefferies 1986; Cripps 1988, 1989b, 1991), but he suggested assigning it to a new genus, \textit{Proscotiaecystis}, morphologically close to but distinct from \textit{Thoralicystis}. Ubaghs (1994) justified this decision based on the structurally different organizations of lamellate organs in \textit{Proscotiaecystis} (consisting of densely packed but distinct cothurnopore
U-shaped plates) and in other scotiaecystids (with numerous lamellae corresponding to fused, adjacent, undistinct U-shaped plates) (see also Lefebvre & Vizcaïno 1999).

The morphology and plate pattern of Bohemiaecystis were reevaluated by Gil Cid et al. (1996d), who assigned to this genus a new species (B. jefferiesi) from the Upper Ordovician of the southern Central Iberian Zone, Spain. Based on overall similarities between B. bouceki and B. jefferiesi (lamellate organ, thecal outlines), they concluded that the Bohemian form probably possessed only one posterior spine. The genus Bohemiaecystis (with high lamellae and G) was thus presented as morphologically distinct from both Scotiaecystis (with low lamellae and G) and Thoralicystis (with high lamellae and both D and G) (Gil Cid et al. 1996d; Domínguez et al. 2002b; Marti Mus 2002). However, based on the reexamination of the original type material of B. bouceki, Lefebvre & Vizcaïno (1999) suggested that D and G were very likely both present in the type-species of Bohemiaecystis (see also Ubaghs & Robison 1988). This observation implied that Bohemiaecystis bouceki and all taxa assigned to Thoralicystis shared the same plate pattern (with two posterior spines) and similarly built lamellate organs with high lamellae protruding into the thecal cavity (Lefebvre & Vizcaïno 1999; Lefebvre 2000a, 2001, 2005; Lefebvre & Fatka 2003; Noailles 2016; Lefebvre et al. 2017b). Consequently, Lefebvre & Vizcaïno (1999) suggested that Bohemiaecystis, because of its original definition (lacking both D and G; Ubaghs 1968) and the uncertainty on its precise number of posterior spines (none, one or two depending on the authors), should be synonymised with the better-known genus Thoralicystis, originally clearly defined as possessing high lamellae and both D and G (see Chauvel 1971). In recent years, the observation of the three known specimens of scotiaecystids from the Dobrotivá Formation of Bohemia confirmed the occurrence of two posterior spines in B. bouceki (see below) and, thus, that Bohemiaecystis and Thoralicystis share identical lamellate organs and plate patterns.
Consequently, it is suggested herein that *Thoralicystis* Chauvel, 1971 represents a junior synonym of *Bohemiaecystis* Caster in Ubaghs, 1968 (see above).

In their systematic revision of the order Cornuta, Lefebvre & Vizcaño (1999) considered that *Proscotiaecystis*, *Scotiaecystis* and *Thoralicystis* formed a well-defined monophyletic subfamily (*Scotiaecystinae*) within cothurnocystids (see also Lefebvre 2000a, 2001, 2005). This clade was defined by the possession of a lamellate organ, the presence of a strong spike on Mc, the absence of a spinal blade on M₃, and the loss of three skeletal elements (A₀, M₄, M‴) (Lefebvre & Vizcaño 1999). In this revised classification, the three cornute genera could be differentiated based on the structure of their lamellate organ and their number of posterior spines: *Proscotiaecystis* (with D, G and densely packed cothurnopore U-shaped plates), *Scotiaecystis* (with G and lamellipores), and *Thoralicystis* (with D, G and lamellipores). In this scheme, the single-spined Spanish scotiaecystid described by Gil Cid et al. (1996d) was re-assigned to *Scotiaecystis*. In the last twenty years, the discovery of several new late Cambrian–Tremadocian cornutes with previously undocumented plate patterns provided new avenues for the identification of plate homologies in stylophorans (see above; Ware & Lefebvre 2007; Lefebvre & Ausich 2021). These new findings do not confirm the validity of the plate homologies suggested by Lefebvre & Vizcaño (1999) for scotiaecystids, but instead they support the view that these taxa are characterised by the insertion of one additional marginal (Ms) between the spinal-bearing M₃ and Z (Cripps 1988, 1989b, 1991; Daley 1992; Martí Mus 2002).

These new late Cambrian–Tremadocian stylophorans also display an unexpectedly wide morphological disparity for their respiratory structures. For example, densely packed cothurnopore U-shaped plates are no longer restricted to *Proscotiaecystis* (Figs 5b, 11a). Similar structures also occur in *Flabellicarpus* (see Martí Mus 2002), the Tizagaouine cornute (Fig. 15c; see Ware & Lefebvre 2007), and possibly also in a poorly preserved
Furongian stylophoran from Nevada (*Scotiaecystis?* sp. in Sumrall *et al.* 1997). The term 'proto-lamellate organ' was coined by Lefebvre *et al.* (2017b) for these respiratory structures, morphologically intermediate between standard cothurnopores (with numerous sutural pores sheltered within opposite U-shaped plates) and the lamellate organs of *Bohemiaecystis* and *Scotiaecystis* (with numerous lamellipores separated by lamellae made of the fused walls of adacent U-shaped plates).

Recent advances in plate homologies and new patterns of character distribution in early stylophorans (e.g. respiratory structures) both question the definition and precise outlines of the clade Scotiaecystidae. For example, considering the insertion of Ms within the marginal frame in between M₃ and Z as the main apomorphy of the family would imply a relatively wide definition of scotiaecystids. This clade would then include *Archaeocothurnus* along with *Bohemiaecystis, Proscotiaecystis* and *Scotiaecystis* (Cripps 1991). Conversely, if the occurrence of lamellipores is retained as the defining apomorphy of the Scotiaecystidae, then this family would include only the two genera *Bohemiaecystis* and *Scotiaecystis* (see e.g. Ubaghs 1968, 1970; Parsley 1997; Lefebvre *et al.* 2017b). However, in the last thirty years, the general consensus was rather to consider the family Scotiaecystidae as the clade uniting all taxa assigned either to *Bohemiaecystis, Proscotiaecystis, Scotiaecystis* and/or *Thoralicystis* (e.g. Cripps 1988, 1989b; Daley 1992; Gil Cid *et al.* 1996d; Lefebvre & Vizcaïno 1999; Lefebvre 2000a, 2001, 2005; Martí Mus 2002; Ruta 2003; Ware & Lefebvre 2007). This concept is retained here.

The occurrence of proto-lamellate organs in other, unrelated stylophorans (e.g. *Flabellicarpus, Tizagzaouine cornute*) implies that scotiaecystids cannot be defined based solely on the nature of their respiratory structures, but also on their plate pattern. They share with *Archaeocothurnus* (Fig. 15a–b) the possession of Ms, but they differ from it by the loss of M₄ (see above). It is unclear if *Archaeocothurnus* possesses two or three adorals (see
Ubaghs & Robison 1988; Sumrall et al. 1997), but only two of them are clearly present in all scotiaecystids (loss of A0; Ubaghs 1968, 1970; Cripps 1988, 1989b, 1991; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Martí Mus 2002). Similarly, the posterior closure of the thecal frame is poorly documented in Archaeocothurnus (Ubaghs & Robison 1988; Sumrall et al. 1997). In most specimens, this area is poorly preserved. At least one element (M5) is definitively present in A. goshutensis (scotiaecystid condition), but the possibility that M5 and M’s both occur (plesiomorphic condition) cannot be entirely ruled out (Figs 15a–b; see Sumrall et al. 1997, fig. 7.3-4).

The brief historical overview of the systematics of scotiaecystid cornutes (see above) highlights the difficulties in identifying which characters (i.e. number of posterior spines and/or morphology of respiratory structures) are best suited for the definition of genera in this family. Some classifications have focused exclusively on plate patterns, thus leading to the identification of only two genera (Bohemiaecystis and Scotiaecystis; Parsley 1997). Others have partially mixed characters based on marginal plates and respiratory structures, generally leading to the identification of three distinct genera: either Bohemiaecystis, Scotiaecystis and Thoralicystis (Chauvel 1971; Cripps 1988, 1989b, 1991; Gil Cid et al. 1996; Martí Mus 2002) or Proscotiaecystis, Scotiaecystis and Thoralicystis (Lefebvre & Vizcaïno 1999; Lefebvre 2001, 2005; Lefebvre & Fatka 2003; Lefebvre et al. 2006; Noailles 2016). More rarely, all four genera Bohemiaecystis, Proscotiaecystis, Scotiaecystis and Thoralicystis have been considered as valid (Domínguez et al. 2002b; Ruta 2003). This situation has remained long complicated by the uncertainties about the precise number of posterior spines in the type-species of Bohemiaecystis: none (Ubaghs 1968, 1970; Chauvel 1971), one (G; Cripps 1988, 1989b, 1991; Gil Cid et al. 1996; Martí Mus 2002), or two (D and G; Ubaghs & Robison 1988; Lefebvre & Vizcaïno 1999). Based on all available fossil evidence (including the description of several new taxa and the revision of all previously described Middle and Late...
Ordovician peri-Gondwanan scotiaecystids; see below), four distinct morphotypes are identified herein within the family Scotiaecystidae. These four morphotypes are defined on their skeletal plate pattern and their respiratory structures. It is suggested here to assign taxa belonging to these four morphotypes to four distinct genera.

The first morphotype corresponds to scotiaecystids with a proto-lamellate organ (Fig. 5b) and two articulated posterior spines (D and G). This combination of characters matches exactly the diagnosis proposed by Ubaghs (1994) for the genus *Proscotiaecystis* (see also Lefebvre & Vizcaïno 1999; Lefebvre 2001). Within the family Scotiaecystidae, the morphology of *P. melchiori* (Ubaghs, 1983) from the Landeyran Formation (late Floian) of the Montagne Noire (France) appears, in many respects, as the most plesiomorphic (Fig. 11a; Cripps 1991; Gil Cid et al. 1996d; Lefebvre & Vizcaïno 1999; Martí Mus 2002). As in *Archaecothurnus* and many other cornutes (e.g. *Chauvelicystis*, *Cothurnocystis*, *Nanocarpus*, *Persiacarpos*, *Ponticulocarpus*), the digital and glossal are both present and articulated to the posterior margin of the thecal frame (Ubaghs 1983; Ubaghs & Robison 1988; Lefebvre & Vizcaïno 1999). It is very likely that *Proscotiaecystis* derives from an *Archaecothurnus*-like ancestor by the loss of M₄, and the acquisition of a proto-lamellate organ (Cripps 1991; Gil Cid et al. 1996d; Lefebvre 2005). The marginal frame of *Proscotiaecystis* consists of two adorals (A'₁, A₁) and 12 marginals (D, G, M'₁₋₄, M₁₋₃, M₅, Ms, Z).

The second morphotype (Fig. 11b) includes scotiaecystids with two posterior spines (D and G) and a raised lamellate organ, with lamellipores separated by high lamellae deeply protruding within the thecal cavity (Fig. 5c). These features were originally used by Chauvel (1971) to erect the genus *Thoralicystis*. However, new fossil evidence demonstrates that the same combination of characters occurs also in *Bohemiaecystis bouceki* (Ubaghs & Robison 1988; Lefebvre & Vizcaïno 1999; Lefebvre 2001). This implies that *Thoralicystis* Chauvel,
1971 represents a junior synonym of *Bohemiaecystis* Caster in Ubaghs, 1968 (see above).

Although the marginal frames of *Bohemiaecystis* and *Proscotiaecystis* are identical in terms of constitutive skeletal elements (same two adorals and 12 marginals), their patterns are slightly different. In *Bohemiaecystis*, the digital is not articulated to the posterior, but to the left side of the thecal frame (see below).

The third scotiaecystid morphotype comprises taxa with a single posterior spine (D lost) and a flat lamellate organ (Fig. 5d), with lamellipores separated by low lamellae not extending into the thecal cavity. This combination of characters corresponds precisely to the original diagnosis of the genus *Scotiaecystis* (Fig. 11d; Caster & Ubaghs in Ubaghs 1968; Chauvel 1971; Cripps 1988, 1989b, 1991; Gil Cid *et al.* 1996d; Parsley 1997; Martí Mus 2002). This morphotype is observed in two Laurentian, highly derived scotiaecystids from the Upper Ordovician of northern Ireland (*S. collapsa*) and Scotland (*S. curvata*). Their marginal frame is built of two adorals (A'₁ and A₁) and 11 marginals (G, M'₁₋₄, M₁₋₃, M₅, Ms, Z).

The fourth morphotype (Fig. 11c) corresponds to scotiaecystids with a single posterior spine (D lost) and a raised lamellate organ, morphologically similar to that occurring in *Bohemiaecystis*. This combination of characters was long thought to be characteristic of the genus *Bohemiaecystis* (see Cripps 1988, 1989b, 1991; Gil Cid *et al.* 1996d; Dominguez *et al.* 2002b; Martí Mus 2002; Gutiérrez-Marco *et al.* 2018). However, the occurrence of two posterior spines in *B. bouceki* (type-species of *Bohemiaecystis*) implies that single-spined scotiaecystids with a raised lamellate organ belong to a different genus. Although their marginal frame is made of the same 13 skeletal elements as in *Scotiaecystis* (*A'₁, A₁, G, M'₁₋₄, M₁₋₃, M₅, Ms, and Z*), cornutes belonging to the fourth morphotype are morphologically distinct. Their lamellate organ is raised and *Bohemiaecystis*-like, and their left anterior thecal corner is made by M'₂ (instead of M'₃ in *Scotiaecystis*). A new generic name, *Thoralicarpus*
gen. nov., is proposed herein for these scotiaecystids morphologically intermediate between

*Bohemiaecystis* and *Scotiaecystis*.

The new systematic subdivision of the family Scotiaecystidae into the four genera *Bohemiaecystis* (Fig. 11b), *Proscotiaecystis* (Fig. 11a), *Scotiaecystis* (Fig. 11d), and *Thoralicarpus* (Fig. 11c) is largely consistent with previous works identifying various morphotypes within this family, and probably describes best the various observed combinations between the two main characters (posterior spines and respiratory structures).

**Genus Bohemiaecystis** Caster in Ubaghs, 1968

*Type species.* *Bohemiaecystis bouceki* Caster in Ubaghs, 1968

**Diagnosis.** A genus of scotiaecystids with lamellipores separated by numerous, high lamellae protruding into thecal cavity; D articulated to M'4 on left thecal side.

**Remarks.** The plate pattern of *Bohemiaecystis* and, in particular, its precise number of posterior spines articulated to the theca (digital and glossal) have long remained poorly documented and controversial, because of the diagnosis of its type-species, *B. bouceki* Caster in Ubaghs, 1968, originally based on two incomplete specimens (holotype NMP.L17728 and paratype NMP.L32304; see below). The careful reexamination of the type material of *B. bouceki*, coupled with the observation of one more specimen (CMC.IP.50176) from the same lithostratigraphic unit (Dobrotivá Formation), confirms the occurrence of two posterior spines (see discussion below; Ubaghs & Robison 1988; Lefebvre & Vizcaïno 1999; Lefebvre 2001), and thus, the synonymy of the genus *Thoralicystis* Chauvel, 1971 with *Bohemiaecystis* Caster in Ubaghs, 1968 (see above).
Within scotiaecystids, *Bohemiaecystis* is morphologically very close to both *Proscotiaecystis* and *Thoralicarpus* gen. nov. (see below). The plate patterns of *Bohemiaecystis* (Fig. 11b) and *Proscotiaecystis* (Fig. 11a) are identical and consist of two adorals (A₀ lost) and the same 12 marginals (D, G, M'₁-₄, M₁-₃, M₅, Ms, Z). Although these taxa have been often assigned to a same, single genus (see e.g., Cripps 1988, 1989b, 1991; Gil Cid et al. 1996d; Parsley 1997; Martí Mus 2002), they are considered here as belonging to two distinct genera, mostly because of their different respiratory structures. *Proscotiaecystis* possesses a proto-lamellate organ (Fig. 5b) morphologically comparable to those occurring in several other stylophorans (e.g. *Flabellicarpus*, *Tizagzaouine cornute*), whereas *Bohemiaecystis* shares with all more derived scotiaecystids the presence of a lamellate organ (Ubaghs 1994; Lefebvre & Vizcaïno 1999; Lefebvre 2001; Lefebvre et al. 2017b). Because of their similarly built, raised lamellate organs all taxa here assigned to the two genera *Bohemiaecystis* and *Thoralicarpus* gen. nov. have been often grouped together in a same genus (see e.g. Cripps 1988, 1989b, 1991; Gil Cid et al. 1996; Martí Mus 2002; Gutiérrez-McCulloch et al. 2018). However, *Bohemiaecystis* possesses two posterior spines (D and G), whereas a single one (G) is present in *Thoralicarpus* gen. nov. (D lost; see above).

As defined here, the genus *Bohemiaecystis* forms a well-defined clade of Early–Middle Ordovician (peri-)Gondwanan scotiaecystids (see below). Its type species, *B. bouceki*, originally described in the Dobrotivá Formation (late Darriwilian) of Bohemia (Czech Republic), represents the youngest known occurrence of the genus. Other described taxa here assigned to *Bohemiaecystis* include *B. griffei* (Ubaghs, 1970) from the Saint-Chinian Formation (late Tremadocian) and *B. ubaghsi* (Lefebvre & Vizcaïno, 1999) from the Landeyran Formation (late Floian) of the Montagne Noire (France), as well as *B. zagoraensis* (Chauvel, 1971) from the upper part of the Fezouata Shale (early–mid Floian) in the Central Anti-Atlas (Morocco). Other yet undescribed occurrences of the genus *Bohemiaecystis* are
present in the Upper Member of the Guayoc Chico Group (early Tremadocian) of Jujuy Province, Argentina (Nohejlová et al. 2018) and the lower part of the Fezouata Shale (late Tremadocian) of the Zagora area, Morocco (Lefebvre et al. 2016a, 2019a). Two additional occurrences of scotiaecystids are also assigned herein to the genus *Bohemiaecystis*: the first one is from the Guezzart Formation (late Darriwilian), Alnif area, eastern Anti-Atlas, Morocco (*B. chouberti* sp. nov., see below; Chauvel 1971, 1978; Derstler 1979; Gutiérrez-Marcos et al., 2003; Lefebvre & Fatka 2003) and the second one, from the Tachilla Formation (early–mid Darriwilian), Tiznit area, western Anti-Atlas, Morocco (*B.?* sp., see below).

All taxa assigned to the genus *Bohemiaecystis* display a relatively wide morphological diversity in terms of thecal outlines, strength of thecal ornamentation, and relative proportions of their marginals. With the single exception of *B. ubaghsi*, six rings are present in the proximal aulacophore of all known occurrences of *Bohemiaecystis* (see below; e.g. Ubaghs 1968, 1970, 1983; Chauvel 1971; Lefebvre & Vizcaïno 1999). The more reduced number of rings in *B. ubaghsi* (three to four) questions the possibility that this very small-sized scotiaecystid corresponds either to the juvenile stages of a larger, yet unknown, late Floian species of *Bohemiaecystis* or to a paedomorphic form (see e.g. Ubaghs 1983; Lefebvre & Vizcaïno 1999). In *B. ubaghsi*, it is also likely that the proportionately large extension of the two posterior blades (glossal and spinal) represents another juvenile morphological feature (see discussion below). The same disproportionate expansion of these two processes in small-sized scotiaecystids from the Fezouata Shale, Morocco (see Lefebvre et al. 2019a fig. 9) suggests that these cornutes may correspond either to juveniles of a larger taxon (e.g. *B. zagoraensis*) or to a strongly paedomorphic new species. Abundant material collected in the last twenty years in the Zagora area will certainly help clarifying this point, as well as critically reevaluating the morphology of *B. zagoraensis* (originally described based on a
single, incomplete specimen in upper aspect; see Chauvel 1971) through a comparison with the very similar looking coeval form from the Montagne Noire (B. griffei).

**Bohemiaecystis bouceki** Caster in Ubaghs, 1968

Figures 11b, 26a, 60–62

*1968 Bohemiaecystis bouceki* Caster in Ubaghs, S550, figs 338.2a-c, 349.1-2

1970 *Bohemiaecystis bouceki* Caster – Ubaghs, p. 56

1972 *Bohemiaecystis bouceki* Caster – Jefferies & Prokop, p. 76, fig. 1

1979 *Bohemiaecystis bouceki* Caster – Philip, p. 449, fig. 6e

1986 *Bohemiaecystis bouceki* – Jefferies, p. 334, fig. 9.6

1988 *Bohemiaecystis bouceki* Caster – Cripps, p. 1069, figs 16, 18, table 2

1988 *Bohemiaecystis* sp. – Parsley, p. 357

1988 *Bohemiaecystis bouceki* Caster – Ubaghs & Robison, p. 15, fig. 11.8

1989a *Bohemiaecystis bouceki* Caster – Cripps, p. 56

1989b *Bohemiaecystis bouceki* Caster – Cripps, p. 217, figs 1, 2

1991 *Bohemiaecystis bouceki* Caster – Cripps, p. 348, figs 14, 15, 17, table 4

1994 *Bohemiaecystis bouceki* Caster – Cripps & Daley, p. 125, table 2

1996d *Bohemiaecystis bouceki* Caster – Gil Cid et al., p. 313, figs 2.15, 3E

1996 *Bohemiaecystis* sp. – Gee, p. 257, fig. 4.17e

1997 *Bohemiacystics* [sic] sp. – Parsley, p. 227, fig. 6, appendix 2

1998b *Bohemiacystics* [sic] sp. – Parsley, p. 112

1999 *Thoralicystis bouceki* (Caster) – Lefebvre & Vizcaïno, p. 433, figs 10.2, 11.3, 14.2-3,

26.1

1999 *Bohemiaecystis bouceki* Caster – Prokop & Petr, p. 64, table 1
2001 *Thoralicystis bouceki* (Caster) – Lefebvre, p. 613, fig. 15.2

2002 *Bohemiaecystis bouceki* Caster – Domínguez *et al.*, p. 50

2002 *Bohemiaecystis bouceki* Caster – Martí Mus, p. 109, tables 1,2, figs 9J, 11

2003 *Thoralicystis* sp. – Lefebvre & Fatka, p. 90

2003 *Bohemiaecystis bouceki* Caster – Ruta, p. 564, fig. 2

2005 *Thoralicystis bouceki* (Caster) – Lefebvre, p. 482, figs 2, 3

2006 *Thoralicystis bouceki* (Caster) – Lefebvre *et al.*, appendix

2007a *Thoralicystis bouceki* (Caster) – Lefebvre, p. 186

2009 *Bohemiaecystis bouceki* Caster – Rahman *et al.*, p. 426, table 2

2016 *Thoralicystis* sp. – Noailles, p. 6, fig. 2.9, table 1

**Holotype.** NMP.L17728 (coll. Hanuš): part and counterpart of fully articulated, almost complete specimen (Figs 61a–b, 62a–b). Lower aspect of holotype exposing proximal aulacophore and most of lower thecal surface (complete marginal frame, fully articulated left and right infracentral areas). Opposite side of holotype with stylocone, proximal rings, and incompletely preserved upper thecal surface (lamellate organ, zygal crest, fully articulated supracentral pavement). Left and posterior portions of theca not visible in upper aspect. Posterior spines (D and G) not preserved on part and counterpart. Spinal blade apparently blunt, but possibly posteriorly truncated. In the original description of *B. bouceki*, no specimen was explicitely designated as holotype by Caster (in Ubaghs 1968). In the collections of the National Museum, Prague, NMP.L17728 is identified as the holotype, because it corresponds to the single fully illustrated specimen of *B. bouceki* figured in the *Treatise on Invertebrate Paleontology* (i.e. both thecal sides and closer view on the lamellipores; Ubaghs 1968, figs 338.2a,b, 349.1,2)
Paratype. NMP.L32304 (coll. Hanuš): part and counterpart of fully articulated theca (Figs 61c–d, 62c–d). Aulacophore not preserved. Lower thecal surface almost complete, with large portions of undisturbed left and right infracentral areas. Digital articulated to M′. Upper thecal surface incomplete (left half and adorals missing), exposing numerous articulated supracentraals, well-preserved lamellate organ and most right marginals. In the collections of the National Museum, Prague, specimen NMP.L32304 is labeled as paratype of *B. bouceki*, based on its figure in the original description of this species (Ubaghs 1968, fig. 338.2c).

Other material. CMC.IP.50176 (coll. Bouček): largely excavated (prepared) anterior portion of fully articulated theca in upper aspect (no counterpart), revealing part of high lamellate organ in right anterior corner of supracentral area. Fully articulated aulacophore collapsed on its left side, i.e. exposing right lateral aspect of proximal rings, stylocone, eight proximal-most ossicles and associated cover plates. This specimen was probably not available when Caster originally described *B. bouceki* (in Ubaghs 1968), as its label indicates that it was acquired by the University of Cincinnati Museum in 1974. A cast of CMC.IP.50176 is available in the collections of Lyon 1 University (UCBL.FSL.711923).

Horizon and localities. All three specimens of *B. bouceki* were collected in the Dobrotivá Formation (Dw3, late Darriwilian), Barrandian area, Czech Republic. In its original description, *B. bouceki* was also reported from the underlying Šárka Formation (Dw1–2, Darriwilian) (see e.g. Ubaghs 1968, 1970; Derstler 1979). However, none of the two specimens originally examined by Caster (in Ubaghs 1968) for the original description of *B. bouceki* was collected in the Šárka Formation. The confusion possibly comes from the two localities, where the holotype and paratype were found, and which both contain 'Šárka' in their name. The type locality of *B. bouceki* is not precisely known. Locality details on the
label of the holotype NMP.L17728 refer to Praha-Šárka (Fig. 22.1), i.e. several fields and outcrops located NW of Prague in Barrande's time and no more accessible due to the development of the city. Paratype NMP.L32304 was collected in Šárka field, near Hammernikova villa (Fig. 22.2). This locality is now situated within the city of Prague, near the primary school of Vokovice (Nad Lávkou street). The third specimen is from Malé Přílepy (Fig. 22.3), about 18 km SW of Praha-Šárka.

Diagnosis. A species of Bohemiaecystis with broad, thick-framed, weakly ornamented sabot-shaped theca, with single small knob on lower surface of both M'2 and M2; spinal blade short and blunt; M1 long, forming right anterior thecal corner; Ms short; anterior and right branches of Z almost perpendicular to each other, both longer than left branch; right infracentral area almost as long as wide; proximal aulacophore consisting of six rings.

Description. Theca sabot-shaped, relatively broad, slightly wider than long (in both holotype and paratype: TW=30 mm, TL=24 mm), almost bilaterally symmetrical in upper aspect (Figs 26a, 60). Thecal frame consisting of two adorals (A'1, A1), ten thick and broad marginals (M'1-4, M1-3, M5, Ms, Z), and posterior spine-shaped skeletal elements: D and G(?). Anterior thecal margin particularly short, almost restricted to wide median concave re-entrant at aulacophore insertion. Left and right anterior thecal corners poorly differentiated, with smooth transition between strongly convex lateral thecal margins and gently curved adaxial portions of anterior marginals M1 and M'2. Left thecal side longer than right one, extending from M'2 to posterior extremity of M5. Short concave notch at left posterior thecal corner, along Z-M5 suture, possibly for glossal insertion. Right thecal margin regularly arched from abaxial portion of M1 to distal extremity of short, blunt spinal blade. Posterior thecal margin straight to slightly convex, delimited abaxially by two short posterior extensions produced by Z, on the left
along posterior extremity of left infracentral area), and M$_3$ on the right (spinal blade). Zygal bar wide, gently curved, more or less parallel to left thecal margin, separating left and right infracentral areas on lower thecal surface. Left infracentral area elongate, crescent-shaped, with strongly convex abaxial edge, slightly concave adaxial margin (along zygal bar), widest between Z-M$_1'$ suture and M$_1'$, and decreasing in width both anteriorly and posteriorly. Left infracentral area entirely framed by six marginals (M$_1'$-4, M$_5$ and Z). Right infracentral area broad, slightly elongate transversely, delimited by six skeletal elements (M$_1'$, M$_1$-3, Ms and Z). Right infracentral area subtrapezoidal in shape, with short, sinuous anterior edge almost parallel to longer, straight posterior side. Lateral borders of right infracentral area gently convex, posteriorly diverging from each other, with right (abaxial) one slightly longer than left one (along zygal bar). Lower thecal surface almost flat, except along aulacophore insertion (raised antero-adaxial portions of M$_1$ and M$_1'$, below strong aulacophore apophyses) and on lower surface of both M$_2$ and M$_2'$ (each bearing a low elongate abaxial spike-shaped protuberance).

M$_1$ transversely elongate, forming marked, rounded elbow corresponding to right anterior thecal corner, immediately right of aulacophore insertion. Adaxial part of M$_1$ and adjoining anterior (marginal) portion of M$_1'$, each bearing cup-shaped aulacophore apophysis, forming high vertical, anterior wall of theca, posteriorly to aulacophore insertion (Figs 61c, 62c). On lower thecal surface, antero-adaxial margins of M$_1$ and M$_1'$ particularly high, rapidly decreasing in height both abaxially and posteriorly (Figs 61a, c, 62a, c). Right of upper abaxial edge of right apophysis, small cup shaped structure (right scutula) present on internal (upper) side of M$_1$ (Figs 61b, 62b). Small groove (infundibulum) extending upwards and abaxially from postero-abaxial extremity of right scutula towards small notch located on upper edge of M$_1$, right of right scutula, next to aulacophore insertion (Figs 61b, 62b). Anterior oblique groove running from upper edge of right aulacophore apophysis towards
postero-abaxial corner of right scutula and adaxial extremity of infundibulum (Figs 61b, d, 62b, d). Deep anterior transverse groove occurring behind posterior walls of left and right apophyses, on internal (upper) surface of both M'1 and M1 (Figs 61d, 62d). Abaxial portion of M1 almost flat (unornamented) on lower thecal surface, abaxially in contact with M2 along short, straight suture. M2 slightly longer than M1, gently curved, forming most of right thecal margin. Lower surface of M2 almost flat, except low, blunt, elongate spike-shaped structure at about mid-length along abaxial edge (Figs 61a, c, 62a, c). M3 small, Y-shaped skeletal element forming right posterior corner of thecal frame. Anterior and left marginal branches of M3 short, subequal in length, almost perpendicular to each other. Posterior portion of M3 (spinal blade) displaying same orientation as anterior branch. Distal extremity of spinal blade possibly short and blunt, though not clearly distinct in two best preserved specimens (Figs 61a, c, 62a, c). Ms straight to slightly sinuous, shorter than M2, extending along posterior margin of right infracentral area, in contact with both M5 (on the right) and Z (on the left) along short and straight sutures (Figs 61a, c–d, 62a, c–d). Zygal plate (Z) T-shaped, with anterior (zygal) part much longer than posterior branches and proximally sutured to distal (zygal) portion of M'1. Left posterior branch of Z slightly shorter than right one. Anterior and right branches of Z almost perpendicular to each other (Figs 61a, c, 62a, c). Presence of relatively high, longitudinal zygal crest on internal (upper) surface of Z suggested by slightly disrupted pavement of overlying supracentrals, on both sides of it (Figs 61b, 62b). Glossal not observed in holotype and paratype. M5 particularly short, curved skeletal element, forming left posterior thecal corner (Figs 61a, c, 62a, c). M'4 gently curved, longer than M5, with small rounded bump at about mid-length, along abaxial margin (Figs 61c, 62c). Adaxial margin of M'4 slightly concave, along left infracentral area. M'4 sutured to both M'3 (anteriorly) and M5 (posteriorly). Minute, slightly elongate digital (length: 1.5 mm, width: 0.8 mm) articulated to abaxial protuberance of M'4 (Figs 61c, 62c). M'3 gently curved, elongate, apparently
unornamented, longer than \( M_4 \) and about same length as Ms (Figs 61a, c, 62a, c). \( M_2' \) strongly curved, forming left anterior corner of thecal margin, about same size as \( M_1 \). Lower surface of \( M_2' \) with low, elongate, spike-shaped antero-abaxial protuberance, more or less equivalent in size and extension to similar structure on opposite (right) thecal side, on \( M_2 \) (Figs 61a, c, 62a, c). \( M_1' \) T-shaped, with posterior (zygal) branch much longer than particularly short and subequal left and right anterior (marginal) portions (Figs 61a, c, 62a, c). On lower thecal surface, (abaxial) branch of \( M_1' \) much lower than raised right (adaxial) part (along aulacophore apophysis) and adjoining portion of \( M_2' \) (antero-abaxial left protuberance). On upper thecal surface, displaced supracentrals suggesting occurrence of underlying strong longitudinal zygal crest on internal (upper) side of \( M_1' \) (Figs 61b, 62b).

Two adorals preserved in holotype (Figs 61b, 62b). \( A_1' \) transversely elongate, unornamented, longer than \( A_1 \), abaxially sutured to underlying \( M_1' \). \( A_1 \) broad, slightly collapsed in holotype, exposing complex anterior margin, along contact with underlying \( M_1 \).

Anterior portion of \( A_1 \) containing internal transverse groove protected by a raised lip, and leading antero-abaxially to right adoral orifice (Figs 61b, 62b). Supracentrals particularly numerous, small (most of them less than 1 mm wide), polygonal (generally hexagonal), forming thin tessellate membrane on upper thecal surface (Figs 61d, 62d). Lamellate organ elongate, fusiform, complex structure extending obliquely from next to \( A_1-M_1 \) suture (anteriorly) to close to \( M_2-M_3 \) suture (posteriorly) on upper thecal surface (Figs 5c, 61b, d, 62b, d). In both holotype and paratype, lamellate organ about 15 mm long and about 3.5 mm wide, though regularly decreasing in width both anteriorly and posteriorly. In holotype, lamellate organ consisting of over 45 distinct lamellae forming a low, raised structure (Figs 5c, 61b, 62b). Each individual lamella consisting of a thin, delicate (about 0.2 mm thick), more or less rhombic calcite wall, with longest diagonal almost perpendicular to edges of lamellate organ (i.e. lamella length: up to 3.5 mm), and shortest one perpendicular to it (i.e.
lamella height: up to 1.5 mm). Line of maximal height of lamellae running more or less parallel to lateral sides of lamellate organ, and about two thirds distance away from its abaxial border, i.e. along sutures between anterior (abaxial) and posterior (adaxial) U-shaped plates (Figs 5c, 61b, d, 62b, d). Each lamella protruding both above upper supracentral area and below it, deep into intrathecal cavity (Figs 5c, 61b, d, 62b, d). Lamellipores narrower (about 0.07 mm wide) along long, gently sloping anterior (abaxial) portion of lamellate organ, and wider (about 0.12 mm) in shorter and steeper posterior (adaxial) part of it (Figs 5c, 61b, 62b).

Thickness of lamellae and width of lamellipores both remaining constant everywhere within the lamellate organ, independently of their location in it. No evidence of periproct on lower thecal surface. Most likely area for anal opening (i.e. at left posterior extremity of supracentral area, anteriorly to M₅) not preserved in three available specimens (Figs 61b, d, 62b, d). Left infracentral area consisting of numerous polygonal (mostly hexagonal) small, tessellate skeletal elements, frequently more elongate next to zygal bar (Figs 61a, c, 62a, c).

Left infracentrals slightly larger (up to 1.4 mm wide) than most supracentrals. Right infracentrals typically broad, tessellate, polygonal (hexagonal) plates, larger than left infracentrals (up to 1.7 mm wide), with some of them more elongate along zygal bar (Figs 61a, c, 62a, c).

Proximal aulacophore slightly longer than wide (about 6.3 mm long and 4.2 mm wide in holotype), and consisting of six, well-defined telescopic rings (Figs 61a–b, 62a–b). Each proximal ring made of four skeletal elements: two symmetrical (left and right), strongly curved inferolaterals forming the lower surface and lateral walls; and two small sub-quadrangular tectals (about 0.8 mm wide and 0.7 mm long) forming a delicate arch above the two underlying inferolaterals (Figs 61a–b, 62a–b). Raised anterior margin of each ring overlapping depressed posterior portion of next, more distal one or, proximal portion of stylocone (Figs 61b, 62b). Stylocone moderately elongate (3.4 mm long in holotype), cone-
shaped, wider posteriorly (2.8 mm in holotype) than anteriorly (1.6 mm in holotype) (Figs 61b, 62b). Lower surface of stylocone entirely smooth and rounded (CMC.IP.50176). Upper surface of stylocone (NMP.L17778) and following ossicles (CMC.IP.50176) with well-defined median longitudinal groove and transverse channels leading to lateral depressions (Figs 61b, 62b). Longest observed portion of distal appendage consisting of eight articulated ossicles and associated pairs of articulated cover plates (CMC.IP.50176). Lower surface of ossicles smooth and rounded. Two pairs of opposite cover plates apparently articulated to stylocone, and a single pair to each more distal ossicle (CMC.IP.50176). Cover plates, relatively high, fan-shaped elements, with fibrillar, radiating ornamentation on their external side (CMC.IP.50176). Each cover plate of a same series (left or right) partly overlapping next, more distal one.

Remarks. In his original description of *Bohemiaecystis bouceki*, Caster (in Ubaghs 1968) provided a short diagnosis and figured only two specimens (holotype and paratype). The reexamination of Caster's original type material and the identification of a third specimen of *B. bouceki* (labelled as 'Phyllocystis' sp.) in the collections of the Cincinnati Museum Center made it possible to produce the first detailed description of this taxon, but also to evidence several previously undocumented aspects of its morphology (e.g. small digital articulated to M'4, internal structures on M1, adorals, right adoral orifice, ossicles and cover plates). The presence of D in *B. bouceki*, along with the possession of a lamellate organ made of high lamellae, both unambiguously support the identification of *Thoralicystis* as a junior synonym of *Bohemiaecystis*. The glossal is not preserved in the three available specimens of *B. bouceki*. However, several lines of (indirect) evidence suggest that this plate was very likely originally present (Fig. 60). For example, the small notch at the M2-Z suture indicates that a third plate was probably inserted posteriorly to them. In scotiaecystids, all blade-like posterior
expansions (digital, glossal, spinal) are frequently disarticulated away from the theca and thus, often not preserved (see below). Moreover, G is present in all scotiacystids, independently of whether they have a digital (Bohemiaecystis griffei, B. zagoraensis, B. ubaghsi, Proscotiaecystis melchiori) or not (Scotiaecystis, Thoralicarpus). The reexamination of the type material of B. bouceki also questions the size and shape of its spinal process. Available evidence suggests that this posterior spike was probably short and blunt (Fig. 60; see e.g. Ubaghs 1968; Ubaghs & Robison 1988; Gil Cid 1996d; Lefebvre 2001). However, the possibility that the M3-spike was longer cannot be entirely ruled out, given the poor preservation of its distal extremity in both the holotype (Figs 61a, 62a) and the paratype (Figs 61c, 62c).

The relatively broad, weakly ornamented, gently rounded, sabot-shaped thecal outlines of B. bouceki are morphologically close to those of both Proscotiaecystis melchiori (Fig. 11a) and Thoralicarpus jefferiesi (see below). However, B. bouceki differs from P. melchiori in the presence of a lamellate organ, the possession of wider marginals, a narrower left infracentral area, a straight to slightly convex posterior thecal margin (along Ms), and also in the lateral position of D. Main differences between B. bouceki and T. jefferiesi concern the presence of D (it is lost in T. jefferiesi), the shape of M2 (it is strongly curved in T. jefferiesi) and the size of M5 (broader and shorter in T. jefferiesi). In contrast, thecal outlines of B. bouceki are markedly different from those of all earlier (late Tremadocian) members of the same genus.

Bohemiaecystis griffei, B. ubaghsi and B. zagoraensis are characterised by strongly ornamented, transversely elongate boot-shaped thecae, with delicate marginals and particularly long posterior blade-like processes (D, G and spinal) (Ubaghs 1970; Chauvel 1971; Lefebvre & Vizcaíno 1999). Moreover, their posterior zygal plate (Z) is shaped differently: its anterior and right branches are not perpendicular to each other (they form an
acute angle) and they are both shorter than the left one. Finally, B. bouceki further differs from B. ubaghsi in the possession of more numerous proximal rings (six).

**Bohemiaecystis chouberti** sp. nov.

Figures 18b–c, 26b, 63–69

1971 genre AVI – Chauvel, p. 53, fig. 2b–d.

1978 Cornuta indet. – Chauvel, p. 61, fig. 14

1979 Cornuta, Cothurnocystidae, undetermined forms – Derstler, 1979, p. 101

2003 Cornuta indet. (gen. AVI) – Gutiérrez-Maro et al., p. 158

2003 *Scotiaecystis?* sp. – Lefebvre & Fatka, p. 90

2006b genre AVI – Destombes, p. 31

**Derivation of name.** The species is dedicated to the French geologist Georges Choubert (1908–1986), who largely contributed to the stratigraphy of the Ordovician succession in the Anti-Atlas and provided the first systematic description of echinoderm remains in the Ordovician of Morocco.

**Holotype.** Specimen A (Figs 18b, 64a–b, 66a–c, 67c) on slab UCBL.FSL.173120 (coll. Gutiérrez-Maro): part and counterpart of almost complete, slightly disarticulated large, isolated individual. Most of lower side of holotype preserved, with complete marginal frame, glossal, partly disrupted proximal aulacophore, and portion of distal appendage made of 16 articulated ossicles and associated cover plates. Digital, stylocone and infracentrals not preserved. Upper side of holotype consisting of almost complete marginal thecal frame, glossal blade, poorly preserved lamellate organ, and isolated portion of distal aulacophore
with at least 10 pairs of opposite, closed cover plates. Left and right adorals (A', A), digital, infracentrals, spinal (M3), supracentrals, proximal rings and stylocone not preserved.

Paratypes. Specimens B–K on slab UCBL.FSL.173120 (coll. Gutiérrez-Marco): Specimen B (Figs 18b, 64c–d, 66c, 67c, 68b–c) almost complete, large, isolated, slightly disarticulated individual lying next to and upside down compared to holotype. Lower surface of specimen B consisting of incomplete thecal frame (D, G, M4, Ms, and posterior parts of M3 and Z missing), largely disrupted proximal aulacophore, and posterior part of fully articulated distal appendage with stylocone and at least 10 poorly preserved ossicles. In upper aspect, specimen B exposing almost complete theca with adorals and lamellate organ (D, G and supracentrals not preserved), proximal rings and relatively long portion (12.5 mm) of poorly preserved distal appendage. Specimens C and D partly overlapping each other, with C showing same orientation as holotype, and D, upside down. Lower side of specimen C exposing well-preserved left posterior portion of thecal frame with D, G, M3, M4, M5, Z, and parts of both M1, M2 and Ms (Figs 64e, 67a, 68a). Specimen C better exposed in upper aspect, with nearly complete theca (D, G, M3, lamellate organ and supracentrals not preserved), fully articulated proximal aulacophore, stylocone and several more distal ossicles with ajar cover plates (Figs 64f, 67b). Specimen D poorly preserved, disarticulated theca. Specimens E–K, all poorly preserved, more or less strongly disarticulated, with same orientation as B and D. Specimen E lying next to C and D, consisting of incomplete theca (M1–4, M1, Z) and proximal aulacophore. Specimen F slightly disarticulated, exposing posteriorly truncated theca (D, G, M3–4, M3, M5, Ms and Z missing), proximal aulacophore and stylocone. Specimen G incomplete, disarticulated theca lying against conulariid. Upper surface of specimen H with well-preserved lamellate organ. Upper surface of specimen I consisting of posterior portion of strongly disarticulated theca with M1–2, M1–2, lamellate organ, proximal aulacophore,
stylecone and at least 15 next ossicles with no attached cover plates. Specimen J poorly preserved portion of thecal frame (M₁ and M₂), partly overlapped by distal aulacophore and proximal rings of specimen K.

*Other material.* Single slab (no counterpart) containing at least 22 tightly packed, partly overlapping, randomly oriented individuals (A–V), most of which (21) are in upper aspect (IGR.PAL.16685, coll. Destombes; Figs 18c, 65, 68d, 69). Most specimens consisting of fully articulated to slightly disarticulated, almost complete theca (D and G not preserved), proximal aulacophore and more or less extensive portion of distal appendage (stylecone, ossicles). Fine morphological structures obscured by coarse grain size of sandstones. Lamellate organ rarely distinct, supracentrals not preserved. Cornutes on this slab correspond to the material originally described by Chauvel (1971) as genus AVI.

*Horizon and localities.* The type-locality of *B. chouberti* is a small excavation (TA-F5) in dark ferruginous quartzitic sandstones forming the top of the Guezzart Formation (Dw3, late Darriwilian), about 12 km S of Alnif, on the western flank of Jbel Bou Isidane, western Maïder, eastern Anti-Atlas, Morocco (Fig. 17.3). This excavation yielded the slab containing the holotype and all associated paratypes (UCBL.FSL.173120). The second slab containing about 20 additional specimens of *B. chouberti* (IGR.PAL.16685) was collected in the same stratigraphic horizon, about 200 m S of TA-F5, at Destombes' locality 1826 (Fig. 17.2; see Chauvel 1971).

*Diagnosis.* A species of *Bohemiaecystis* with thick-framed, moderately ornamented, boot-shaped theca, with spike-like tubercles on lower surface of M₂ and M₃; spinal forming long, flat and blunt process; M₁ long, forming right anterior thecal corner; Ms long; anterior and
right branches of Z forming acute angle with each other, both slightly shorter than left branch;
right infracentral area transversely elongate; proximal aulacophore consisting of six rings.

Description. Subtrapezoidal, boot-shaped, transversely elongate theca framed by relatively wide and thick marginals (Fig. 63). Lower thecal surface almost flat, except two relatively large, strong spike-shaped, blunt, antero-abaxial protuberances borne by M'₂ (on the left) and M₂ (on the right), and slightly raised antero-adaxial portions of M₁ and M₁ (below aulacophore apophyses). Theca slightly higher anteriorly, slightly decreasing in height posteriorly. Anterior thecal margin relatively short, forming wide, shallow, concave embayment at aulacophore insertion. Antero-abaxial thecal corners rounded, made by M₁ (on the right) and M'₂ (on the left). Left anterior thecal corner shorter, more strongly curved and protruding more anteriorly than right one. Left thecal side convex, regularly curved, gently rounded. Right thecal margin shorter, slightly curved anteriorly (abaxial part of M₁ and proximal part of M₂), almost straight posteriorly (distal part of M₂, spinal blade). Posterior thecal margin very long, sinuous, forming very wide concave shallow embayment delimited abaxially by two protuding lateral processes: relatively elongate spinal blade (on the right) and shorter, blunt glossal (on the left). Relatively wide range of thecal sizes observed on two available slabs. Thecal width (TW) measured between abaxial edges of M₂-M₃ suture (on the right) and M'₃-M'₄ contact (on the left) (Fig. 26b). Thecal length (TL) estimated perpendicularly to TW between anterior-most extremity of M'₂ and distalmost edge of M₅ (Fig. 26b). In all measurable individuals, TW/TL~1.2. Holotype, largest observed specimen (TW=19.2 mm, TL=16.3 mm). Most individuals on slab UCBL.FSL.173120 larger than those from Destombes' locality 1826 (e.g. paratype B: TW=18.7 mm, TL=15 mm; paratype C: TW=18.2 mm, TL=14.3 mm; paratype F: TW=13.2 mm). On slab IGR.PAL.16685, TW comprised between 11.8 mm (specimen A) and 7.9 mm (specimens B and E).
M₁ transversely elongate, wide, sinuous, with rounded convex anterior margin and concave, gently curved, opposite distal edge. Antero-adaxial portions of M₁ and M'₁ forming high vertical, cup-shaped, symmetrical aulacophore apophyses posteriorly to proximal rings (Figs 64d, 68c). M₁ laterally in contact with M'₁ (on the left) and M₂ (on the right) along short and straight sutures. Internal structures on upper surface of M₁ poorly preserved (e.g. anterior oblique groove, infundibulum), except right scutula, corresponding to small shelf along abaxial upper edge of right apophysis (Figs 64b, f, 66b, 67b). M₂, elongate, slightly curved, longer than M₁, with strong spike-shaped blunt protuberance in median position, along abaxial edge of lower side (Figs 64a, c, 65c, 66a, 68b). M₃, as long as M₂, Y-shaped, with two very short marginal branches, and particularly elongate posterior (spinal) process (Figs 64c–d, 65a, 68b–d). Spinal blade flattened, relatively wide, with subparallel lateral sides and blunt distal tip. Ms narrow and elongate, longer than M₂ and M₃, forming sinuous posterior thecal margin between M₃ (on the right) and Z (on the left) (Figs 64a–d, 65a, 66a–b, 68b–d). Distal edge of Ms straight to slightly concave. Opposite (anterior) margin of Ms nearly straight to slightly convex. Posterior zygal plate Y-shaped, consisting of three subequal, relatively wide branches sutured to M'₁ (anteriorly), M₃ (on the right) and both G and M₅ (on the left) (Figs 64a–b, d–e, 65a, 66a–b, 67a, 68c–d). Anterior (zygal) and right (marginal) parts of Z joining at acute angle (about 75°). Posterior margin of Z weakly curved and concave. Upper (internal) surface of Z bearing posterior part of strong longitudinal zygal crest (Figs 64d, f, 65a, 67b, 68c–d). M₅, particularly short, strongly curved (C-shaped), forming left posterior rounded extremity of thecal frame (Figs 64a–b, d–f, 65a, 66a–b, 67a–b, 68a, c–d). Glossal relatively short, subtriangular, wider anteriorly and regularly tapering towards blunt distal extremity (Figs 64a–b, e, 66a–b, 67a). Glossal anteriorly sutured to both Z (along short contact) and, mostly, nearly straight posterior margin of M₅. M'₄ short, elongate, gently curved, with slightly concave adaxial (right) margin (Figs 64a–b, d–f, 65a, 66a–b, 67a–b, 68a, c–d).
Abaxial (outer) edge of $M'_4$ regularly convex, with small distal rounded process for insertion of digital (Figs 64e, 67a, 68a). Digital tiny, elongate, narrow, movable skeletal element articulated posteriorly to abaxial protuberance on $M'_4$ (D about 1 mm long and 0.3 mm wide in paratype C, UCBL.FSL.173120; Figs 64e, 67a, 68a). $M'_3$ elongate, gently curved, as long as $M_2$, with slightly concave adaxial (right) margin, in contact with both $M'_4$ (posteriorly) and $M'_2$ (anteriorly) along short, straight sutures (Figs 64a–b, d–f, 65b, d, 66a–b, 67a–b, 68a, c).

$M'_2$ as long as $M_1$, strongly curved, with short, wide anterior branch almost perpendicular to longer, narrower posterior portion (Figs 64a–d, 65, 66a–b, 67a, 68b–c). Antero-abaxial margin of $M'_2$ rounded, with large, blunt, spike-shaped protuberance on its lower surface. $M'_1$ elongate, T-shaped, with two very short anterior (marginal) parts and very long posterior (zygal) branch. $M'_1$ slightly longer than both $M_2$ and $M'_3$, shorter than Ms (Figs 64a, c, 66a, 68b). Right margin of zygal part of $M'_1$ (along right infracentral area) weakly concave and regularly curved. Opposite edge of posterior branch of $M'_1$ (along left infracentral area) sinuous, anteriorly concave (at junction with antero-abaxial branch), posteriorly weakly curved and gently convex. On upper thecal surface, antero-abaxial portion of $M'_1$ forming transversely elongate, quadrangular, elevated shelf, left of aulacophore apophysis. Internal (upper) side of posterior branch of $M'_1$ bearing anterior portion of zygal crest.

Infracentra not preserved because of coarse lithology. Left infracentral area entirely closed, longitudinally elongate, narrower anteriorly (along $M'_1$ and $M'_2$), wider posteriorly (along $M'_3$–4, $M_5$ and Z) (Figs 64a, c, e, 66a, 67a, 68b). Left (abaxial) margin of left infracentral area regularly curved and gently convex. Opposite (right) edge of left central area, weakly concave along zygal bar. Anterior and posterior extremities of left infracentral area rounded. Right infracentral area larger than left one, transversely elongate, subtrapezoidal, with nearly parallel anterior and posterior sides, and distally slightly diverging, straight to slightly convex lateral sides. Anterior margin of right infracentral area...
sinuous, with median concavity. Opposite (posterior) edge of right infracentral area longer, straight to slightly concave.

Two small, strongly unequal adorals, at anterior extremity of upper thecal surface, posteriorly to aulacophore insertion, in between shelves borne by M'_1 (on the left) and M_1 (on the right) (Figs 64d, 65a, 68c–d). Left adoral A'_1 depressed, elongate transversely, with slightly raised anterior and abaxial edges. Right adoral A_1 pentagonal, shorter and broader than A'_1, with distinct anterior notch along suture with M_1 (right adoral orifice), and low oblique ridge more or less parallel to suture with A'_1, extending adaxially to right adoral orifice from slightly raised antero-adaxial edge of A_1 to postero-abaxial extremity of right adoral. Supracentraals polygonal, poorly preserved, hardly distinct in most specimens, because of coarse lithology. Lamellate organ best preserved in holotype (Figs 64b, 66b), elongate, fusiform to slightly sigmoidal, extending obliquely from postero-abaxial margin of A_1 towards posterior extremity of M_2. In holotype, lamellate organ consisting of at least 30 (possibly around 45?) relatively high and thin lamellae (about 0.2 mm thick). On upper surface, antero-abaxial edge of each lamella longer and more gently sloping than postero-adaxial one. In other specimens, precise morphology of lamellate organ obscured by coarse lithology (Figs 64d, 68c) or poorly preserved, with only several broken lamellae (Figs 65a, 68d). No clear evidence of periproct in any specimen.

Proximal aulacophore consisting of six distinct telescopic rings, each made of four plates: two inferolaterals and two tectals. Within a same ring, left and right inferolaterals symmetrical to each other. Each inferolateral consisting of two perpendicular branches, contributing to almost flat lower portion and slightly convex lateral flanks of proximal aulacophore (Figs 64c, f, 67b, 68b). Tectals seldom preserved, much smaller than inferolaterals, broad, subquadrangular, restricted to adaxial upper portion of each proximal ring (Figs 65a, 68d). Each proximal ring partly overlapping posterior portion of next, more
distal one, or proximal part of stylocone. Stylocone elongate, funnel-shaped, with wide posterior concave portion and narrower, straight, semi-cylindrical anterior part (Figs 64c, f, 67b, 68b). Upper (internal) surface of stylocone with deep longitudinal median groove ending posteriorly into distinct V-shaped notch, at contact with wide posterior depressed area (Figs 64f, 67b). Lower (external) surface of stylocone and next ossicles rounded and smooth. Relatively long more distal portions of appendage preserved either as isolated stumps or still attached to stylocone, proximal rings and theca (e.g. over 30 articulated ossicles in specimen K, IGR.PAL.16685). Upper (internal) surface of ossicles with deep longitudinal median groove and, apparently, no transverse channels (see e.g. isolated portion of distal aulacophore, made of about 15 attached ossicles, next to paratype B, UCBL.FSL.173120). One pair of opposite, relatively high cover plates articulated on left and right abaxial sides of upper surface of each ossicle, often preserved in closed or ajar position. Possibly two pairs(?) of cover plates articulated to stylocone (specimen A, IGR.PAL.16685). Precise morphology of cover plates difficult to document because of poor preservation.

Remarks. The cornutes from the type-locality (TA-F5) can be confidently assigned to the family Scotiaecystidae, based on the presence of a lamellate organ and a distinct Ms marginal. Moreover, in spite of their preservation in relatively coarse sandstones, the occurrence of a small digital articulated to M'₄ (paratype B, UCBL.FSL.173120) and the possession of high lamellae rising above the supracentral area and extending deep into the thecal cavity (holotype, UCBL.FSL.173120) both clearly support the placement of these cornutes within the genus *Bohemiaecystis*. The scotiaecystids from Jbel Bou Isidane share several similarities with both Early Ordovician (B. griffei, B. ubaghsi, B. zagoraensis) and late Darriwilian (B. bouceki) members of the genus *Bohemiaecystis*. For example, the possession of a relatively long Ms, a wide and oblong spinal blade, and a zygal plate with its anterior and right branches
forming an acute angle are characters found both in late Tremadocian species of *Bohemiaecystis* and in the specimens from the Guezzart Formation. Similarly, the occurrence of a relatively large, thick marginal frame with a transversely elongate M₁ forming the right anterior thecal corner are features shared by both *B. bouceki* and the specimens from TA-F5. However, the morphology of *Bohemiaecystis* specimens from Jbel Bou Isidane is also markedly distinct from that of all other described taxa belonging to the same genus. For example, the TA-F5 scotiaecystids differ from earlier representatives of the genus *Bohemiaecystis* in the possession of a wider, thicker marginal frame, a more elongate M₁ forming the right anterior thecal corner, a much shorter glossal, a more reduced ornamentation on the lower thecal surface (M₂ and M₂ spikes, shorter spinal blade), and also in the morphology of their posterior zygal plate, with three branches subequal in length (the left posterior branch of Z is significantly longer than the two other ones in late Tremadocian taxa). The *Bohemiaecystis* material from TA-F5 also differs from *B. bouceki* in the occurrence of a more elongate Ms (this plate is longer than M₂ in the Moroccan material, whereas it is shorter in *B. bouceki*), a stronger ornamentation on the lower thecal surface, and in the possession of a morphologically distinct posterior zygal plate. In TA-F5 scotiaecystids, the three branches of Z are subequal in length and the anterior and right ones are forming an acute angle, whereas in *B. bouceki*, the zygal branch of Z is significantly longer than the two posterior ones, and its anterior and right branches are perpendicular to each other. The morphology of the Jbel Bou Isidane scotiaecystids is thus unique, and in many respects, relatively intermediate between those of earlier (Early Ordovician) and coeval (late Darriwilian) representatives of the genus.

The more numerous and smaller specimens occurring on the slab from Destombes' locality 1826 (IGR.PAL.16685) correspond to the material originally described by Chauvel (1971) as genus AVI. Possible affinities of these cornutes with scotiaecystids, and more precisely with
Bohemiaecystis, were discussed and tentatively rejected by Chauvel (1971), because of the poor preservation of the material and the absence of clear evidence of respiratory structures (lamellipores). However, the reexamination of Chauvel's (1971) original specimens demonstrates that poorly preserved remains of lamellipores are present in some individuals (e.g. specimen A, IGR.PAL.16685; Figs 65a, 68d), and moreover, that a distinct Ms marginal is distinctly occurring in most specimens, between the posterior zygal plate (Z) and the spinal-bearing M3. These two characters definitively support affinities with the scotiaecystid genera Bohemiaecystis, Scotiaecystis and Thoralicarpus. Although they are incompletely preserved (e.g. D, G missing) and significantly smaller than the specimens from TA-F5, the cornutes from Destombes' locality 1826 are considered here as conspecific and thus, also assigned to B. chouberti. This interpretation relies on the almost identical plate patterns exhibited by scotiaecystids from the two localities, and also on their occurrence in the same stratigraphic horizon, at the top of the Guezzart Formation. The only morphological difference observed between the two assemblages from localities TA-F5 and 1826 concerns the relative proportion of the spinal blade. This oblong spike has the same shape and the same length (about 4.5 mm) in both small individuals from locality 1826 (e.g. specimen A, IGR.PAL.16685: TW=11.8 mm) and the much larger ones from TA-F5 (e.g. paratype B, UCBL.FSL.173120: TW=18.7 mm). This difference, with a proportionately much longer spinal blade in small specimens can be interpreted in two different ways. The first one is to consider that two morphologically close, but distinct taxa are co-occurring in the same horizon, one characterised by a long spinal (locality 1826), and the other one, by a shorter M3 process (TA-F5). However, comparison with the situation in other boot-shaped cornutes known by a high number of specimens and a wide range of sizes, such as Cothurnocystis elizae (B. Lefebvre, pers. obs. Dec. 2008) and Thoralicarpus bounemrouensis (see below) shows that relative proportions of some thecal plates can vary dramatically during ontogeny. For example, in these two cornute...
taxa, the length of posterior spines (glossal, spinal) is almost identical in all specimens, so that these processes are proportionately much more extensive in small (young) individuals than in very large (gerontic) ones. It is thus very likely that the same situation occurs in scotiaecystids from the Guezzart Formation, so that smaller individuals from locality 1826 with a proportionately longer spinal blade and larger ones from TA-F5 all probably belong to a single species: *B. chouberti*.

*Bohemiaecystis*? sp.

Figures 70–71

**Material.** IGR.PAL.16698 (Destombes coll.): Two unrelated slabs (no counterpart), each displaying one incomplete, slightly disarticulated individual. Best preserved specimen (IGR.PAL.16698.A; Figs 70a, 71a) corresponding to large portion of theca in lower aspect (M'_1–4, M_1, M_5, M_6, Z, and part of M_2) and associated fully articulated proximal aulacophore and stylocone. Second individual (IGR.PAL.16698.B; Figs 70b, 71b) much smaller, more incompletely preserved, in upper aspect, with adorals, parts of several marginals (M'_1–2, M_3 and M_6), fragments of a lamellate organ, disrupted proximal rings, and stylocone.

**Horizon and locality.** The two slabs were collected in Oct. 1986 at Destombes' locality 2410, eastern flank of Jbel Ouarzemine, W of Aït Waziz, about 78 km south of Agadir, western Anti-Atlas, Morocco (Fig. 17.1), in siltstones of the Tachilla Formation, early–middle Darriwilian (Dw1–2), Middle Ordovician.

**Description.** Theca boot-shaped, with two strong antero-abaxial spikes on lower surface of M'_2 (on the left) and M_2 (on the right) (Figs 70a, 71a). Anterior marginals (M_1–2, M'_1–2) wider
and stouter than more delicate and thinner posterior skeletal elements (M’3–4, M3, M5, Ms, Z).

Thecal outlines anteriorly straight to slightly concave. Lower surface of anterior thecal margin sinuous with two depressed areas (across the M’1-M’2 and M1-M2 sutures) delimited by three raised areas formed by left and right antero-abaxial protuberances (on M’2 and M2, respectively) and aulacophore apophyses (antero-adaxial parts of M’1 and M1). Left anterior thecal corner rounded, formed by M’2. Left thecal side relatively elongate, almost straight, formed by distal part of M’2, M’3, M’4 and anterior portion of M5. Thecal outlines posteriorly sinuous, almost straight along Ms, concave and gently curved along Z. M5 forming rounded, left posterior thecal corner. Right thecal side poorly preserved. Right posterior thecal corner made by short M3 with strong, elongate spinal blade. Precise thecal dimensions of specimens difficult to measure due to incomplete preservation, but individual IGR.PAL.16698.A clearly larger (TW>22 mm, TL≈18mm) than IGR.PAL.16698.B (estimated TW probably around 15 mm).

M1 relatively elongate transversely, sinuous, with gently curved, convex anterior margin, and slightly concave, opposite, distal edge (Figs 70a, 71a). Lower surface of M1 consisting of two subequal parts: flat abaxial one sutured to M2, right of aulacophore insertion, and convex, high adaxial one, posteriorly to appendage insertion. Upper surface of M1 and putative internal structures not preserved. M2 incompletely preserved in IGR.PAL.16698.A (adaxial part only; Figs 70a, 71a). Lower surface of M2 with large, rounded, blunt abaxial protuberance, possibly forming right anterior thecal corner. M3 Y-shaped, with two particularly short marginal branches, and long, relatively wide, posterior spinal blade (Figs 70b, 71b). Marginal (anterior and left) portions of M3 joining at acute angle. Ms elongate, nearly straight to slightly sinuous, relatively narrow, in contact with both M3, on the right (Figs 70–71) and Z, on the left (Figs 70a, 71a) along short sutures. Posterior zygal plate Y-shaped, with left (marginal) branch longer than anterior (zygal) and right (marginal) ones.
(Figs 70a, 71a). Anterior and right parts of Z almost perpendicular to each other. M5 poorly preserved, short, narrow, strongly curved (with distal convex margin and anterior concave edge), forming left posterior thecal corner (Figs 70a, 71a). M'4 poorly preserved, straight, narrow, elongate, shorter than similarly shaped more anterior marginal, M'3 (Figs 70a, 71a). M'2 forming rounded left anterior thecal corner, with anterior, adaxial branch almost perpendicular to longer, narrower, posterior part. Lower surface of M'2 bearing strong, abaxially and downward directed spike-shaped protuberance (Figs 70–71). M'1 T-shaped, with two relatively short, wide and stout anterior (marginal) branches and more delicate, gently curved posterior (zygal) part (Figs 70a, 71a). Right and posterior branches of M'1 meeting at obtuse angle. Lower (external) surface of M'1 with almost flat left and posterior branches, but raised right adaxial part, below left aulacophore apophysis.

Infracentrals not preserved. Left infracentral area closed, delimited by six marginals (M'1–4, M5 and Z), longitudinally elongate, narrower both anteriorly and posteriorly, wider between M'3–M'4 suture (on the left) and contact between anterior and left branches of Z (on the right) (Figs 70a, 71a). Right infracentral area incompletely preserved, transversely elongate, very likely sub-trapezoidal in shape, with almost parallel anterior and posterior edges, and distally diverging lateral sides (Figs 70a, 71a).

Adorals, two in number, subequal in size, forming anterior thecal margin on upper thecal surface, posteriorly to aulacophore insertion (Figs 70b, 71b). Left adoral A'1 transversely elongate, hexagonal. Right adoral A1 broader, subpentagonal, with deep groove leading to anterior notch (right adoral orifice). Supracentrals not preserved. In one individual (IGR.PAL.16698.B; Figs 70b, 71b), small portion of lamellate organ preserved next to M3, consisting of eight high, thin lamellae.

Proximal aulacophore consisting of six telescopic rings. Lower and lateral sides of each ring made of two symmetrical, opposite (left and right) curved inferolaters (Figs 70a, 71a).
Tectals not observed. Raised distal portion of each ring partly overlapping depressed proximal part of next, more anterior ring or posterior extremity of stylocone. Stylocone elongate, slightly wider proximally than distally, consisting of an anterior narrower, semi-cylindrical part and a posterior, wider funnel-shaped portion (Figs 70–71). Lower surface of stylocone gently rounded and smooth. Upper surface of stylocone too poorly preserved to document internal structures. Isolated stump of distal appendage consisting of at least 18 slightly disarticulated ossicles (in lower aspect) occurring next to individual IGR.PAL.16698.B (about 12 mm away from stylocone). All ossicles with rounded, smooth lower surface. Upper surface of ossicles and cover plates not observed.

Remarks. The cornutes from the Tachilla Formation can be identified as scotiaecystids, based on the presence of a lamellate organ and a distinct marginal Ms in between the spinal-bearing M3 and the posterior zygal plate Z. Moreover, the possession of high lamellae (Figs 70b, 71b) suggests affinities with either Bohemiaecystis or Thoralicarpus. However, the poor preservation of the two incomplete specimens from Jbel Ouarzemine does not make it possible to document if a digital was originally present (Bohemiaecystis) or not (Thoralicarpus).

Comparison of the scotiaecystids from Destombes' locality 2410 with all other described species belonging to the two genera Bohemiaecystis and Thoralicarpus suggests that they are morphologically closer to both B. griffei (late Tremadocian, France) and B. zagoraensis (early–mid Floian, Morocco) than to other taxa. For example, the Tachilla scotiaecystids differ from B. ubaghsi (late Floian, France) in the possession of six proximal rings (instead of four), the presence of a strong protuberance on the lower surface of M2 (this plate is unornamented in B. ubaghsi), and in the morphology of the posterior zygal plate (its anterior and right branches are particularly short in B. ubaghsi). Contrary to the situation in B. bouceki
and *B. chouberti* (late Darriwilian; see above), and the various taxa assigned to the genus
*Thoralicarpus* (see below), all characterised by relatively thick and broad marginals, the
thecal frame of scotiaecystids from Jbel Ouarzemine is, at least laterally and posteriorly, made
of relatively narrow and delicate plates. Another major difference with all these taxa is the
morphology of M₃: its two marginal branches are joining at low, acute angle in the specimens
from locality 2410, whereas they are perpendicular to each other (or even meeting at a slightly
obtuse angle) in *B. bouceki*, *B. chouberti* (see above) and *Thoralicarpus* (see below). A third
difference between the Tachilla scotiaecystids and all younger representatives of the genera
*Bohemiaecystis* and *Thoralicarpus* is the morphology of the posterior zygal plate: its left
marginal branch is much longer than the two other (anterior and right) ones in the material
from Jbel Ouarzemine, whereas it is of the same length (*B. chouberti*) or generally shorter
than the zygal branch in other taxa (*B. bouceki*, *T. bounemrouensis*, *T. guilloui*, *T. jefferesi*, *T.*
*prokopi*).

Conversely, these three characters (i.e. narrow marginals, marginal branches of M₃
meeting at acute angle, posterior zygal plate with a long left posterior branch) are shared by
the specimens from Destombes' locality 2410, *B. griffei* and *B. zagoraensis*. Other
morphological similarities between the Tachilla cornutes and these two scotiaecystid taxa
concern the morphology of the left infracentral area, the ornamentation (in particular, the
strong spike-shaped protuberance on M'₂), and the possession of a relatively short M₁, not
involved in the right anterior thecal corner. The strong morphological similarities between the
Jbel Ouarzemine scotiaecystids and these two Early Ordovician taxa (*B. griffei* and *B.
zagoraensis*) suggest that the material from Destombes' locality 2410 more likely belongs to
*Bohemiaecystis* than to *Thoralicarpus*. However, in the absence of evidence supporting the
presence of the digital, this taxonomic affiliation is only tentatively suggested here
(*Bohemiaecystis*?).
Comparison with *B. griffei* and *B. zagoraensis* further suggests that the Tachilla scotiaecystids cannot be assigned to any of these two taxa. The two main differences concern the shape of the posterior zygal plate (its anterior and right branches are almost perpendicular to each other in the Jbel Ouarzemine material, whereas they are meeting at an acute angle in *B. griffei* and *B. zagoraensis*), and the possession of relatively wide, broad anterior marginals (M′1–2, M1–2), whereas these plates are narrower and more delicate in the two Early Ordovician taxa. Consequently, the two incomplete, poorly preserved scotiaecystid specimens from the Tachilla Formation, which are morphologically very close, though distinct from both *B. griffei* and *B. zagoraensis*, are here tentatively assigned to the same genus, but left in open nomenclature (*Bohemiaecystis?* sp.), pending more, better preserved specimens are found.

Genus *Thoralicarpus* gen. nov.

*Type species.* *Thoralicarpus bounemrouensis* sp. nov.

*Derivation of name.* The genus is named after the French palaeontologist Marcel Thoral (1900–1956), who described several new echinoderm taxa, including various cornute stylophorans, in the Lower Ordovician of the Montagne Noire.

*Diagnosis.* A genus of scotiaecystids with lamellipores separated by numerous, high lamellae protruding into thecal cavity; D absent (lost).

*Remarks.* The genus *Thoralicarpus* is morphologically intermediate between *Bohemiaecystis* and *Scotiaecystis* (see above). *Thoralicarpus* shares with *Bohemiaecystis* the possession of a raised lamellate organ made of high lamellae, but it differs from it in the loss of the digital.
Thoralicarpus shares with Scotiaecystis the possession of a single posterior spine (D lost), but its lamellate organ is raised (instead of flat in Scotiaecystis) and its marginal M₂ is large and forming the left anterior corner of the theca (whereas in Scotiaecystis, M₂ is short and the left anterior thecal corner is made by M₃).

As defined here, Thoralicarpus forms a well-defined clade of relatively large Mid–Late Ordovician (peri-)Gondwanan scotiaecystids (see below). This genus includes T. bounemrouensis sp. nov. from the Izegguirene Formation (early Sandbian), eastern Anti-Atlas (Morocco), T. guilloui (Lefebvre & Vizcaïno, 1999) from the Traveusot Formation (late Darriwilian), Brittany (France), T. jefferiesi (Gil Cid, Domínguez Alonso, Silván Pobes & Ródenas, 1996d) from both the Cantera Shale (late Sandbian–early Katian), Central Iberian Zone (Spain) and the Letná Formation (Sandbian), Bohemia (Czech Republic), T. prokopi sp. nov. from the both the upper part of the Letná Formation (Sandbian) and the overlying Vinice Formation (late Sandbian–early Katian), Bohemia (Czech Republic), and T. aff. prokopi from the Šárka Formation (early–middle Darriwilian), Bohemia (Czech Republic).

Thoralicarpus bounemrouensis sp. nov.

Figures 11c, 18a, 26c, 72–82
Derivation of name. The new species is designated after its type-locality, Bou Nemrou, a hill in the western Tafilalt area, eastern Anti-Atlas, Morocco.

Holotype. UCBL-FSL.425000 (Reboul coll.): best preserved and most complete available specimen, in upper aspect (no counterpart), with fully articulated theca (including both glossal and spinal posterior blades), well preserved lamellate organ, slightly disarticulated proximal aulacophore, and long, fully articulated portion of distal appendage with stylocone, 31 ossicles and all associated pairs (left and right series) of cover plates in closed position (Figs 75a, 77a). Supracentrals not distinct, due to preservation in coarse sandstones.

Paratypes. Twenty-three specimens collected in the type-locality of *T. bounemrouensis* (Bou Nemrou) and within the same stratigraphic horizon as the holotype are considered here as paratypes. Their wide range of thecal sizes (Fig. 73) offers the possibility to document ontogenetic and intraspecific variability (see discussion below). Most individuals consist of a fully articulated theca (G and/or M3 generally missing), often with proximal aulacophore, stylocone and more or less extensive portions of distal appendage, with closed or ajar cover plates. In most individuals, preservation in relatively coarse, purple-reddish sandstones makes the observation of minute morphological details particularly difficult (e.g. plate sutures, integumentary platelets, lamellae, internal structures on stylocone and ossicles). All specimens occur on distinct slabs, but several of them are associated with eocrinoids (*Ascocystites*; MHNM.15690.9, 15, 49, 58), mitrate stylophorans (*Anatifopsis* and/or *Eumitrocystella*; MHNM.15690.12, 55, 76, 106) and trilobites (MHNM.15690.106). Part and counterpart are available for only eight specimens: MHNM.15690.12, 49, 58, 68, 70, 80–81, 106 (Reboul coll.). However, none of them could be selected as the holotype, because of their incomplete preservation (e.g. glossal and M3 are missing in all them). Four other individuals
are only known in lower aspect: UCBL-FSL.713378 (Auvray coll.) and MHNM.15690.56, 76, 86 (Reboul coll.). Finally, eleven other specimens are only preserved in upper aspect: UCBL-FSL.424997, 424999 (Reboul coll.), and MHNM.15690.9, 15, 31, 46, 55, 82, 85, 101–102 (Reboul coll.).

Additional material. Several specimens were collected in Feb. 1990 by J. Destombes, R.P.S. Jefferies and J. Savill at Jbel Izegguirene (Destombes' locality 2479; Gutiérrez-Marko et al. 2003; Destombes 2006a). This material, which is now deposited in the palaeontological collections of the Natural History Museum, London (B. Lefebvre, pers. obs. Dec. 2008) is morphologically identical to the specimens from the type locality.

Horizon and locality. The holotype and paratypes were collected in quarries excavated within sandstones of the Izegguirene Formation, early Sandbian (Sa1), Upper Ordovician, at the summit of Bou Nemrou hill, E of Ksar Tamarna, about 30 km SW of Erfoud, Jbel Tijarfaïouine Massif, western Tafilalt, eastern Anti-Atlas, Morocco (Fig. 17.5). Additional specimens were observed in Destombes' locality 2479, Jbel Izegguirene, about 15 km NW of Tazarine, central Anti-Atlas, Morocco, which is the type locality of the Izegguirene Formation, early Sandbian (Sa1), Upper Ordovician and the type-locality of Destombesicarpus izegguirenensis (see above; Fig. 17.4).

Diagnosis. A species of Thoralicarpus with a long, angular left thecal margin. M2 gently curved. Spinal blade narrow, elongate and oblong. Ms particularly long. Glossal short, oblong, narrow process. Posterior zygal plate with long marginal branches, the right one making an acute angle with the zygal bar.
Description. Theca with transversely elongate, boot-shaped to nearly bilaterally symmetrical outlines (Fig. 72). Thick, almost pentagonal marginal frame consisting of two adorals (A'1 and A1) and 11 marginals (G, M'1-4, M1-3, M5, Ms, Z). Left and right anterior thecal margins converging towards anterior extremity of theca provided by strongly curved M'2, left of aulacophore insertion. Left anterior side relatively short, almost straight, consisting of posterior part of M'2 and proximal portion of M'3. Right anterior thecal margin slightly longer, sinuous, concave along M'1 and adaxial part of M1 (aulacophore insertion), but gently convex abaxially (right part of M1 and anterior portion of M2). Lateral thecal sides almost parallel to each other, almost perpendicular to, and extending more distally than, posterior margin. Left thecal margin gently curved, consisting of posterior part of M'3, M'4, M5 and glossal. Opposite (right) thecal side almost straight, shorter, extending from posterior half of M2 (anteriorly) to distal tip of elongate spinal blade borne by M3 (posteriorly). Posterior thecal margin particularly long, forming wide embayment delimited abaxially by two posterior processes: glossal (on the left) and spinal (on the right). Posterior thecal side consisting of two unequal, straight to slightly convex portions meeting at posterior extremity of zygal bar with an obtuse angle: a particularly long one, made of Ms and right branch of Z (along right infracentral area), and a much shorter one, consisting of the left marginal part of Z (along left infracentral area). Theca very slightly decreasing in height distally. Lower thecal surface flat to slightly concave, except three downward protruding areas: at aulacophore insertion, below apophyses (antero-adaxial portions of M'1 and M1), and two strong abaxial protuberances borne by M'2 (on the left) and M2 (on the right). Wide range of observed thecal sizes. Thecal width (TW) measured from M'4-M5 suture (on the left) to M2-M3 contact (on the right) (Fig. 26c), varying from 5.5 mm (MHNM.15690.55) to 30.6 mm (MHNM.15690.101) (Fig. 73: mean estimated value for TW: 21 mm), and with holotype (UCBL-FSL.425000) one of the largest specimens (TW=29 mm). Thecal length (TL) measured perpendicularly to TW, between anterior-most
extremity of M’₂ and distal-most edge of left branch of Z (Fig. 26c). TL ranging from 4.3 mm (MHNM.15690.55) to 22.2 mm (MHNM.15690.101), with a mean value of 15.2 mm. In Bou Nemrou specimens: TW/TL=1.38 +/- 0.1.

M₁ sinuous (S-shaped), transversely elongate, in contact with both M’₁ (adaxially) and M₂ (abaxially) along short sutures (Figs 74, 78c–d, f, 79a, 80b). Anterior margin of M₁ strongly convex, forming high vertical cup-shaped right apophysis, posteriorly to aulacophore insertion (e.g. MHNM.15690.15, 85, 106). Lower surface of M₁ almost flat, except strongly downward protruding antero-abaxial part (below right aulacophore apophysis). Upper (internal) surface of M₁ with narrow notch (infundibulum) leading adaxially to posterior extremity of small shelf (right scutula) on upper abaxial edge of right aulacophore apophysis (Figs 75f, 79d). Anterior oblique groove not clearly distinct below and adaxially to right scutula. Anterior transverse groove, corresponding to shallow, narrow depressed area running posteriorly to left and right aulacophore apophyses, on internal (upper) surfaces of both M’₁ and M₁, respectively (Figs 76c, 77b). M₂ elongate, consisting of two subequal, almost straight, anterior and distal parts, joining at high, obtuse angle (about 145° +/− 5°) forming right anterior thecal corner (Figs 74–80). In some rare individuals, M₂ either more weakly curved, almost straight (Figs 74d, 80b) or, conversely, slightly more bent (anterior and posterior parts forming an angle of 125° in holotype; Figs 75a, 77a). On abaxial edge of lower surface of M₂, strong, spike-shaped, blunt protuberance directed downwards and laterally, at junction between its anterior and posterior parts (Figs 74, 78c, e–f, 79a, 80b). M₃ absent in most specimens, Y-shaped, with two very short marginal branches, and elongate, relatively narrow, oblong posterior spinal blade (Figs 74e–f, 75a, 77a, 78f). M₃ in contact with both M₂ (anteriorly) and Ms (on the left) along short, straight sutures. Right margin of M₃ almost straight, along abaxial edges of its anterior and posterior branches. Posterior and left branches of M₃ almost straight, perpendicular to each other and united along regularly curved, concave
left posterior margin. Left and anterior parts of M₃ similarly almost perpendicular to each other. Antero-adaxial margin of M₃ strongly concave. Spinal process directed downwards, almost flat, thin, with almost subparallel lateral sides and blunt to slightly truncated distal extremity. Length of spinal blade comparable in all three specimens (6 to 6.5 mm), independently of thecal size: UCBL-FSL.425000 (TW=29 mm), 713378 (TW=19.3 mm) and MHNMM.15690.56 (TW=23.5). Fibrillar, radiating ornamentation along distal tip and lateral edges of spinal blade (Figs 74f, 78f). Ms longest marginal plate either straight (Figs. 75b, d, 77c, 78b, d, 79b) or gently curved, with either weakly concave (Figs 74e, 75c, 79f) or slightly convex posterior margin (Figs 74d, 76c, 77b, 80b). Posterior zygal plate made of three branches of comparable lengths, sutured to M₁ (anteriorly), Ms (on the right) and both G and M₅ (on the left) (Figs 74a–c, e, 75, 76a–c, e, 77, 78b–e, 79a–e, 80a). Marginal (posterior) parts of Z slightly wider than anterior (zygal) one. Right and anterior branches of Z meeting at acute angle varying from about 65° (Figs 75a–b, 77a, 79b) to around 75° (Figs 75e, 76e, 78c, 79c, 80a). Posterior margin of Z concave, with left and right branches, both straight to slightly curved, meeting at obtuse angle, varying from about 140 to 150°. Internal surface of anterior branch of Z bearing strong, posterior portion of longitudinal zygal crest (Figs 75, 76a–c, e, 77, 78a–b, 79b–f, 80a). M₅ shortest marginal, L-shaped, unornamented, made of two unequal parts, almost perpendicular to each other (Figs 74a, c, 75a–e, 76c, 77, 78b–c, 80a). Anterior portion of Ms straight, involved in left thecal margin, sutured (proximally) to M'₄. Right (posterior) branch of M₅ much shorter, straight, in contact with both Z (adaxially) and mostly, with glossal (distally). Antero-adaxial margin of Ms strongly concave. Glossal rarely preserved, consisting of flat, oblong, elongate, posterior blade, with subparallel, nearly straight lateral sides and blunt to truncated distal tip (Figs 74a, e, 75a, 77a, 78e). Proximal portion of G slightly wider, tightly sutured to both Z (along short contact, antero-adaxially) and M₅ (along longer suture, antero-abaxially). Width of glossal blade comparable in all
specimens (1.5–2 mm), independently of thecal size. M’\textsubscript{4}, elongate, gently curved, unornamented, relatively narrow, about the same size as M\textsubscript{1}, with slightly convex abaxial margin, and weakly concave, opposite, adaxial side (Figs 74a, c, e–f, 75a–e, 76a–c, e, 77, 78b–f, 79b–c, e–f, 80a). M’\textsubscript{3} elongate, longer than M’\textsubscript{4}, shorter than M\textsubscript{2}, gently to relatively markedly curved (Figs 74, 75a–e, 76a–c, e, 77–78, 79a–c, e–f, 80a). Lower surface of M’\textsubscript{3} generally smooth (Figs 74c, f, 78c–d, f), but sometimes displaying low longitudinal abaxial crest (Figs 74a, 78e) or strong spike-shaped protuberance directed laterally (Fig. 74e). M’\textsubscript{2} strongly curved, forming anterior-most extremity of theca, with short, wider antero-adaxial part in contact with M’\textsubscript{1}, and longer posterior part, distally sutured to M’\textsubscript{3}. In anterior thecal corner, lower surface of M’\textsubscript{2} bearing strong, downward and slightly posteriorly directed, rounded, blunt protuberance (Figs 74, 78c–f, 79a, 80b). Antero-adaxial and posterior branches of M’\textsubscript{2} meeting at obtuse angle (from about 110 to 130\degree). M’\textsubscript{1} T-shaped, with two short anterior (marginal) parts in contact with M’\textsubscript{2} (on the left) and M\textsubscript{1} (on the right), and longer, narrower, gently curved posterior branch forming proximal portion of zygal bar and distally sutured to Z (Figs 74–80). Lower surface of M’\textsubscript{1} almost flat, except strongly protruding downward antero-adaxial portion, below aulacophore apophysis. M’\textsubscript{1} contributing to anterior thecal wall and forming cup-shaped, anteriorly concave left apophysis posteriorly to aulacophore insertion. Left apophysis similarly shaped and symmetrical to adjoining right apophysis borne by M\textsubscript{1} (Figs 74c, 75f, 76c, 77b, 79d). On upper (internal) surface of M’\textsubscript{1}, left scutula corresponding to small shelf along upper abaxial edge of left aulacophore apophysis (Figs 75f, 76c, 77b, 79d). Strong anterior portion of longitudinal zygal crest on upper (internal) surface of posterior branch of M’\textsubscript{1} (Figs 75–77, 78a–b, 79b–f, 80a). Left margin of zygal branch of M’\textsubscript{1} straight to slightly convex, and opposite (right) margin, straight to weakly concave (Figs 74a, c, 75a, e, 76e, 77a, c, 78b, d–e, 80a).
Infracentrals generally not distinct due to coarse lithology (Figs 74d, f, 78c, f, 79a, 80b). In rare better preserved specimens, infracentrals corresponding to relatively small (0.4 to 0.7 mm wide), thin, polygonal (typically penta- or hexagonal) skeletal elements forming tessellate pavement (Figs 74a, 78e). Left and right infracentral areas particularly extensive on lower thecal surface, separated by straight to gently curved, relatively narrow, oblique zygal bar. Left infracentral area longitudinally elongate, crescent-shaped, entirely framed by six marginals (M'_1-4, M_s, Z), narrower proximally (along M'_1-2 and anterior part of M'_3), wider distally (along Z, M_s, M'_4 and posterior part of M'_3) (Figs 74–75, 76a–c, e, 77–80). Anterior and posterior extremities of left infracentral area short, gently curved and convex. Abaxial (left) margin of left infracentral area markedly convex, longer than opposite, adaxial (right), slightly concave edge. Right infracentral area moderately elongate transversely, subtrapezoidal in shape, entirely closed by six marginals (M'_1, M_1-3, M_s, Z), with almost parallel anterior and posterior sides, and two distally diverging lateral margins (Figs 74–80). Anterior edge of right infracentral area (adaxial part of M'_1 and M_1) slightly concave, much shorter than posterior margin (along M_s and right branch of Z). Abaxial side of right infracentral area (along abaxial part of M_1, M_s, and anterior portion of M_3) slightly longer and more convex than opposite, left margin (along zygal bar).

On upper thecal surface, two small, thin, subequal adorals (A'_1, A_1) closing marginal frame above aulacophore apophyses (Figs 75d, f, 76b, e, 79c–d). Both adorals slightly depressed, moderately elongate transversely, meeting along raised, straight adaxial longitudinal suture. A'_1 almost trapezoidal, with parallel anterior and posterior edges, longer and almost perpendicular to left (abaxial) margin in contact with underlying M'_1 (Figs 75d–e, 76e, 77c, 78b, 79c, 80a). Adaxial margin of A'_1 oblique and slightly longer than opposite (left) side. Morphology of right adoral more complex, ear-shaped, with relatively depressed adaxial part (along A_1-A'_1 suture) and V-shaped, anteriorly convex, abaxial transverse ridge (Figs 75d, f,
79c–d. Left branch of ridge forming a lip more or less parallel to slightly raised anterior margin of A1. Right adoral orifice (hydropore) located along suture with M1, at anterior extremity of deep oblique groove encased between raised anterior portion of A1 and left branch of adoral ridge. Right portion of adoral ridge corresponding to raised abaxial margin of A1, right of hydropore.

Some supracentrals hardly distinct in few individuals (Figs 75f, 78b, 79d), generally along disrupted portions of supracentral area along underlying zygal crest. Supracentrals polygonal, forming tessellate pavement, but too poorly preserved for any precise measurement. Lamellate organ extending obliquely in right side of supracentral area, more or less parallel to right thecal margin, from postero-abaxial extremity of A1 (anteriorly) to distal extremity of M2 (posteriorly) (Figs 75a–b, d–f, 76–77, 78a–b, 79b–e, 80a). Lamellate organ elongate, slightly sigmoid, fusiform, strongly decreasing in width both anteriorly and posteriorly. Number of lamellae (NL), length (LOL) and maximal width of lamellate organ (LOW) all increasing with thecal size (see Fig. 81). Lamellae thin (0.2 mm thick), high, almost vertical, nearly rhombic calcite walls. Each lamella protruding deep below supracentral membrane within intrathecal cavity (Figs 74f, 78f). Uppermost extremities of lamellae forming a high oblique sinuous crest, more or less parallel to right thecal margin and outlines of lamellate organ, well-above supracentral area. Upper margins of each lamella strongly unequal in length, with gently sloping antero-abaxial portion much longer than nearly vertical postero-adaxial edge (Figs 75a–b, d–f, 77a, c, 78a, 79b, d–e, 80a). Weathered lamellae showing composite structure, with tightly sutured walls of two adjoining U-shaped plates (Figs 76a, 78b). No clear evidence of lamellate organ in smallest observed individual (MHN.15690.55, TW=5.5 mm; Figs 75c, 79f), but lamellipores present in slightly larger specimen (MHN.15690.12, TW=6.5 mm). Periproct rarely preserved, corresponding to
small, polyplated, cone-shaped pyramid, made of elongate platelets, at left posterior extremity of supracentral area, along concave antero-adaxial margin of M₅ (Figs 75e, 80a).

Proximal aulacophore cylindrical, almost as high as wide, longitudinally elongate, consistently made of six bilaterally symmetrical telescopic transverse rings, even in smallest observed individuals (Figs 75c, 79f). Each ring made of four tightly sutured skeletal elements: two inferolaterals and two tectals (Figs 74a–e, 75, 76b–e, 77, 78a–e, 79–80). Within a same ring, symmetrical inferolaterals, strongly curved, C-shaped, meeting adaxially along longitudinal midline on lower surface (Figs 74d–e, 78c, 80b), expanding upwards to form almost vertical, slightly convex lateral walls (Figs 76c, 77b) and partly contributing, abaxially, to upper side (Figs 75e, 76e, 78a, 79c, f). Tectals, much smaller, almost quadrangular, flat, symmetrical, restricted to upper side (Figs 75b, 76e, 78a, 79b–c). Within a same ring, tectals meeting adaxially along longitudinal midline. Tectals and inferolaters contributing almost equally to upper surface of each ring (Figs 75c, e, 79f, 80a). Anterior part of each ring overlapping proximal region of next, more distal ring or posterior portion of stylocone (Figs 74a–e, 75, 76b–e, 77, 78a–e, 79–80).

Stylocone broad, funnel-shaped, about twice larger proximally than distally, slightly longer than wide (Figs 74a, c–e, 75, 76c–e, 77, 78c–e, 79–80). Morphology of stylocone comparable in both small and large-sized individuals. Size of stylocone increasing with thecal size. Lower surface and lateral sides of stylocone rounded, totally smooth (Figs 74a, c–e, 78c–e, 79a, 80b). On upper (internal) surface, large proximal part of stylocone forming deep, concave area entirely surrounded by proximal rings (Figs 75e–f, 79d, 80a). More distal upper (internal) surface of stylocone bearing relatively distinct longitudinal median groove, deeply encased between lateral lips, and posteriorly ending in strong V-shaped notch communicating with proximal stylocone cavity (Figs 75e, 80a). Two opposite pairs of cover plates articulated to abaxial edges of stylocone, generally closed or slightly ajar above longitudinal median groove.
(Figs 75, 76c–e, 77, 79b–f, 80a). Very long portions of fully articulated more distal appendage preserved in many individuals, typically comprising 8–15 (Figs 74c, 75b, f, 76c, 77b, 79a–b, d), but sometimes over 30 ossicles and associated pairs of cover plates (Figs 74d, 75a, e, 76d, 77a, 80a–b). Ossicles semi-cylindrical, about twice wider than long, with smooth, rounded lower and lateral sides, and almost flat upper (internal) surface bearing deeply encased longitudinal median groove (Figs 74a, c–d, 75e, 78e, 79e, 80a–b). Putative occurrence of transverse channels along longitudinal median groove impossible to document due to coarse lithology (Figs 75e–f, 79d–e, 80a). One pair of opposite (left and right) cover plates articulated to abaxial edges of upper surface of each ossicle (eFigs 75e–f, 79d–e, 80a).

In all observed specimens cover plates preserved in closed or slightly ajar position. In closed position, each pair of cover plates overlapping proximal portion of next, more distal pair. Cover plates relatively high, more or less fan-shaped, possibly with fibrillar ornamentation (e.g. MHNM.15690.106).

Remarks. The Bou Nemrou specimens can be assigned to the family Scotiaecystidae, based on the presence of a lamellate organ and a Ms marginal. Within scotiaecystids, they can be further identified as belonging to the genus *Thoralicarpus*, based on the high, rhombic morphology of their lamellae and the absence of any digital. The occurrence of abundant, well-preserved, fully articulated specimens of scotiaecystids in Bou Nemrou suggests that the absence of D is certainly original. This interpretation is also corroborated by the smooth, gently and regularly curved abaxial margin of M', which lacks any sign of articulation surface for the digital. The large number of fully articulated scotiaecystid specimens (23 individuals) collected in Bou Nemrou, as well as their wide range of sizes (5.5 mm < TW < 30.6 mm) offer the rare opportunity to document both intraspecific and ontogenetic variability (assuming that smaller-sized individuals are younger than large-sized ones). Although some
minor inter-individual variations can be observed within the available sample (e.g. small
variations in the curvature of some marginals, slight differences in angles between plates or
branches of a same plate; see above), thecal outlines and the general morphology (shape and
relative proportions) of marginals, infracentral areas, proximal rings and stylocone are
remarkably conservative and apparently, size-independent. Two notable exceptions are the
posterior processes (glossal and spinal): their size and morphology are almost the same in
both small and very large individuals (Fig. 82). This implies that the relative size of the
glossal and spinal blades is diminishing during growth, i.e. that the possession of well-
developed, extensive posterior processes possibly represents a paedomorphic feature in
scotiaecystids (the same pattern also occurs in *Ceratocystis perneri* and *Cothurnocystis elizae*;
B. Lefebvre, pers. obs., Dec. 2008). Within a same lamellate organ, the thickness of lamellae
is constant (0.2 mm) and independent of the length of the lamellae. New lamellae are
regularly added during ontogeny (Fig. 81), so as to maintain the same relative size of the
lamellate organ on the upper thecal surface. All specimens from Bou Nemrou, and
morphologically similar ones from Jbel Izegguirene, are thus considered here to belong to the
same species.

Two other, previously described cornute taxa are assigned here to the same genus as the
scotiaecystids from the Izegguirene Formation: *T. guilloui* (Lefebvre & Vizcaïno, 1999) and
*T. jefferesi* (Gil Cid, Domínguez Alonso, Silván Pobes & Escribano Ródenas, 1996d). The
Moroccan specimens are morphologically much closer to *T. guilloui* than to *T. jefferesi*. For
example, the Bou Nemrou *Thoralicarpus* differs from *T. jefferesi* in the shape and length of
its two posterior processes (they are much shorter, broader and wider in *T. jefferesi*; see
below), the relative proportions of several marginals (e.g. M₁ and Ms are much shorter in *T.
jefferesi*; see below), thecal outlines (e.g. more gently curved right side and, conversely, more
angular left thecal margin in Moroccan specimens), and also in the morphology of the
posterior zygal plate. The three branches of Z are subequal in length in Bou Nemrou scotiaecystids, whereas its anterior part is much longer than marginal ones in *T. jefferiesi* (see below). Moreover, the right and zygal branches of Z are meeting along an acute angle in the Moroccan material (see above), whereas these two parts are perpendicular to each other in *T. jefferiesi*. In marked contrast, the Bou Nemrou *Thoralicarpus* shares with *T. guilloui* the possession of relatively similarly shaped posterior processes (glossal, spinal) and Z, relatively elongate M₁ and Ms, and a markedly curved M'₃ (see below). However, *T. guilloui* differs from Moroccan scotiaecystids in the possession of a more transversely elongate theca, with a markedly angular M₂ (whereas this marginal is gently curved in the Bou Nemrou material) and an almost rectangular right infracentral area (whereas it is subtrapezoidal in specimens from the Izegguirene Formation). Moreover, the spinal blade of *T. guilloui* is markedly oblique to the right thecal margin, whereas this is not the case in Bou Nemrou specimens. All these differences with the holotype and single known specimen of *T. guilloui* are considered here as significant and largely outside of the range of inter-individual variations observed in Moroccan specimens. Consequently, scotiaecystids from Bou Nemrou, which are morphologically distinct from both *T. guilloui* and *T. jefferiesi*, are here assigned to a new species, *T. bounemrouensis*.

*Thoralicarpus guilloui* (Lefebvre & Vizcaïno, 1999)

Figures 21b, 26d, 83–85

1996d *Bohemiaecystis* sp. – Jefferies in Gil Cid et al., p. 318

*1999 Scotiaecystis guilloui* Lefebvre & Vizcaïno, p. 450, figs 22.12, 25, 26.3

2000a *Scotiaecystis guilloui* Lefebvre & Vizcaïno – Lefebvre, p. 111, fig. 4

2002b *Bohemiaecystis guilloui* (Lefebvre & Vizcaïno) – Domínguez et al., p. 50
2003  *Scotiaecystis* sp. – Lefebvre & Fatka, p. 90

2006  *Scotiaecystis guilloui* Lefebvre & Vizcaïno – Lefebvre *et al.*, appendix

2007a  *Scotiaecystis guilloui* Lefebvre & Vizcaïno – Lefebvre, p. 186

2008  *Scotiaecystis guilloui* Lefebvre & Vizcaïno – Lefebvre *et al.*, p. 15

2015a  *Scotiaecystis guilloui* Lefebvre & Vizcaïno – Lefebvre *et al.*, p. 307

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**Holotype.** UCBL-FSL.170875 (coll. Guillou): single slab of micaceous siltstones containing large, slightly disarticulated individual in upper aspect (no counterpart) with complete marginal frame (adorals, G, M′1–4, M1–3, Ms, M, Z), disrupted supracentral area, well-preserved lamellate organ, fully articulated proximal aulacophore, stylocone and next three ossicles (the third one being incomplete). This specimen (Figs 84–85) is the only known specimen of *T. guilloui*. In the original description of this taxon, it was designated as holotype by Lefebvre & Vizcaïno (1999). Its morphology is reevaluated here, so as to facilitate comparisons with other taxa assigned to the same genus.

**Horizon and locality.** The holotype occurs on a small elongate slab (about 4 x 15 cm) of dark greenish micaceous siltstones collected within the upper part of the Traveusot Formation, late Darriwilian (Dw3), Middle Ordovician, in a temporary excavation made in the mid-1990s at La Saudrais, Guichen, Ille-et-Vilaine, Brittany, France (Fig. 20.3).

**Diagnosis.** A species of *Thoralicarpus* with a long, angular left thecal margin. M2 angular and strongly curved. Spinal blade narrow, elongate and oblong. Ms particularly long. Glossal short and oblong narrow process. Posterior zygal plate with long marginal branches, the right one making an acute angle with the zygal bar.
Description. Large, transversely elongate, nearly rectangular, almost bilaterally symmetrical theca, with two relatively short and narrow distal processes, at opposite postero-abaxial corners: glossal (on the left) and spinal (on the right) (Fig. 83). Rectangular aspect of theca reinforced by strong bending of M₂ (on the right) and M'_2 (on the left). Curvature of elongate left thecal margin resulting in placement of proximal-most left marginals (M'_2 and anterior part of M'_3) into anterior thecal side. Thecal frame relatively broad (about 1.7 +/- 0.1 mm wide), made of two adorals (A'_1, A_1) and 11 marginals (G, M'_1-₄, M₁-₃, M₅, Ms, Z). Theca slightly decreasing in height towards left posterior extremity. Anterior thecal margin particularly elongate, with deep, wide, median concave embayment for aulacophore insertion (adaxial parts of M'_1 and M₁). Left portion of anterior thecal margin strongly curved, protruding more anteriorly than opposite (right) one, and consisting of abaxial part of M'_1, M'_2 and anterior portion of M'_3. Right of aulacophore insertion, thecal margin almost straight, made of abaxial part of M₁ and left branch of M₅. Left antero-abaxial thecal corner relatively faint, obtuse (about 135°), provided by M'_3. Opposite (right) antero-abaxial corner particularly angular (90°), made by strongly curved M₂. Lateral thecal sides particularly short, parallel to each other, almost straight, subequal in length, consisting of M₅, M'_₄ and posterior part of M'_₃ (on the left), and of distal part of M₂ and proximal portion of M₃ (on the right). Postero-abaxial thecal corners made by M₃ (oblique spinal blade, on the right) and G (on the left). Posterior thecal margin elongate, almost straight, subparallel to anterior thecal side, and consisting of Z, Ms and left part of M₃. Lower surface of theca and putative ornamentation not documented in single available specimen. Thecal width (TW=31 mm) measured between abaxial edges of both M₂-M₃ suture (on the right) and median part of M'_₄ (on the left) (Fig. 26d). Thecal length (TL=19 mm) estimated perpendicularly to TW, from proximalmost extremity of M'_2 (anteriorly) and distalmost part of Z (posteriorly) (Fig. 26d).
M₁ transversely elongate, sinuous, with long, convex, gently rounded anterior margin and more weakly curved, slightly concave, opposite (posterior) edge (Figs 84–85). Adaxial-most anterior portion of M₁ forming high, thin vertical wall (right apophysis) posteriorly to aulacophore insertion. Small shelf on uppermost, abaxial edge of right apophysis possibly corresponding to right scutula. Other putative internal structures (e.g. infundibulum, anterior oblique groove, anterior transverse groove) not observed, because of overlapping, collapsed, right adoral. M₁ in contact with both M’₁ (on the left) and M₂ (on the right) along short and straight sutures. M₂ particularly long, strongly arched, with subequal left and posterior parts almost perpendicular to each other (Figs 84–85). M₂ forming strongly convex, rounded right anterior thecal corner. M₃ Y-shaped, with two subequal marginal branches and slightly longer thinner, almost flat, downwards directed spike-shaped process (spinal). Marginal portions of M₃ shorter than those of M₂. Anterior and left branches of M₃ meeting at slightly obtuse angle (100°). Spinal blade oblong, elongate, relatively narrow, with nearly parallel lateral sides and truncated, blunt distal extremity. Spinal markedly oblique, making an angle of about 130° with both left and posterior thecal margins (Figs 84–85). M₅ longest marginal (13.6 mm long), transversely elongate, almost straight, in contact with both M₃ (on the right) and Z (on the left) (Figs 84–85). Posterior zygal plate T-shaped, with posterior (marginal) branches subequal in length, slightly shorter than anterior (zygal) part (Figs 84–85). Posterior margin of Z almost straight. Right and anterior branches of Z meeting each other with an acute angle (70°). Antero-abaxial edge of Z (along left infracentral area) gently curved and concave. Strong longitudinal zygal crest on upper (internal) surface of anterior branch of Z. M₅ shortest marginal, curved, L-shaped, forming left posterior corner of marginal frame (Figs 84–85). Anterior portion of M₅ weakly curved, with slightly convex abaxial edge. Right part of M₅ straight, shorter and almost perpendicular to anterior portion, with slightly concave distal margin. Antero-adaxial edge of M₅ regularly curved and concave. Glossal relatively short,
flat, pear-shaped, slightly elongate (about 3.4 mm wide, 4.4 mm long), possibly broken posteriorly (Figs 84–85). Anterior half of glossal broad, wide, probably originally in contact with distal edges of both Z and M₅ (G preserved slightly detached posteriorly to marginal frame). Posterior half of G much narrower (2.1 mm wide), with subparallel lateral sides, and blunt, possibly truncated distal extremity. Anterior and left margins of G almost perpendicular to each other and gently curved. Right side of G with strong median concavity between convex (rounded) anterior portion and almost straight distal edge. M'₄ relatively short (5.5 mm long), longitudinally elongate along left thecal margin, weakly curved, with slightly convex abaxial edge (Figs 84–85). M'₃ longer than M'₄, elongate, with marked curvature (135°) in median part separating two almost straight, subequal anterior and posterior halves (Figs 84–85). M'₂ L-shaped, elongate, slightly shorter than M'₃, with strongly curved, rounded anterior margin, and concave opposite (posterior) edge (Figs 84–85). Abaxial part of M'₂ almost straight, distally sutured to M'₃, much longer than adaxial portion, in contact with M'₁. M'₁ T-shaped with two short anterior (marginal) parts and long, relatively narrow posterior branch forming anterior portion of oblique zygal bar (Figs 84–85). Antero-adaxial portion of M'₁ bearing high, thin, cup-shaped vertical wall (left apophysis) posteriorly to aulacophore insertion. Uppermost abaxial edge of left apophysis apparently bent into short, narrow, almost horizontal posterior shelf (left scutula). Upper (internal) surface of posterior branch of M'₁ bearing anterior portion of strong longitudinal zygal crest. Posterior branch of M'₁ and anterior part of Z contributing equally to zygal bar.

Infracentrals not observed (covered by overlying, collapsed supracentrals). Outlines of left and right infracentral areas relatively distinct, delimited by zygal bar and marginal frame (Figs 84–85). Left infracentral area longitudinally elongate, crescent-shaped, narrower anteriorly (along M'₁, M'₂ and proximal part of M'₃) than posteriorly (along Z, M₅, M'₄ and distal part of M'₃), with short, rounded, strongly convex anterior and posterior extremities.
Adaxial margin of left infracentral area (along zygal bar) elongate, slightly concave, shorter and less curved than markedly convex opposite (abaxial) one, along left thecal side. Right infracentral area almost rectangular, transversely elongate, with very sinuous anterior margin (along M₁ and adaxial parts of M₂, and M’₁) almost parallel to opposite, straight, posterior edge (along left part of M₃, Ms and right branch of Z). Lateral sides of right infracentral area almost parallel to each other, with right one (along posterior part of M₂ and anterior branch of M₃) straight, slightly shorter than weakly curved, slightly convex, opposite (left) one, along zygal bar.

Two thin, morphologically distinct adorals closing marginal frame posteriorly to aulacophore insertion, above left and right apophyses (Figs 84–85). Left adoral (A'₁) depressed (strongly concave upper, external surface), pentagonal, in contact with both M’₁ (abaxially) and right adoral, A₁ (adaxially). A₁ almost subequal in size with A'₁, but morphologically more complex, with short, adaxial depressed area, and strong inverted U-shaped ridge in abaxial portion enclosing deep, narrow longitudinal groove leading anteriorly to right adoral orifice (hydropore) along contact with M₁. Supracentrals (Figs 84–85) particularly numerous, thin, polygonal (mostly hexagonal) forming tessellate anisotropic pavement, with largest elements (1.6–1.8 mm wide) in central part of upper surface, and smallest ones (0.7–0.9 mm) along marginal frame and around lamellate organ. Lamellate organ (Figs 84–85) partly collapsed, slightly disarticulated anteriorly, extending obliquely from postero-abaxial extremity of A₁ (proximally) to posterior extremity of M₂ (distally). Lamellate organ elongate (about 8.5 mm long and 2 mm maximal width), fusiform, strongly decreasing in width anteriorly and posteriorly. Lamellate organ consisting of at last 25 thin (0.2 mm thick) vertical walls (lamellae), protruding well-above supracentral area. Upper edge of each lamella consisting of elongate, straight to slightly concave, gently sloping antero-abaxial part, and much shorter, straight to slightly concave, nearly vertical postero-adaxial
portion. Junction of these two portions corresponding to highest raised part of each lamella, and also suture between its tightly fused anterior and posterior elements. In left posterior extremity of supracentral area, along concave antero-adaxial margin of Ms, small (≈1.1 mm wide), distinct, protruding anal pyramid, consisting of numerous acicular platelets (Figs 84–85).

Proximal aulacophore relatively large (about 4.7 mm wide), made of six, well-defined telescopic, V-shaped, anteriorly concave, transversely elongate, bilaterally symmetrical rings (Figs 84–85). Each ring consisting of four skeletal elements: two tectals and two inferolaters. Tectals short (about 1 mm wide), quadrangular, restricted to adaxial portion of upper surface. Inferolaters forming abaxial portions of upper surface and lateral sides of each ring. Proximal portion of each ring slightly depressed and more or less strongly overlapped by distal margin of next, more posterior ring. Most distal ring enclosing proximal portion of stylocone. Stylocone funnel-shaped, particularly broad and massive, almost as wide as long (≈2.4 mm), tapering distally (Figs 84–85). Lateral sides of stylocone reticulate, gently rounded. Upper surface with well-defined narrow (≈0.16 mm wide) median longitudinal median groove, laterally delimited by narrow ridges (about 0.12 mm thick) interrupted by two pairs (left and right) of transverse channels (each about 0.08 mm wide) leading to lateral depressions. Next two ossicles and posterior half of third (more distal) one preserved (Figs 84–85). Proximal ossicles short, transversely compressed (about 1.4 mm wide, and 0.7 mm long), with rounded lateral sides and upper (internal) surface showing same internal structures as on stylocone (e.g. longitudinal median groove, transverse channels). At least three cover plates preserved, disarticulated, left of aulacophore. Cover plates fan-shaped, relatively high, elongate (about 1.7 mm long, 1 mm maximal width), thin, oblong, nearly flat, except short, narrow, thick base for articulation (Figs 84–85). Anterior margin of cover plate nearly
straight, upper and posterior edges rounded. Wide, upper portion of cover plates with radiating fibrillar ornamentation.

Remarks. Although more detailed and precise, the reevaluation of the morphology of the holotype and single known specimen of *T. guilloui* is largely congruent with its original description (see Lefebvre & Vizcaíno 1999). The main difference concerns the glossal. Two elongate and narrow isolated skeletal elements occurring posteriorly to the theca were considered by Lefebvre & Vizcaíno (1999) as probable fragments of a particularly long glossal. This interpretation is considered here as unlikely. Many other skeletal fragments, not necessarily related to the holotype of *T. guilloui* are found on the same slab. Moreover, in all other scotiaecystids, the two posterior processes are generally of relatively comparable length (see above and below). Finally, a relatively large and elongate, sub-triangular skeletal element is occurring next to the posterior margin of both Ms and Z. This plate, which was overlooked by Lefebvre & Vizcaíno (1999), represents a more convincing glossal than the two isolated fragments situated much farther away from the theca. Its location, shape and size are very similar to those of the glossal in other scotiaecystids, and in particular, in *T. bounemrouensis* (see above).

*Thoralicarpus guilloui* (Fig. 83) is morphologically close to *T. bounemrouensis* (see above; Fig. 72). Main differences concern the more rectangular, transversely elongate outlines of *T. guilloui*, the morphology of M₂ (weakly curved in *T. bounemrouensis*, whereas it is strongly bowed in *T. guilloui*), and the oblique orientation of the spinal blade (130° with the right thecal margin in *T. guilloui*, instead of 180° in *T. bounemrouensis*). *T. guilloui* differs more significantly from *T. jefferiesi* (see below; Fig. 86). Their thecal outlines are very distinct (short, broad and rounded in *T. jefferiesi*, more transversely elongate and quadrangular in *T. guilloui*). The left thecal margin of *T. jefferiesi* is short and regularly convex, whereas it is
more angular in *Thoralicarpus guilloui*, with two distinct, nearly straight anterior (*M'_2–3*) and posterior (*M'_3–4, M_5*) portions. The glossal is short, small and subtriangular in *T. jefferiesi*, whereas it is distally more elongate in *T. guilloui*. *M_1* is short and broad in *T. jefferiesi*, but elongate in *T. guilloui*. *M_2* is more strongly curved in *T. guilloui* than in *T. jefferiesi*. The spinal blade is longer and narrower in *T. guilloui*. *M_s* is short and sinuous in *T. jefferiesi* (e.g. shorter than *M_2*), whereas it is straight and the longest marginal in *T. guilloui*. The three branches of *Z* are almost subequal in length in *T. guilloui*, whereas the anterior one is much longer than the two posterior parts in *T. jefferiesi*. Moreover, the right and zygal parts of *Z* are almost perpendicular to each other in *T. jefferiesi*, whereas they are meeting with an acute angle in *T. guilloui*. The numerous morphological similarities between *T. guilloui* (late Darriwilian, Brittany) and *T. bounemrouensis* (early Sandbian, Anti-Atlas) can result from comparable modes of life (ecophenotypy) and/or suggest closer affinities than with *T. jefferiesi* (late Sandbian–early Katian, Bohemia and Central Iberian Zone; see below).

*Thoralicarpus jefferiesi* (Gil Cid, Domínguez Alonso, Silván Pobes & Escribano Ródenas, 1996d)

Figures 26e, 86–91

1996d *Bohemiaecystis jefferiesi* Gil Cid et al., p. 318, figs. 2.15, 3F, 4.5, 5–12

1999 *Bohemiaecystis* sp. – Domínguez et al., p. 210, fig. 1.5

1999 *Scotiaecystis jefferiesi* (Gil Cid et al.) – Lefebvre & Vizcaíno, p. 433, figs 10.3, 26.2

2000a *Scotiaecystis jefferiesi* (Gil Cid et al.) – Lefebvre, p. 118

2001 *Scotiaecystis jefferiesi* (Gil Cid et al.) – Lefebvre, p. 608

2002b *Bohemiaecystis jefferiesi* Gil Cid et al. – Domínguez et al., p. 50

2002 *Bohemiaecystis jefferiesi* Gil Cid et al. – Arroyo & Lara, p. 103
Holotype. UCM.EO.035 (Gil Cid coll.): part and counterpart of incomplete, partly disarticulated specimen, with large, central portion of theca relatively well preserved (adorals, G, infracentrals, lamellate organ, M'1, M1, Ms, part of Ms, supracentrals, Z), but left and right sides either disrupted (M'2–4) or missing (M3, most of M2) (Figs 87a–b, 89). Aulacophore strongly disarticulated consisting of six disrupted rings, stylocone and next, more distal ossicle, and few isolated cover plates. This specimen, which is the best preserved and most complete individual collected in the type locality, was originally designated as holotype by Gil Cid et al. (1996d).

Paratypes. Four other specimens, UCM.EO.036–38, 40 (Gil Cid coll.), all collected in the same locality and horizon as the holotype, were originally designated as paratypes (Gil Cid et al. 1996d). Paratype UCM.EO.036 (part and counterpart) corresponding to strongly dislocated theca, with large portions of disrupted integumentary areas surrounded by disorganised marginals (M'1–3, M1–3, Ms, Z) (Figs 88a, c, 90b–c). Small part of lamellate organ preserved. Large portions of theca missing (adorals, glossal, M'4, Ms, spinal blade) and aulacophore not preserved. Paratype UCM.EO.037 (part and counterpart) consisting of few scattered skeletal
elements probably originally belonging to one single individual: integumentary platelets, marginals (M₂, M₅, Ms, Z), and ambulacral cover plates (Fig. 88b, d). Paratype UCM.EO.038 corresponding to disarticulated, incomplete specimen in upper aspect (no counterpart), with partly dislocated theca (A₁, G, M'₁, M'₄, M₁₋₂, M₅, Ms, small portions of M'₂ and M'₃), relatively well-preserved, collapsed proximal rings, and stylocone (Figs 88e, 90a). Lamellate organ not preserved. Paratype UCM.EO.040 consisting of two isolated marginals (M'₁, M₁) in lower aspect (no counterpart) and disarticulated nearby proximal rings.

Other material. UCM.EO.039 (Gil Cid, Domínguez Alonso, Silván Pobes & Escribano Ródenas coll.), from the type locality of *T. jefferiesi*, corresponds to a single isolated curved marginal (part and counterpart), morphologically identical to M'₂ in co-occurring individuals of *T. jefferiesi*. A single specimen (part and counterpart) from the Letná Formation, Barrandian area (Czech Republic), is also assigned here to *T. jefferiesi*: CGS.LK.17 (Kašička coll.). It corresponds to an almost complete, slightly disarticulated theca (infracentrals, lamellate organ, marginals, supracentrals), with two associated rings of proximal aulacophore (distal appendage missing) (Figs 87c–d, 91). Adorals and part of supracentral area not preserved. Specimen occurring on two small slabs along with solutian remains (*Dendrocystites*).

Horizon and locality. The holotype, paratypes and specimen UCM.EO.039 were all collected at La Palomera, about 3 km west of the town of El Viso del Marqués, Ciudad Real, Spain (VM on Fig. 24a, c), on float siltstone blocks from the Cantera Shale, late Sandbian–early Katian (Sa₂–Ka₁), Upper Ordovician. The other specimen was found in a *Dendrocystites*-dominated layer occurring in the stratigraphically lower temporary excavation made in Borová Street, along the slope of Děd Hill, Zahořany, Czech Republic (Fig. 22.5), within
sandstone units of the upper part of the Letná Formation, late Sandbian (Sa2), Upper Ordovician.

Diagnosis. A species of *Thoralicarpus* with a short, rounded left thecal margin. M₂ curved.

Spinal blade short, wide and blunt. Ms short. Glossal short and subtriangular. Posterior zygal plate with short marginal branches, the right one perpendicular to the zygal bar.

Description. Theca sabot-shaped, broad, weakly elongate transversely, with almost bilaterally symmetrical, subelliptical outlines. Integumentary areas delimited by thick and relatively wide marginal frame consisting of two adorals (A'₁, A₁) and 11 marginals (G, M'₁₋₄, M₁₋₃, M₅, Ms, Z) (Fig. 86). Marginals regularly decreasing in both height and thickness distally (e.g. in holotype, width of marginals varying from 3 to 4.7 mm anteriorly, to about 2.2 mm along posterior margin; in smaller specimen CGS.LK.17, marginal width comprised between 1.6–2.7 mm anteriorly and around 1 mm posteriorly). Anterior thecal margin almost as long as posterior one, sinuous, with wide, shallow concave median embayment at aulacophore insertion (adaxial portions of M'₁ and M₁), delimited abaxially by two rounded, anteriorly convex and protruding areas formed by M'₂ (on the left) and M₁ (on the right). Left anterior thecal corner formed by M'₂, and right anterior one, by M₂. Left thecal margin regularly curved and convex, longer than opposite, nearly straight, right side. Postero-abaxial thecal corners provided by two short posterior processes: particularly wide and massive spinal (M₃, on the right) and small, triangular glossal (on the left). Posterior thecal margin forming wide sinuous embayment delimited abaxially by G and spinal process, with two small concave areas, laterally, on the left (posteriorly to zygal bar) and on the right (at M₃-Ms suture) separated by gently curved, slightly convex median region (along Ms and right branch of Z). Lower thecal surface almost flat to possibly weakly concave, except slightly protruding
downwards lower adaxial portions of M'\textsubscript{1} and M\textsubscript{1} (below aulacophore apophyses), relatively
strong downward-oriented anterior protuberances borne by M'\textsubscript{2} and M\textsubscript{2}, and wide spinal
process (M\textsubscript{3}) directed both downwards and posteriorly. Thecal dimensions (Fig. 26e) difficult
to measure, due to strong disarticulation of most specimens from the type locality. Thecal
width (TW) estimated between M'\textsubscript{3}-M'\textsubscript{4} contact (on the left) and M\textsubscript{2}-M\textsubscript{3} suture (on the right).
Theclal length (TL) estimated perpendicularly to TW, i.e. between anterior-most part of either
M'\textsubscript{2} (on the left) or M\textsubscript{1} (on the right) and distal-most extremity of either M\textsubscript{5} or adjoining left
branch of Z. Both dimensions measured precisely only in CGS.LK.17 (TW≈21.5 mm, TL≈17
mm), suggesting a TW/TL ratio of about 1.3. In paratype UCM.EO.038 (TW=19.4 mm,
TL=18.4 mm), TW under-estimated due to collapse and disarticulation of left thecal margin.
Holotype, largest known specimen (TL≈29 mm) with estimated TW probably originally close
to 38 mm.

M\textsubscript{1} massive, broad, thick, transversely elongate, with rounded, convex anterior margin and
shorter, slightly concave posterior edge (Figs 87a, c, 89a, 91a). M\textsubscript{1} laterally in contact with
both M'\textsubscript{1} (adaxially) and M\textsubscript{2} (abaxially) along relatively short sutures. Lower surface of M\textsubscript{1}
almost flat, except in slightly protruding antero-adaxial part (below right apophysis). Anterior
edge of M\textsubscript{1} forming high vertical wall, with adaxially, posteriorly to aulacophore insertion,
well-defined cup-shaped, concave right apophysis, framed abaxially by low vertical crest
(Figs 87b, 89b). Lower surface of M\textsubscript{1} protruding slightly more anteriorly than right apophysis.
Infundibulum corresponding to cavity deeply encased abaxially to right apophysis, on
posterior (internal) wall of M\textsubscript{1} (Figs 6b–c, 88a). Upper extremity of infundibulum forming
well-defined rounded, convex, shallow structure delimited by low ridge (probably
corresponding to similar rounded opening on adjacent adoral A\textsubscript{1}, i.e. right adoral orifice).
Well-defined oblique groove running (adaxially) from upper edge of right apophysis towards
(abaxially) median part of left side of infundibulum. Right scutula corresponding to small
shelf on upper adaxial edge of right apophysis, immediately above anterior oblique groove.

Anterior transverse groove extending from lower extremity of infundibulum (abaxially) along lower portion of posterior wall of right apophysis (adaxially). M2 longest marginal, angular, strongly curved, forming right anterior thecal corner (Figs 87c–d, 88a, e, 90a–b, 91a–b).

Anterior and posterior parts of M2 meeting at obtuse angle (≈120°). M2 more or less subtriangular in cross-section, with high, gently convex, rounded external (upper abaxial) wall, strongly depressed, concave internal (upper adaxial) side, and almost flat lower surface, except low, blunt, relatively elongate spike-shaped protuberance, at junction between anterior and posterior parts of M2 (Figs 87a, c, 89a, 91a). On lower thecal surface, adaxial margin of M2 (along right infracentral area) gently rounded, forming wide, obtuse (125–130°) concavity. On opposite (upper) thecal surface, adaxial margin of M2 (along supracentral area), concave, longer, more angular (about 110°). M3 not preserved in original type material, except putative small, incomplete (marginal) portion in paratype UCM.EO.036 (Figs 88a, 90b). In CGS.LK.17, M3 Y-shaped, with two short, narrow marginal branches, and longer, much wider posterior (spinal) process (Figs 87c–d, 91a–b). Morphology of spinal process unknown in all specimens from the type locality. In CGS.LK.17, spinal corresponding to relatively thick, downwards and posteriorly directed massive process, with a wide, blunt, truncated posterior margin (Figs 87c–d, 91a–b). Lower surface of spinal gently convex, weakly rounded, extending into relatively high, almost parallel lateral walls. Upper surface of spinal nearly flat, smooth, separated from underlying lateral sides by sharp longitudinal edges.

Ms transversely elongate, markedly shorter than M2, weakly curved, with long, slightly convex posterior margin, and gently concave opposite (anterior) edges (Figs 87, 88a, c, e, 89–91). Ms in contact with both M3 (on the right) and Z (on the left) along short, straight sutures.

Posterior zygal plate Y-shaped, with longitudinally elongate anterior (zygal) part and two particularly short, transverse, posterior (marginal) left and right branches (Figs 87a, c, 88a–b,
Right and anterior parts of Z almost perpendicular to each other. Lower surface of Z almost flat to slightly concave. Posterior margin of Z with strong median concavity, distally to zygal bar and at junction between left and right branches. Left branch of Z slightly bent downwards abaxially. Zygal part of Z with straight, parallel lateral sides, anteriorly in contact with M'\textsubscript{1} along short suture. Internal (upper) surface of anterior branch of Z bearing strong longitudinal zygal crest (Figs 87d, 88c–e, 90a–b, 91b). M\textsubscript{5} smallest marginal, particularly broad, forming left posterior thecal corner (Figs 87, 88e, 89, 90a, 91). Abaxial side of M\textsubscript{5} gently convex, finely serrated in holotype (Figs 87a–b, 89a–b). Posterior margin of M\textsubscript{5} slightly shorter, straight to weakly concave. Antero-adaxial margin of M\textsubscript{5} rounded, concave. Glossal particularly short (about 3.7 mm long and 2.6 mm wide in holotype), subtriangular in shape, almost flat, longitudinally elongate, with nearly straight left margin and longer, rounded, strongly convex right side converging distally into blunt extremity (Figs 87a–b, 88e, 89a–b, 90a). Anterior margin of G with short re-entrant for insertion along and in between Z-M\textsubscript{5} suture. Marginal M'\textsubscript{4} longitudinally elongate, with curved, convex abaxial margin, and straight to weakly concave adaxial edge (Figs 87a, c–d, 88e, 89a, 90b, 91). Anterior extremity of M'\textsubscript{4}, in contact with M'\textsubscript{3}, wider than distal extremity, along suture with M\textsubscript{5}. Lower surface of M'\textsubscript{4} and next, more anterior marginal, M'\textsubscript{3} flat and unornamented. M'\textsubscript{3} slightly longer than M'\textsubscript{4}, similarly elongate, with regularly curved, convex abaxial margin bearing one or two low, short, blunt laterally-oriented protuberances (Figs 87b–c, 88a, c, 89b, 90b–c, 91a). Opposite (right) margin of M'\textsubscript{3} almost straight to weakly concave. M'\textsubscript{2} massive, high, thick, L-shaped, with short anterior and longer posterior branches joining at slightly obtuse angle (100°) at left anterior thecal corner (Figs 87a–c, 88a, c, 89, 90b–c, 91a). Strong rounded blunt protuberance on abaxial edge of lower surface of M'\textsubscript{2}, at junction between anterior and posterior parts. Internal (upper) side of M'\textsubscript{2} deeply concave (Figs 87a, 88c, 89a, 90c). M'\textsubscript{1} Y-shaped, with very short anterior (marginal) branches and long posterior part
forming anterior half of zygal bar (Figs 87a, c, 88a, 89a, 90b, 91a). $M'_1$ largely in contact with $M_1$ (adaxially) and also in contact, along shorter sutures with $M'_2$ (abaxially) and Z (posteriorly). All junctions between adjacent branches of $M'_1$ gently rounded and markedly concave. Lower surface of $M'_1$ almost flat, except antero-adaxial corner, slightly protruding below and proximally to left aulacophore apophysis. Anterior part of $M'_1$ forming narrow and high vertical wall (e.g. in UCM.EO.036, front edge of $M'_1$ about 2 mm wide and 3 mm high; Figs 88a, 90b). Left of aulacophore insertion, abaxial part of anterior side of $M'_1$ forming high vertical proximal thecal margin. Posteriorly to aulacophore insertion, adaxial part of anterior (vertical) margin of $M'_1$ comprising well-defined, narrow, cup-shaped, proximally concave left apophysis (e.g. in UCM.EO.036, left apophysis about 0.8 mm wide and 1.5 mm high). Left apophysis morphologically similar, but symmetrical to right one (borne on anterior margin of $M_1$, see above). Left apophysis framed abaxially by low, slightly rounded ridge. Strong eyebrow-shaped crest above upper portion of left apophysis, probably corresponding to floor of left scutula. In upper adaxial edge of left scutula, shallow groove connecting it, posteriorly, to intrathecal cavity. Strong longitudinal median crest (anterior portion of zygal crest) running on upper (internal) surface of posterior branch of $M'_1$ (Figs 88a, e, 90a–b). Lateral sides of straight to gently curved posterior (zygal) branch of Z almost parallel to each other. Left edge of zygal bar slightly convex, whereas opposite (right) edge, weakly concave. Zygal bar markedly oblique on lower thecal surface.

Infracentral areas largely unequal in size, with right one significantly more extensive than left one (e.g. in CGS.LK.17, area of right infracentral area $\approx 115 \text{ mm}^2$, whereas area of left infracentral area $\approx 45 \text{ mm}^2$; Figs 87a, 91a). Right infracentral area moderately elongate transversely, subtrapezoidal, with almost parallel anterior and posterior margins (Figs 87a, 91a). Right infracentral area delimited by six marginals ($M'_1$, $M_{1-3}$, Ms, Z). Anterior edge of right infracentral area sinuous, straight to weakly concave (along posterior adaxial portions of
M₁ and M₁), much shorter than slightly convex opposite (posterior) margin (along left part of M₃, Ms, and right branch of Z). Lateral sides of right infracentral area of comparable lengths, gently convex, slightly diverging distally. Left infracentral area relatively narrow, longitudinally elongate, crescent-shaped, slightly narrower anteriorly than posteriorly (Figs 87a, c, 89a, 91a). Left infracentral area totally enclosed within six marginals (M'₁₋₄, Ms, Z).

Abaxial margin of left infracentral area gently curved, regularly convex, slightly longer than opposite (adaxial) weakly concave edge, along zygal bar. Anterior and posterior extremities of left infracentral area short, rounded and convex. Infracentrals tessellate, polygonal (typically hexagonal), thin, fewer and significantly larger in right infracentral area than in left one (Figs 87a, c, 89a, 91a). In holotype (Figs 87a, 89a), most of right infracentral area consisting of particularly large skeletal elements (typically 2–3.2 mm wide), with the exception of narrow postero-abaxial zone (along right and posterior thecal margins) made of smaller platelets (0.5–2 mm). No platelets inserted in between large plates. Left infracentral area of holotype (Figs 87a, 89a) with largest plates occurring in anterior half of left infracentral area (most of them are 1–2 mm wide), progressively decreasing in size distally.

Similar pattern in specimen CGS.LK.17 (Figs 87c, 91a), with right infracentral area made of about 60 large skeletal elements, most of them 1.5–2.5 mm wide, with some smaller plates along postero-abaxial margins, and left infracentral area consisting of over 80 platelets, typically 0.7–1.2 mm wide.

Adorals thin, slightly unequal in size, forming delicate V-shaped arch over aulacophore apophyses, along anterior margin of upper thecal surface (Figs 87b, 89b). Left adoral (A'₁) polygonal, depressed, with slightly raised anterior and adaxial lips. A'₁ slightly oblique, transversely elongate, abaxially in contact with M'₁ along short, straight suture, and adaxially, with right adoral (A₁). A₁ oblique, transversely elongate, sub-pentagonal, slightly longer than A'₁ and morphologically more complex. Adaxial portion of A₁ depressed with raised lip along
suture with A'. Upper surface of A₁ bearing narrow, longitudinal groove extending from middle part of plate (posteriorly) to right adoral orifice (anteriorly, at contact with M₁).

Groove delimited by low, narrow, inverted U-shaped ridge (laterally and posteriorly). Right part of A₁ much thicker than left (depressed) area, forming low inflated protuberance along abaxial edge of groove and right adoral orifice. Supracentrals numerous, polygonal, forming thin tessellate upper integument (Figs 87b, d, 88e, 89b, 90a, 91b). In holotype (Figs 87b, 89b), supracentrals displaying clear radiating (rosette) pattern, with concentric circles of hexagonal plates around large central octogonal element (2.9 mm wide). Within a same circle, supracentrals all about of the same size (e.g. in first circle: 2.2–2.5 mm). Supracentrals decreasing in size away from large central element. Same concentric pattern around large central octogonal plate occurring in supracentral area of CGS.LK.17 (Figs 87d, 91b).

Lamellate organ in right anterior corner of supracentral area, extending obliquely from near postero-abaxial edge of A₁ (proximally) to posterior extremity of M₂ (distally) (Figs 87b, d, 89b, 91b). Lamellate organ fusiform, decreasing in width both anteriorly and posteriorly, protruding both above supracentral area (Figs 87b, d, 89b, 91b) and deeply into thecal cavity (Figs 88c, 90c). Lamellate organ consisting of numerous (at least 25 in CGS.LK.17, probably more in holotype; Figs 87b, d, 89b, 91b), thin (0.2 mm thick), rhombic, vertical lamellae. Antero-abaxial and postero-adaxial portions of each lamella meeting along well-defined suture, corresponding to former boundary between anterior and posterior U-shaped elements (Figs 87b, 88c, 89b, 90c). On upper thecal surface, antero-abaxial portion of each lamella longer and more gently sloping than short, steep postero-adaxial part. Periproct not observed.

Proximal aulacophore consisting of six, bilaterally symmetrical, transversely elongate, relatively narrow, telescopic rings (Figs 87a–b, 88e, 89, 90a). Each ring made of a pair of C-shaped, large inferolaterals and two small, quadrangular, flat tectals. Within a same ring, inferolaterals forming slightly convex lateral (vertical) sides and contributing equally to flat
lower surface. Lower and abaxial branches of a same inferolateral almost perpendicular to each other, meeting along sharp, angular edge externally, but along smooth, regular concavity internally (Fig. 87a–b, 88c, 89, 90c). Abaxial (vertical) branch of each inferolateral about twice longer than lower one. Tectals restricted to adaxial portion of upper surface of each ring (Figs 87b, 88e, 89b, 90a). Slightly raised distal margin of each ring partly overlapping depressed proximal neck of next, more anterior one or proximal portion of stylocone. Stylocone massive, broad, short (3 mm long and 3 mm wide in holotype; Figs 87a, 89a), comprising wide posterior funnel-shaped portion with regularly rounded lower and lateral sides, hosting deep proximal (internal) cavity, and much shorter, narrower, semi-cylindrical distal part (about 0.8 mm long and 1.6 mm wide). Proximal cavity of stylocone entirely enclosed by distal-most proximal rings (Figs 87a, 89). Upper surface of distal part of stylocone bearing distinct longitudinal median groove, deeply encased between lateral lips interrupted by paired transverse channels. Lower surface of stylocone and next ossicles regularly rounded and smooth. Upper surface of ossicles bearing same internal structures as in stylocone (e.g. longitudinal median groove, transverse channels) (Fig. 89b). In holotype, first ossicle about 1.6 mm wide and 1 mm long, with entirely flat, smooth anterior (distal) surface, originally in contact with next, second ossicle. Several scattered, disarticulated cover plates occurring next to stylocone and proximal rings in holotype (Figs 87a–b, 89). Cover plates large, thin, fan-shaped, with delicate fibrillar ornamentation radiating away from thicker, smooth, narrow, basal umbo. Upper edge of cover plates rounded.

Remarks. The reevaluation of the morphology of T. jefferiesi largely confirms most salient morphological features originally described by Gil Cid et al. (1996d). However, the reexamination of the holotype and paratypes of T. jefferiesi also indicates that some aspects of its original reconstruction (Gil Gid et al. 1996d, fig. 7) were at least partly conjectural. For
example, the morphology of the spinal process cannot be documented based on the original type material. Marginal branches of M₃ are poorly preserved in one individual (UCM.OE.036; Figs 88a, 90b), and M₃ is entirely lacking in all other specimens. The morphology of the distal aulacophore (22 ossicles shown in Gil Cid et al. 1996d, fig. 7) cannot be confidently reconstructed beyond the stylocone and the next two ossicles. The anal pyramid probably occurred at the left posterior extremity of the supracentral area, as illustrated by Gil Cid et al. (1996d, fig. 7A). However, the periproct is not preserved in any specimen from the type locality. Comparison with other scotiaecystids suggests that the anal pyramid was possibly closer to the antero-adaxial margin of M₅. Finally, the reexamination of the type material confirms the occurrence of ornamentation on the lower surface of M₂, M₃ and M₂, but it does not show any clear evidence of putative protuberances on M₁, M₄ and M₅, as suggested by Gil Cid et al. (1996d, fig. 7).

A relatively complete, well-preserved additional specimen of *Thoralicarpus* (CGS.LK.17; Figs 87c–d, 91) from the upper part of the Letná Formation (Barrandian area, Czech Republic) is tentatively assigned here to *T. jefferiesi*. This identification relies on its morphology, largely congruent, in all aspects, with that of the more incomplete and disarticulated type specimens from the Cantera Shale (Central Iberian Zone, Spain): similar outlines, identical plate patterns and same relative proportions of skeletal elements. Consequently, in the absence of any significant morphological difference with the type material of *T. jefferiesi*, CGS.LK.17 probably represents the single known occurrence of this taxon outside of its type-locality. The unique Czech specimen of *T. jefferiesi* was collected in a level yielding abundant remains of the solutan *Dendrocystites barrandei*, which is also co-occurring with *T. jefferiesi* in the Cantera Shale (see Gil Cid et al. 1996d, Gutiérrez-Maro et al. 2018). If specimen CGS.LK.17 is correctly identified as *T. jefferiesi*, its excellent preservation offers the possibility to document some previously poorly known morphological
features of this taxon. In the original reconstruction of *T. jefferiesi* (Gil Cid *et al.* 1996d), the
morphology of its spinal process largely relied on a comparison with *Bohemiaecystis bouceki*.
Specimen CGS.LK.17 suggests that the spinal of *T. jefferiesi* was wider, thicker and more
massive than initially expected.

The morphology of *T. jefferiesi* (Fig. 86) appears clearly distinct from those of both *T.
bounemrouensis* (Fig. 72) and *T. guilloui* (Fig. 83). *Thoralicarpus jefferiesi* is characterised
by broader, more sabot-shaped thecal outlines, a more gently rounded left thecal side, shorter
G, M₁ and Ms, a wider and more massive spinal process, and a differently shaped posterior
zygal plate (with short posterior branches and the right one perpendicular to the anterior
branch of Z). As already pointed out by Gil Cid *et al.* (1996d), the broad, sabot-shaped thecal
outlines of *T. jefferiesi* are morphologically closer to those of *Bohemiaecystis bouceki* (Fig.
60). This morphological similarity can suggest affinities between these two taxa and/or
simply reflect comparable modes of life or associated environmental conditions. However, *T.
jefferiesi* differs from *B. bouceki* in the loss of the digital (no evidence of any facet for the
articulation of D along abaxial margin of M'₄), the possession of a shorter, L-shaped M₅ (it is
straight and more elongate in *B. bouceki*) and of a more curved, angular M₂. Within
scotiaecystids, relatively comparable broad, sabot-shaped outlines also occur in
*Proscotiaecystis melchiori* (see above; Fig. 11a). However, *P. melchiori* differs from both *B.
bouceki* and *T. jefferiesi* in the presence of a proto-lamellate organ. Moreover, *P. melchiori*
possesses a digital, a short, oblong spinal blade, and five proximal rings (see Ubaghs 1983).

*Thoralicarpus prokopi* sp. nov.

Figures 23, 26f, 92–98, 99a–b

2014 *Scotiaecystis* sp. – Noailles *et al.*, p. 457
Derivation of name. The species is dedicated to the late Czech palaeontologist Rudolf Jan Prokop (1934–2018), who was a specialist of Palaeozoic echinoderms and described several stylophoran taxa from the Prague Basin.

Holotype. CGS.OZ.194 (coll. Zicha; Figs 93a, 94a, 96a, 97a): part and counterpart of almost complete, fully articulated theca (adorals, G, M'_1-4, M_1-3, M_5, Ms, Z), with proximal aulacophore strongly bent rightwards, stylocone, and long portion of distal appendage comprising over 20 articulated ossicles, with associated slightly open cover plates. In spite of preservation in coarse sandstones, delicate skeletal structures (e.g. infracentrals, lamellate organ, spinal blade, supracentrals) are relatively distinct. CGS.OZ.194 is designated here as holotype, because it is the most complete, fully articulated specimen known in both lower and upper aspect.

Paratypes. Twenty-one individuals collected in the same stratigraphic horizon and locality as the holotype are designated here as paratypes: CGS.OZ.149–150, 189–193, 195–208 (coll. Zicha; Figs 23a–b, 93b–f, 94b–e, 96b–f, 97b–f, 98). This choice is motivated by the wide range of sizes displayed by this sample of 21 specimens, which makes it possible to document both intraspecific and ontogenetic variability within a same assemblage. Although all paratypes occur in the same lithology (coarse sandstones), quality of preservation is also variable, with e.g. delicate skeletal structures (integumentary platelets, lamellate organ) sometimes better preserved (e.g. CGS.OZ.200). Part and counterpart available for most paratypes (CGS.OZ.149–150, 189–193, 195–196, 198–201, 203, 205–206), except for five of them, only known in upper aspect (CGS.OZ.197, 202, 204, 207–208). Most paratypes fully articulated, but with left and right posterior parts of theca (glossal, spinal blade, M_3) often
missing. Proximal rings and more or less extensive portions of distal appendage preserved in most individuals, with cover plates generally closed or slightly ajar above stylocone and ossicles.

Other material. Two distinct stratigraphic levels in the upper part of the Letná Formation and the lowermost part of the overlying Vinice Formation yielded 11 additional specimens preserved in finer-grained lithology (clayey shales, fine siltstones) than in type locality: CGS.LK.5–14, 16 (coll. Kašička). CGS.LK.14 (Figs 95b, 99b) corresponding to slightly disarticulated individual in upper aspect (no counterpart), with almost complete theca (adorals, G, M’1–4, M1–3, M5, Ms, Z, most supracentrals, fragments of lamellate organ) and small stump of proximal aulacophore. Spinal blade and distal appendage missing. CGS.LK.16 (Figs 23c, 94f, 99a) consisting of large portion of slightly disarticulated individual in upper aspect (no counterpart), with incomplete theca (A1, M’1–2, M1–3, Ms, Z, most supracentrals, part of lamellate organ, distal extremity of M’4 and large portion of spinal blade), fully articulated proximal aulacophore, stylocone and next two ossicles occurring on same slab as strophomenid brachiopods and abundant remains of well-preserved, complete solutans (Dendrocystites barrandei). Other individuals corresponding to fully articulated portions of lower (CGS.LK.6, 9–10; Fig. 95a) or upper thecal surfaces (CGS.LK.13), strongly disarticulated thecae (CGS.LK.7–8, 12) and isolated scotiacystid marginals (CGS.LK.5, 11).

Horizons and localities. Holotype and all paratypes were collected at Chrustenice (Fig. 22.6), about 11.5 km NE of Zahořany, Prague Basin, Czech Republic, within grey to yellow, thinly laminated sandstones in the uppermost part of the Letná Formation, late Sandbian (Sa2), Upper Ordovician. Specimen CGS.LK.16 was sampled in the same locality and horizon as CGS.LK.17 (Thoralicarpus jefferiesi, see above), i.e. within a Dendrocystites barrandei
dense bed occurring in a temporary excavation made in Borová Street, along the slope of Děd Hill, Zahořany, Prague Basin, Czech Republic (Figs 22.5, 23c), within the upper part of the Letná Formation, late Sandbian (Sa2), Upper Ordovician. This *Dendrocystites*-dominated bed is probably stratigraphically slightly lower than the level exploited at Chrustenice. This horizon also yielded remains of a third specimen of *Thoralicarpus* (CGS.LK.15), too poorly preserved to be assigned to either *T. jefferiesi* or *T. prokopi*. Finally, all other individuals of *T. prokopi* (CGS.LK.5–14) were found in the same locality as CGS.LK.15–17 (i.e. Borová Street, Děd Hill, Zahořany, Barrandian area, Czech Republic; Fig. 22.5), but in micaceous shales occurring higher in the section, in the lowermost part of the Vinice Formation, latest Sandbian–earliest Katian (Sa2–Ka1), Upper Ordovician, i.e. stratigraphically slightly higher than the type-locality.

**Diagnosis.** A species of *Thoralicarpus* with a long, straight to gently curved left thecal margin. $M_2$ gently curved. Spinal blade long, wide, subtriangular, with a blunt distal tip. $M_5$ long. Glossal short and subtriangular. Posterior zygal plate with long marginal branches, the right one making an acute angle with the zygal bar.

**Description.** Theca sabot-shaped, asymmetrical, with sub-triangular outlines (Fig. 92). Lower thecal surface almost flat to slightly concave, except two well-developed antero-abaxial protuberances borne by $M'_2$ (on the left) and $M_2$ (on the right) and raised antero-adaxial portions of both $M'_1$ and $M_1$ (below aulacophore apophyses). Thecal height slightly decreasing antero-posteriorly. Theca framed by two delicate adorals ($A'_1$ and $A_1$) and 11 relatively thick and wide marginals ($G, M'_1$–$4, M_1$–$3, M_5, M_6, Z$). Anterior thecal margin short, slightly oblique to main axis, corresponding to wide, shallow embayment at aulacophore insertion, delimited laterally by rounded antero-abaxial thecal corners. On upper surface,
anterior thecal margin V-shaped, regularly curved, concave, made of A', M' and adaxial part of M' (on the left), A1, and short adaxial part of M1 (on the right). On lower surface, anterior thecal edge shallower, more sinuous, because of short convex adaxial extension of M' and M1 protruding slightly anteriorly, below aulacophore apophyses. Left anterior thecal corner rounded, formed by strongly bowed M'2, extending more anteriorly than much fainter opposite (right) thecal corner provided by gently curved M1, right of aulacophore insertion. Left and right thecal sides strongly unequal in size, both convex, weakly curved, and extending more distally than posterior thecal margin into moderately elongate, flat distal processes: glossal (on the left) and M3-spinal (on the right). Sub-triangular aspect of thecal outlines resulting from faint transition between anterior and right thecal sides, forming together more or less continuous, sinuous margin extending from M'2 (anteriorly) to distal extremity of spinal blade (posteriorly). Posterior thecal margin corresponding to wide embayment bounded abaxially by the two posterior processes (glossal and spinal). Posterior edge of theca slightly oblique to main axis, elongate, sinuous, and mostly made by Ms and posterior (marginal) branches of Z. Lower thecal surface divided into two unequal infracentral areas by nearly straight, oblique zygal bar, more or less parallel to left thecal side. Thecal width (TW) estimated between M3-M'4 suture (on the left) and contact between M2 and M3 (on the right) (Fig. 26f). TW measurable only in 9 individuals (out of 33), because of incomplete preservation of posterior parts of theca and/or disarticulation. Measured values for TW varying from 9.4 mm (smallest known individual: CGS.OZ.206) to 16.7 mm (CGS.LK.14), but TW probably over 25 mm in incomplete, largest observed individuals (CGS.LK.7, CGS.OZ.191). Thecal length (TL) measured perpendicularly to TW, between anterior-most extremity of M'2 (proximally) and posterior-most edge of left branch of Z, along suture with G (distally). Holotype relatively large individual within observed sample (TW=14.6 mm, TL=12.4 mm). Ratio TW/TL around 1.23 +/- 0.05, independent of thecal size.
transversely elongate, slightly curved, consisting of two distinct parts connected by a slightly narrower neck (Figs 93, 96, 97c, e). Right of aulacophore insertion, abaxial portion of M₁ elongate, with anteriorly convex, gently rounded edge, posteriorly concave margin, and short, straight abaxial suture with M₂. Right part of M₁ subtriangular in cross-section, with almost flat lower surface, concave posterior (internal) side, and convex, subvertical anterior (outer) wall. Posteriorly to aulacophore insertion, left portion of M₁ shorter, wider, protruding both downward and anteriorly, adaxially in contact with M₁ along relatively long suture. Anterior edge of adaxial part of M₁ folded upward into vertical wall (right apophysis), posteriorly to aulacophore insertion (Figs 94b–c, e, 95b, 97d, 98d, f, 99b). Upper (internal) surface of adaxial portion of M₁ almost flat, except right portion of anterior transverse groove running posteriorly to right apophysis (Figs 95b, 99b). Front (anterior) view of right apophysis impossible to observe in most specimens, because of preservation of fully articulated proximal aulacophore. Right apophysis forming semi-circular, relatively wide, concave, deep anterior cavity, almost symmetrical to adjacent left apophysis (on anterior edge of M₁) (e.g. CGS.OZ.191). Small, subtriangular, shallow depression on upper abaxial edge of right apophysis probably corresponding to right scutula (Figs 94c, 98f). In CGS.OZ.191, faint portion of narrow groove running along postero-adaxial edge of left scutula and upper abaxial margin of right apophysis very likely representing part of anterior oblique groove. In all available specimens, infundibulum not observed, hidden by slightly collapsed right adoral. M₂ elongate, weakly curved, with slightly convex abaxial edge and lightly concave opposite, adaxial margin (Figs 93, 94a–b, d–f, 95b, 96a–d, f, 97a, d, f; 98a–e, 99a–b). Lower surface of M₂ flat, except in middle position along abaxial margin, low, longitudinally elongate, spike-shaped protuberance oriented posteriorly (Figs 93, 96). M₃ Y-shaped, forming right posterior thecal corner, with two very short marginal branches and long, posterior spike-shaped (spinal) process (Figs 93a, c–f, 94b, d–f, 95b, 96a–d, f, 97d, 98a, c–e). Left and anterior part of M₃
almost perpendicular to each other. Antero-adaxial margin of M₃ regularly curved and concave. Abaxial margin of M₃ almost straight to slightly convex along anterior (marginal) and posterior (spinal) branches. Spinal blade relatively thin, sub-triangular, relatively wide proximally and tapering distally into blunt posterior extremity. Upper surface of spinal process strongly curved downwards and posteriorly, smooth, bounded by two lateral relatively sharp edges. Lower surface of spinal process almost flat to slightly convex. Length of spinal process comparable in all observed specimens (about 3 mm long), independently of thecal size. Ms transversely elongate, sinuous, longest marginal, in contact with both M₃ (on the right) and Z (on the left) along short, straight sutures (Figs 93a–b, e–f, 94a–b, d–f, 95b, 96a, c, f, 97a–d, f, 98a–e). Posterior zygal plate Y-shaped, with three distinct branches almost subequal in length and width (Figs 93a–b, d–f, 95a–b, 96a, c, f, 99b). Anterior portion of Z almost straight, forming posterior part of zygal bar. Posterior margin of Z with shallow median concavity, posteriorly to insertion of zygal bar. Anterior and right branches of Z meeting with an acute angle (≈70°). Antero-abaxial margin of Z (along left infracentral area) regularly curved and concave along widely diverging zygal and left branches (around 135°). Upper (internal) surface of anterior part of Z carrying posterior portion of strong longitudinal zygal crest (Figs 94a–e, 95b, 97a–b, d, f, 98, 99b). M₅ smallest marginal, L-shaped, with short, straight, subequal posterior and left branches, almost perpendicular to each other (Figs 93a, d–f, 94a–b, d, 95a–b, 96a–b, f, 97a–b, d, 98a–c, 99b). Antero-adaxial margin of M₅ regularly curved and concave. M₅ in contact with G (posteriorly), M′₄ (anteriorly) and Z (on the right). Glossal relatively short, broad, subtriangular, wider anteriorly and tapering distally into blunt extremity (Figs 93a, d, f, 94a, 95a–b, 96a–b, f, 97a, 98a, 99b). G almost flat, slightly recurved downwards distally. Abaxial (left) margin of G gently curved, slightly convex, lightly longer than opposite (adaxial), straight to slightly concave adaxial edge. G anteriorly in contact with M₅ along long, transverse suture, and with Z, along much shorter,
oblique suture. Morphology and dimensions of glossal (about 3 mm long and 1.8 mm wide) comparable in all individuals, independently of thecal size. M’4 relatively short, longitudinally elongate, unornamented, with a straight to weakly curved (convex) abaxial margin, and a straight, slightly concave opposite (adaxial) edge (Figs 93, 94a–b, d, 95a–b, 96a–d, f, 97a–d, f, 98b–c, 99b). M’3 similarly shaped as M’4, but slightly longer (Figs 93b–f, 94b–d, 95a–b, 96b–d, f, 97b–d, f, 98b–f, 99b). M’2, J-shaped, strongly curved, forming rounded left anterior thecal corner (Figs 93b–f, 94b–f, 95b, 96b–f, 97b–f, 98, 99a–b). Short anterior (adaxial) and longer posterior portions of M’2 almost perpendicular to each other. Postero-adaxial margin of M’2 strongly curved and concave. As in other lateral marginals (M’3–4, M2), M’2 subtriangular in cross-section, with oblique, weakly convex outer (upper, abaxial) wall, and more concave internal (upper, adaxial) side. Lower surface of M’2 almost flat, except relatively strong, rounded, blunt, spike-shaped protuberance at junction between right and posterior branches. M’1 Y-shaped, with two particularly short anterior (marginal) left and right parts, and longitudinally elongate posterior branch forming anterior portion of zygal bar (Figs 93, 95a, 96, 97c, e). On lower thecal surface, M’1 almost flat, except antero-adaxial region protruding both downwards and slightly anteriorly, at aulacophore insertion. Anteriorly, abaxial part of M’1 forming high, narrow vertical wall, left of aulacophore insertion, in contact with both M’2 (abaxially) and A’1 (adaxially). Posteriorly to aulacophore insertion, proximal portion of adaxial part of M’1 recurved upward into left apophysis (Figs 94c, 95b, 98f, 99b). Left aulacophore apophysis bearing large, semi-circular, deep adaxial cavity. Upper (internal) surface of posterior branch of M’1 with strong longitudinal zygal crest (Figs 94a–d, 95b, 97a–b, d, f, 98, 99b). Posteriorly to left apophysis, upper (internal) surface of adaxial part of M’1 bearing left portion of anterior transverse groove, running from adjacent marginal M1 (on the right) to antero-adaxial extremity of zygal crest (on the left). Posterior branch of M’1 almost straight, contributing to more than half of zygal bar length.
Zygal bar dividing lower thecal surface into two infracentral areas of unequal size. Right infracentral area consistently larger than left one. In holotype (Figs 93a, 96a), area of right infracentral area (ARIA, 47 mm²) about 1.4 time larger than area of left infracentral area (ALIA, 34 mm²). Relative sizes of both integumentary areas variable within observed sample, with ratio ARIA/ALIA ranging from about 1.4 (e.g. holotype) to 1.8 (e.g. CGS.LK.14: ARIA=62.7 mm², ALIA=34.2 mm²; CGS.OZ.189: ARIA=47 mm², ALIA=26 mm²). Variations in ratio independent from thecal size. Infracentrals polygonal, generally hexagonal, forming thin tessellate pavement (Figs 93a, 95a, 96a). Right infracentrals fewer and about twice as large as left ones (CGS.LK.6). No obvious plate pattern observed in both infracentral areas, except occurrence of smaller elements close to marginal frame and more elongate ones along zygal bar. Right infracentral area subtrapezoidal in shape, transversely elongate, entirely framed by six marginals (M'1, M1–3, Ms, Z) (Figs 93a, e–f, 95b, 96a, c, f). Anterior margin of right infracentral area (along adaxial parts of M'1 and M1) short, sinuous, more or less parallel to much longer, sinuous posterior edge (along left branch of M3, Ms and right part of Z). Abaxial and adaxial sides of right infracentral area diverging posteriorly, with left one (along zygal bar) nearly straight, longer and more oblique than gently rounded, slightly convex, opposite (right) one (along abaxial part of M1, M2 and anterior branch of M3). Left infracentral area sub-elliptical, oblique, longitudinally elongate, narrow, slightly wider posteriorly than anteriorly, totally framed by six marginals (M'1–4, Ms, Z) (Figs 93, 95a–b, 96a–d, f, 97c, 99b). Abaxial and adaxial margins of left infracentral area nearly parallel to each other, with right one (along zygal bar) almost straight, and opposite (left) one weakly curved and slightly convex (along posterior part of M'2, M'3, M'4). Anterior and posterior extremities of left infracentral area short, rounded, and strongly convex.

Left and right adorals forming delicate V-shaped anterior thecal margin on upper thecal surface, posteriorly to aulacophore insertion (Figs 94, 95b, 97a–b, d, f, 98, 99a–b). A'1 and A1
slightly unequal in size, meeting adaxially along median axis. $A'_1$ oblique, transversely elongate, sub-pentagonal, depressed, antero-abaxially in contact with underlying $M'_1$ along short suture (Figs 94, 95b, 97a–b, d, f, 98, 99a–b). $A_1$ slightly larger than $A'_1$, oblique, morphologically more complex, antero-abaxially sutured to $M_1$ along relatively long suture (Figs 94, 95b, 97a–b, d, f, 98, 99a–b). Left part of $A_1$ slightly depressed, with raised adaxial lip along contact with $A'_1$. Antero-abaxial margin of $A_1$ with well-defined notch corresponding to right adoral orifice (hydropore) at suture with $M_1$ (Figs 94a, c, 97a, 98e–f).

Hydropore notch surrounded laterally and posteriorly by well-defined inverted U-shaped ridge. Supracentral area consisting of numerous, thin, polygonal (mostly hexagonal), tessellate skeletal elements (Figs 94a, c, f, 95b, 97a, 98f, 99a–b). Supracentrals displaying roughly concentric pattern, with skeletal elements more or less regularly decreasing in size away from central cluster made of the largest plates (Figs 94f, 95b, 99a–b). Lamellate organ rarely preserved, more or less weathered, incomplete and/or dislocated (Figs 94a, c–e, 95b, 97a, 98a, c–d, f, 99b). Lamellate organ fusiform, slightly sinuous, extending obliquely on upper thecal surface from close to postero-abaxial margin of $A_1$ to distal extremity of $M_2$. In best preserved specimens, lamellate organ consisting of over 20 vertical lamellae decreasing in width both anteriorly and posteriorly (Figs 94c, 98f). All lamellae with identical thickness (0.2 mm; e.g. CGS.LK.14, 16, CGS.OZ.191), strongly protruding over supracentral area about 2/3 away from their antero-abaxial margin. On upper surface, antero-abaxial edge of each lamella nearly straight, gently sloping towards marginal frame, and much longer than opposite (postero-adaxial) steeper edge. Lamellipores wider in postero-adaxial part of lamellate organ than in antero-abaxial one (Figs 94c, 98f). Periproct not observed.

Proximal aulacophore consisting of six bilaterally symmetrical, telescopic, transverse rings forming particularly flexible, elongate, cylindrical structure inserted into adaxial region of proximal thecal margin (Figs 93a–c, e–f, 94b, f, 96a–e, 97, 98a–e, 99a). Rings sub-triangular
in cross-section, with two opposite, relatively straight, upper sides meeting adaxially at relatively sharp (acute) angle along median axis, and sloping abaxially towards rounded lateral edges of flat to slightly convex lower surface. Each ring made of four plates: two inferolaterals and two tectals. Inferolaterals symmetrical, strongly curved, C-shaped, forming lower surface and most of lateral (upper) sides of each ring. Tectals much smaller, almost quadrangular, flat, symmetrical, restricted to adaxial part of upper side of each ring. Raised, wider distal edge of each ring overlapping narrower, depressed proximal neck of next, more anterior ring or proximal part of stylocone. Stylocone elongate, funnel-shaped, about twice wider posteriorly (proximal part inserted within distal-most proximal ring) than distally (Figs 93a, c, e, 94b, f, 96a, c–d, 97b–f, 98b, 99a). Lower and lateral sides of stylocone smooth and regularly rounded. Upper (internal) surface of distal part of stylocone with deep longitudinal median groove bounded by two thin abaxial ridges interrupted by two pairs of opposite transverse channels leading to lateral depressions. Two pairs of small, symmetrical pits for articulation of overlying cover plates, along abaxial edges of upper surface of stylocone. Anteriorly to stylocone, relatively long portions of distal aulacophore preserved in several individuals, with over 20 articulated ossicles (Figs 93e, 94b, 96a, c–d, 97b, d–f, 98b). Ossicles relatively short, wider than long, semi-cylindrical, with smooth, rounded, lower surface and flat upper (internal) side. Upper surface of ossicles bearing internal structures (longitudinal median groove, lateral ridges, one pair of transverse channels, two lateral depressions, two abaxial pits for articulation of cover plates) comparable in morphology to those occurring in stylocone (Figs 94b, 97d, 98b). Cover plates often preserved in closed or slightly ajar position above stylocone and ossicles (Figs 97b, d, f, 98b, e). One pair of opposite (left and right) cover plates articulated to abaxial edges of each underlying ossicle, and two pairs to stylocone. In closed position, opposite cover plates meeting adaxially along median axis, forming relatively high roof above stylocone and ossicles, with same steeply sloping sides as
tectals in proximal rings. Cover plates fan-shaped, relatively high, with wide, thin, rounded upper margin and much narrower, thicker, lower base for articulation. Distal part of each cover plate partly overlapping proximal portion of next, more anterior one.

Remarks. Over thirty specimens of scotiaecystids from three distinct localities in the Barrandian area are here considered as conspecific, spanning a relatively short stratigraphic interval bracketed between the upper part of the Letná Formation and the base of the overlying Vinice Formation (late Sandbian–early Katian). This interpretation is based on their similar morphologies, plate patterns and thecal outlines. Observed interindividual variability is relatively low and is based on the relative proportions of the two infracentral areas and, to a lesser extent, the morphology of the posterior zygal plate (e.g. angle between anterior and right branches varying between 65° and 75°). Intraspecific variability is also based on the relative sizes of both glossal and spinal processes, proportionately much longer in smaller (i.e. younger) individuals than in larger (i.e. more mature) ones. As this is also the case in other scotiaecystids (e.g. T. bounemrouensis, see above), the length of these two posterior processes remains the same during growth, and is thus size-independent.

Although these scotiaecystids locally co-occur with Thoralicarpus jefferiesi (known by one specimen from lower-most excavation in Borová street, upper part of the Letná Formation; see above), they are interpreted here as belonging to a distinct species of the same genus: T. prokopi. Their assignment to Thoralicarpus relies on the occurrence of a Ms marginal, a lamellate organ made of high lamellae, and on the absence (loss) of D on the left thecal side. The smooth, regular abaxial margin of M'4 without any socket for the articulation of the digital supports the view that D was originally absent (lost). Thoralicarpus prokopi differs from T. jefferiesi (Fig. 86) in the possession of more triangular thecal outlines, a less rounded left thecal margin, a more oblique zygal bar, more trapezoidal outlines of the right
infracentral area, more elongate M₁ and Ms, a less curved M₂, a more triangular spinal blade, and a differently shaped posterior zygal plate, comprising three subequal branches, with anterior and right ones meeting at acute angle (in T. jefferiesi, the two posterior parts of Z are much shorter than the anterior one, and its right and zygals branches are almost perpendicular to each other; see above). Thoralicarpus prokopi also differs from T. guilloui (Fig. 83) in the occurrence of more triangular, broader thecal outlines, a straighter zygal bar, a weakly curved almost straight left thecal margin, a lightly curved M₂, and a wider spinal blade, which is not oblique to right thecal side. In many respects, T. prokopi appears morphologically closer to T. bounemrouensis (Fig. 72) than to other scotiaecystid taxa (e.g. similarly oriented spinal blade, almost identical M'₁, M'₂, M'₄, M₁, M₂, M₅, Ms, Z). However, the left thecal margin of T. bounemrouensis is more curved (angular) with a bowed M'₃, its zygal bar is lightly more arched, and its posterior processes (glossal, spinal) are narrower, less massive than in T. prokopi. Morphological similarities between T. bounemrouensis and T. prokopi possibly reflect close (phylogenetic) affinities between these two taxa and/or may also result from similar modes of life in shallow settings and relatively coarse lithologies. At generic scale, T. jefferiesi appears as relatively distinct from the three other species, all characterised by elongate marginals M₁ and Ms, and similarly-shaped posterior zygal plates). Moreover, T. bounemrouensis is apparently morphologically intermediate between T. guilloui (e.g. similar strongly curved left thecal margins, narrow oblong posterior processes) and T. prokopi (e.g. comparable weakly curved right thecal margins, and posteriorly-oriented spinal blades).

Thoralicarpus cf. prokopi sp. nov.

Figures 99c–d, 100

1968 Bohemiaecystis bouceki Caster in Ubaghs, S550
Material. NRS.Ec.19934: part and counterpart of an incomplete, partly disarticulated specimen preserved in a concretion (Figs 99c–d, 100). Preserved portion of theca consisting of anterior and right marginals (M'₁₋₂, M₁₋₃), almost complete posterior zygal plate (Z), most of right infracentral area, several patches of left infracentrals, a large portion of disarticulated supracentral area with lamellate organ and two adorals (A'₁ and A₁). Disarticulated proximal aulacophore preserved next to anterior thecal margin; more distal portions of appendage missing. The specimen label provides no clues on its acquisition (date, collector) by the collections of the Naturhistoriska Riksmuseet, Stockholm. It is thus impossible to document if this specimen was known by Caster (in Ubaghs 1968), when he reported the presence of *B. bouceki* in the Šárka Formation. As no other scotiaecystid material is reported from this lithostratigraphic unit, all published references mentioning the occurrence of *B. bouceki* in the Šárka Formation are tentatively assigned to this specimen.

Horizon and locality. The specimen was collected at Praha-Šárka (Fig. 22.1), a cumulative name for several localities situated NW of Prague in Barrand's time, Barrandian area, Czech Republic, Šárka Formation, Darriwilian (Dw₁–Dw₂), Middle Ordovician.

Description. Relatively large, incomplete, disarticulated theca (TL > 26 mm; TW > 30 mm) framed by relatively broad marginals, six of which are well-preserved (M'₁₋₂, M₁₋₃, Z) (Figs 99c–d, 100). Anterior thecal margin particularly short, strongly concave, reduced to aulacophore insertion, and deeply encased between two rounded antero-abaxial corners borne by M₁ (on the right) and M'₂ (on the left). Right thecal margin slightly disarticulated,
extending from abaxial portion of M₁ (anteriorly) to sharp distal extremity of short spinal
blade, on M₃ (posteriorly). Left thecal side restricted to M'₂ (more posterior left marginals not
preserved). On lower thecal surface, zygalar bar complete, gently curved, consisting of two
skeletal elements in marginal position (M'₁, anteriorly and Z, posteriorly), separating two
large infracentral areas. Right infracentral area posteriorly incomplete, sub-trapezoidal in
shape. Left infracentral area partially preserved (abaxial and posterior margins unknown).
Lower thecal surface almost flat, with the exception of right antero-adaxial portions of M₁ and
M'₁ (at aulacophore insertion, below apophyses) and two strong rounded knobs borne by M₂
and M'₂.

M₁ transversely elongate (maximum length, 8.8 mm; width: 2.5 mm), strongly curved into
two subequal portions. Left part of M₁ involved in aulacophore insertion, with strongly
concave anterior margin forming high, vertical, cup-shaped apophysis (Figs 99c, 100a). Right
portion of M₁ almost flat on lower thecal surface, abaxially in contact with M₂ along short and
straight suture. Posterior margin of M₁ strongly concave, along right infracentral area. Upper
surface of M₁ bearing poorly preserved right scutula abaxially to right upper edge of
aulacophore apophysis (Figs 99d, 100b). Well-defined infundibulum forming a small notch
on postero-abaxial extremity of right scutula, in contact with clear, deep anterior oblique
groove on upper side of right aulacophore apophysis, and also anterior transverse groove
running leftwards posteriorly to right and left apophyses, on upper (internal) surface of both
M₁ and M'₁, respectively. M₂ elongate (about 12.5 mm long, 2.5 mm wide), straight to gently
curved, forming most of right thecal margin (Figs 99c–d, 100). Abaxial edge of M₂ slightly
convex. Relatively large, slightly elongate longitudinally (2.3 x 1.5 mm) blunt abaxial knob
on lower surface of M₂. M₃ Y-shaped, forming right posterior thecal corner (Figs 99c–d, 100).
Anterior and left branches of M₃ subequal in length, almost perpendicular to each other and
participating to marginal frame. Posterior portion of M₃ forming wide, flattened, spike-like
process, distally tapering into sharp posterior extremity. Right side of spinal blade almost
straight to weakly convex, in direct continuity with abaxial margin of anterior branch.
Posterior edge of M₃ markedly concave along transition between left marginal portion and left
side of spinal blade. Next to adaxial extremity of left branch of M₃, very small preserved
portion of right extremity of Ms (Figs 99c–d, 100). Zygal plate, Y-shaped, with straight
anterior (zygal) branch much longer than left posterior one (Figs 99c, 100a). Right posterior
branch of Z incompletely preserved (abaxial portion missing). Strong zygal crest on internal
(upper) side of Z (Figs 99d, 100b). Posterior extremity of marginal frame poorly preserved,
with precise abaxial extension of left branch of Z not clear (M₅ or part of it possibly present).
M’₂ elongate (about 8 mm long, 2.3 mm wide), with short, curved anterior portion forming
rounded left anterior thecal corner, and straight, longer posterior part (Figs 99c–d, 100).
Large, blunt, rounded anterior knob on lower surface of M’₂. M’₁ T-shaped, with wide,
elongate, arched posterior (zygal) branch, much longer than left and right anterior (marginal)
parts (Fig. 99c, 100a). Right margin of M’₁ (along right and zygal branches) regularly curved
and concave, along contact with right infracentral area. Left and posterior parts of M’₁ almost
perpendicular to each other. Antero-adaxial part of M’₁ particularly short, restricted to
aulacophore insertion, and bearing high, concave, vertical left apophysis. Antero-abaxial
branch of M’₁ slightly longer than right one, forming depressed area on lower thecal surface,
between raised antero-adaxial part of M’₁ (below left apophysis) and strong anterior knob on
M’₂. High longitudinal zygal crest on upper (internal) surface of posterior part of M’₁.
Adorals, two in number (A’₁ and A₁), unequal in size and morphologically distinct (Figs
99d, 100b). A’₁ elongate (about 4.4 mm long), dumbbell-shaped, with wider abaxial and
adaxial extremities (about 1.6 mm wide) than median part (about 0.8 mm). Left and median
parts of A’₁ tightly sutured to underlying portions of M’₁ (abaxially to left aulacophore
apophysis). Upper (external) surface of A’₁ smooth and almost flat. Right adoral A₁ much
shorter (about 2.5 mm long), collapsed posteriorly to aulacophore insertion and showing strongly arched anterior view, with concave lower (originally above right aulacophore apophysis) and upper (external) surfaces, as well as probable right adoral orifice (antero-abaxially). Large portion of slightly disarticulated lamellate organ (comprising about 25 lamellae) displaced postero-abaxially, partly crushed against posterior adaxial extremity of M₂ and overlying small set of about five in situ lamellae (Figs 99d, 100b). Lamellae vertical, almost rhombic thin calcite walls (about 0.2 mm thick), with their upper and lower corners extending, respectively, high above and deep below supracentral membrane. Antero-abaxial upper edges of lamellae longer and more gently sloping than their postero-adaxial upper margins. Antero-abaxial and postero-adaxial portions of lamellate organ meeting externally along slightly sinuous, oblique, high line of crest corresponding to sutures between anterior and posterior fused U-shaped elements. Supracentrals relatively numerous, polygonal (mostly hexagonal), unusually large (typically 1.6 to 2 mm wide), forming thin, tessellate membrane (Figs 99d, 100b). On opposite thecal surface, right infracentrals similarly polygonal (hexagonal), tessellate, but consistently smaller than supracentrals (1 to 1.5 mm wide), with the exception of few, particularly elongate elements (up to 3.2 mm long) along zygal bar (Figs 99c, 100a). Left infracentrals very numerous, small (0.5 to 1 mm wide) polygonal (hexagonal) tessellate platelets, with the exception of few, longer ones (1.4 to 1.7 mm long) along zygal bar (Figs 99c, 100a). Periproct not observed.

Strongly disarticulated proximal aulacophore consisting of six telescopic rings (Figs 99c–d, 100). Each ring distally overlapping proximal portion of next (more anterior) one. All rings made of two strongly curved, symmetrical inferolaterals (about 1.3 mm wide) forming lower and lateral sides of ring (about 2 and 3 mm long, respectively), and above them, two small, symmetrical and subrectangular tectals (0.7 x 0.9 mm). Distal appendage not preserved.
Remarks. Although incompletely preserved (several marginals missing, precise thecal outlines unknown), specimen NRS.Ec.19934 can be confidently identified as a scotiaecystid cornute, based on the presence of a lamellate organ on its upper surface. Within the family Scotiaecystidae, the morphology of its lamellae (i.e. particularly high, extending well above the supracentral area and also deep inside the thecal cavity) excludes any assignment of this specimen to the genera Proscotiaecystis and Scotiaecystis, but supports its affiliation with either Bohemiaecystis or Thoralicarpus. In specimen NRS.Ec.19934, the absence of the left posterior portion of the theca does not make it possible to document if it originally possessed a digital articulated to it (Bohemiaecystis) or not (Thoralicarpus).

Comparison with other known members of these two genera indicates that the Šárka specimen is morphologically closer to thick-framed Mid–Late Ordovician taxa (B. bouceki, B. chouberti, T. bounemrouensis, T. guilloui, T. jefferiesi, T. prokopi) than to delicately framed Early Ordovician ones (B. griffei, B. ubaghsi, B. zagoraensis). Comparison with thick-framed scotiaecystids further suggests that the Šárka specimen cannot be assigned to B. chouberti, T. bounemrouensis and T. guilloui, all characterised by an elongate, narrow, blunt spinal blade (see Figs 63, 72, 83), whereas M₃ is bearing a wide, strong, subtriangular sharp spike process in NRS.Ec.19934 (Figs 99c–d, 100). The Czech specimen further departs from B. chouberti in the possession of a posterior zygal plate Z with an anterior branch longer than the left posterior one (Figs 99c, 100a). The anterior branch of Z is comparatively much shorter in B. chouberti (see Fig. 63a). The Šárka scotiaecystid also further differs from T. guilloui in the possession of an almost straight to gently curved M₂ (Figs 99c–d, 100), whereas this marginal is strongly curved in T. guilloui (Fig. 83). Specimen NRS.Ec.19934 is also different from T. jefferiesi (Fig. 86), which is characterised by a shorter M₁, a more strongly curved M₂, a wider, differently shaped spinal process and zygal branches of M'₁ and Z subequal in length (whereas the Z one is shorter than the M'₁ one in the Šárka material). The Šárka scotiaecystid
is morphologically closer to the two Bohemian taxa *B. bouceki* (Fig. 60) and *T. prokopi* (Fig. 92). However, the identification of several differences with *B. bouceki* suggests that NRS.Ec.19934 probably belongs to another taxon. For example, thecal ornamentation is distinct and weaker (low elongate spike-shaped ridges on M'₂ and M₂) in *T. bouceki* than in the Šárka specimen (well-defined rounded knobs on both M'₂ and M₂). Moreover, supracentals are extremely numerous and small on the upper surface of *T. bouceki*, whereas in the similarly sized specimen from Šárka, they are fewer and much larger. The left posterior branch of Z is also proportionately shorter in *T. bouceki*. The precise morphology of the spinal blade in *T. bouceki* is not sufficiently well-known (shape, extension; see above) to support any detailed comparison with the situation in NRS.Ec.19934. In contrast, preserved portions of the Šárka scotiaecystid do not show any significant differences with the plate pattern of *T. prokopi*: similarly shaped adorals, marginals, platings of integumentary areas, and thecal ornamentation (on M₂, M'₂ and M₃). However, the morphology of NRS.Ec.19934 is too incompletely known (6 marginals missing: D, G, M'₂-₄ and Ms) to support its definitive assignment to *T. prokopi*. The Šárka specimen is thus tentatively identified herein as *T. cf. prokopi*.

**Palaeobiogeographic affinities**

The exhaustive review of non-hanusiid cornute remains from Darriwilian to Katian rocks of Czech Republic (Bohemia), France (Armorican Massif), Morocco (Anti-Atlas) and Spain (Central Iberian and Ossa Morena zones) confirms the existence of strong faunal affinities between these four regions of the high-latitude Mediterranean Province in Middle and Late Ordovician times (e.g. Chauvel 1941, 1966; Havlíček 1971, 1989; Hammann 1976; Paris & Robardet 1977; Henry 1980; Destombes et al. 1985; Vannier 1986a, b; Babin & Destombes...
In recent years, a major sampling effort in these four peri-Gondwanan regions, in particular in the eastern Anti-Atlas and the Barrandian area, resulted in a wealth of new data and a major reassessment of cornute diversity, stratigraphic range and palaeobiogeographic distribution. All six cornute genera occurring in the Middle and Upper Ordovician of Morocco are also present in at least one other Mediterranean area, and two of them (Domfrontia and Thoralicarpus) are now documented in all four regions. Milonicystis is known in France and Morocco, whereas Arauricystis, Bohemiaecystis and Destombesicarpus are occurring in Czech Republic and Morocco. These strong faunal affinities are further supported by examples of occurrences of the same species in two distinct regions, e.g. Arauricystis clariondi in the Anti-Atlas and Bohemia, Thoralicarpus jefferiesi in the Barrandian area and the Central Iberian Zone. Moreover, morphological differences between closely related species are sometimes subtle and may possibly simply result from slightly different palaeoenvironmental conditions (ecophenotypy).

The Middle–Late Ordovician Mediterranean cornute assemblage has relatively obvious peri-Gondwanan roots. The reevaluation of the morphology and skeletal homologies of Milonicystis suggests that this Darriwilian–Sandbian genus probably derives from Early Ordovician forms closely related to the 'Jbel Tizagzaouine cornute' (see above), from the late Tremadocian of Morocco (Ware & Lefebvre 2007; Lefebvre et al. 2016). Domfrontia (Darriwilian–Katian) represents the youngest known member of the family Amygdalotheidae, which is restricted to the Anti-Atlas and the Montagne Noire in the late Tremadocian–late Floian time interval (Amygdalotheca, Nanocarpus; Ubaghs 1970, 1991; Vizcaïno & Lefebvre 1999; Lefebvre et al. 2016). Similarly, the family Chauvelicystidae is particularly diverse and palaeogeographically widespread in peri-Gondwanan areas in Early Ordovician times, with occurrences in the Montagne Noire, France (Ampelocarpus,
Chauvelicystis, Lyricocarpus; Ubaghs 1970, 1983, 1991; Lefebvre & Vizcaïno 1999), Korea (Sokkaejaecystis; Lee et al. 2005), the Anti-Atlas, Morocco (Ampelocarpus, Chauvelicystis, Sokkaejaecystis; Chauvel 1966, Lefebvre et al. 2016a) and Wales, UK (Prochauvelicystis; Daley 1992). Consequently, Destombesicarpus (Sandbian–Katian) represents the only known younger member of the family Chauvelicycstidae. However, undescribed material from the Pontyfenni Formation (Dapingian) of Wales, possibly represents an earlier record of this genus (see discussion above; Jefferies 1987). The description of Arauricystis in the late Darriwilian of Bohemia and the early Sandbian of Morocco significantly increases the stratigraphic range of this cothurnocystid genus, which was previously known only from the late Tremadocian of the Montagne Noire (Thoral 1935; Ubaghs 1970, 1994; Lefebvre & Vizcaïno 1999). Within cothurnocystids, Arauricystis is probably derived from Persiacarpos and Procothurnocystis-like ancestors (see discussion above). Persiacarpos is known from the late Guzhangian of Iran and probably the late Tremadocian of France (see above; Ubaghs 1970; Rozhnov & Parsley 2017). Procothurnocystis is documented in the late Tremadocian of the Anti-Atlas and the Montagne Noire (Ubaghs 1970; Lefebvre et al. 2016a), the Dapingian of Wales (Woods & Jefferies 1992), and possibly also in the late Furongian–middle Tremadocian of Nevada (Sumrall et al. 2009; Lefebvre et al. 2017a, 2019b). Finally, all earliest occurrences of the family Scotiaecystidae have been reported so far from the Lower Ordovician of the Anti-Atlas, Morocco (Chauvel 1971; Lefebvre et al. 2016a, 2019a), the Montagne Noire, France (Ubaghs 1970, 1983; Lefebvre & Vizcaïno 1999), and Jujuy Province, Argentina (Nohejlová et al. 2018). The presence of Bohemiaecystis in the Darriwilian of Bohemia (B. bouceki, see above; Ubaghs 1968) and Morocco (B. chouberti, B.? sp., see above; Chauvel 1971) represents the youngest record of this genus, previously known in the early Tremadocian–late Floian of Argentina, France and Morocco (Ubaghs 1970; Chauvel 1971; Lefebvre & Vizcaïno 1999; Lefebvre et al. 2016a; Nohejlová et al.
The other scotiaecystid genus, *Thoralicarpus* (Darriwilian–Katian), is endemic to the Mediterranean Province and is probably derived from a *Bohemiaecystis*-like ancestor (see discussion above). Consequently, the six cornute genera occurring in the Middle and Upper Ordovician of the Mediterranean Province illustrate the persistence in high latitude peri-Gondwanan areas of various stylophoran clades already established in these areas in the Early Ordovician.

Comparison of Darriwilian–Katian cornutes from the Mediterranean Province with the few other coeval occurrences reported from other palaeocontinents does not make it possible to establish close affinities between them. This situation probably results from the strong endemicity of high-latitude peri-Gondwanan cornutes, although a possible sampling and/or taphonomic bias cannot be also totally excluded in other regions. No remains of *Darriwilian–Katian amygdalothecids, chauvelicystids, Milonicystis* and related forms have been reported so far from any other palaeocontinent. The late Katian cothurnocystid genus *Cothurnocystis*, which is endemic to Laurentia (Scotland), is probably derived from a *Procothurnocystis*-like ancestor. In the Mediterranean Province, the youngest record of *Procothurnocystis* is in the late Tremadocian of France and Morocco (Ubaghs 1970; Vizcaïno & Lefebvre 1999; Lefebvre et al. 2016a). However, the presence of *P. owensi* in the Dapingian of Wales (Jefferies 1987; Woods & Jefferies 1992) suggests a possible Avalonian origin for Late Ordovician Laurentian cothurnocystids. Similarly, the two late Katian taxa *Scotiaecystis collapsa* (northwestern Ireland) and *S. curvata* (Scotland) correspond to a small clade of Laurentian scotiaecystids. The genus *Scotiaecystis* can be derived either from a *Thoralicarpus*-like ancestor or from an earlier stock of *Bohemiaecystis*-like scotiaecystids. No scotiaecystid remains have been documented so far in the Middle and Upper Ordovician of Avalonia or Baltica. At this stage, it is thus difficult to document if the presence of late Katian cothurnocystids and scotiaecystids in Laurentia results from the immigration of
psychrospheric (cool-adapted) deep faunas and/or from the northern drift of Avalonia away from Gondwana in Middle and Late Ordovician times. During the Sandbian, the taconic orogeny resulted in the drowning of the southeastern margin of Laurentia, which coincided with the immigration of cool-adapted taxa previously unrecorded in this relatively low latitude region (e.g. bivalves, mitrate stylophorans, solutans; Babin 1993; Patzkowsky & Holland 1993; Cope & Babin 1999; Lefebvre 2007a, b; Lefebvre et al. 2013). On the other hand, faunal exchanges between Avalonia, Baltica and Laurentia were enhanced in Late Ordovician times by the progressive closure of the Iapetus Ocean. It thus cannot be excluded that an Avalonian stock of originally peri-Gondwanan stylophorans could have drifted northwards with Avalonia and finally reached Laurentia in late Katian times. Relatively diverse cornute remains are present in the Dapingian and the Darriwilian of Wales (Jefferies 1987; Woods & Jefferies 1992; Botting et al. 2013).

In late Katian times, typical high-latitude echinoderm faunas adapted to cold temperatures and siliciclastic soft sea floors, dominated by aristocystitid diploporites, eocrinoids, glyptocystitid rhombiferans, ophiuroids, solutans and stylophorans were replaced, in most regions of the Mediterranean Province, by more temperate assemblages associated to bryozoan bioherms and carbonate platforms (Lefebvre 2007b; Lefebvre et al. 2013). In Algeria, Czech Republic (Prague Basin), France (Armorican Massif, Corbières, Montagne Noire, Pyrénées), Germany (Thuringia), Italy (Carnic Alps, Sardinia), Portugal, Spain (Central Iberian Zone, Iberian Cordillera) and Morocco (eastern Tafilalt), abundant and diverse late Katian echinoderm faunas are dominated by coronates, crinoids, caryocystitid and hemicosmitid rhombiferans (e.g. Bather 1910; Dreyfuss 1939; Renard 1968; Chauvel & Le Menn 1972, 1979; Chauvel et al. 1975; Gutiérrez-Marco et al. 1996; Le Menn & Spjeldnaes 1996; Vennin et al. 1998; Gutiérrez-Marco 2001; Schallreuter 2005; Botquelen & Le Menn 2006; Touzeau et al. 2012; Jacinto et al. 2015; Sumrall et al. 2015). This major turnover in
echinoderm communities is matched by a similar major faunal shift in brachiopod and
trilobite assemblages in high-latitude peri-Gondwanan areas, correlated with the onset of
warmer (more temperate) environmental conditions: the Boda Event (e.g. Fortey & Cocks
2016; Ernst this volume; Villas & Colmenar this volume). Consequently, the absence of late
Katian cornute remains in the Armorican Massif and the Iberian Peninsula is probably not due
to sampling or taphonomic biases, but likely original. These two regions have yielded
particularly abundant, diverse, and well-studied late Katian temperate echinoderm faunas
(Chauvel & Le Menn 1972, 1979; Chauvel et al. 1975; Gutiérrez-Marco et al. 1996;
Gutiérrez-Marco 2001; Jacinto et al. 2015). In contrast, the occurrence of cornutes in the
Lower Second Bani Formation, Central Anti-Atlas (Domfrontia milnerorum, see above;
Chauvel 1971; Ruta 1999a) and in the Králův Dvůr Formation, Bohemia (Destombesicarpus
budili, Domfrontia aff. milnerorum; see above) suggests that cool-adapted Mediterranean
communities were still present, in some 'refuge areas', in late Katian times. In Morocco,
temperate faunas are apparently restricted to the eastern-most part of the Tafilalt (E of
Erfoud), and cool-adapted assemblages living on soft, siliciclastic substrates occur
everywhere else, in the central and eastern Anti-Atlas (e.g. Álvaro et al. this volume;
Colmenar et al. this volume). In Bohemia, the situation is more complex, with the occurrence
of assemblages typical of the Boda Event in iron ore deposits and pelocarbonate facies (e.g.
Echinosphaerites, Haplosphaeronis, Heliocrinites, Mespilocystites; Mikuláš & Prokop 2003),
whereas cool-adapted faunas are restricted to black shales (e.g. Anatifopsis, Barrandeocarpus,
Destombesicarpus, Diamphidiocystis, Domfrontia; Barrande 1887; Prokop and Petr 1999;
Lefebvre et al. this volume). This pattern is probably related to original subtle variations in
substrates, bathymetry (and thus, water temperature) and/or currents.
Acknowledgments

This paper is a contribution to the International Geoscience Programme (IGCP) projects 653 "The onset of the Great Ordovician Biodiversification Event" and 735 “Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification”.

The authors are particularly grateful to James Sprinkle, Thomas E. Guensburg and Samuel Zamora for their careful and constructive reviews, which greatly improved the quality and relevance of the paper. The authors are particularly indebted to the late Jacques Destombes, who provided precious assistance during field work in the Tafilalt in 2010, as well as much useful information on localities, bibliographic references and geological maps. All colleagues who helped during field work in the Anti-Atlas, Morocco are also warmly thanked: Ali Bachnou, Khadija El Hariri, Christian Gaillard, Ahmad Hafid, Aaron W. Hunter, Nicolas Olivier, Véronique and Roland Reboul. The authors are also very grateful to Ton Agterbos, Francis Auvray, Patrick Catto, Philippe Courville, Christian Gaudu, Christophe Guillou, and Philippe Roussel for donating scientifically important specimens to public collections and/or for providing important data on localities. The access to the material dispersed in various international public collections was greatly facilitated by Didier Berthet (Lyon), Petr Budil (Prague), Sylvain Charbonnier (Paris), Pierre Dalous (Toulouse), Isabel Díaz Megías (Madrid), Tim Ewin (London), Christina Franzen-Bengtson (Stockholm), Damien Gendry (Rennes), Concha Herrero (Madrid), Cindy Howells (Cardiff), Brenda Hunda (Cincinnati), Stéphane Jouve (Marseille), Khaoula Kouraïss (Marrakesh), Yves Laurent (Toulouse), Anne Médard (Marseille), Silvia Menéndez Carrasco (Madrid), Didier Merle (Paris), Sylvie Pichard (Marseille), Abel Prieur (Lyon), Emmanuel Robert (Lyon), and Vojtěch Turek (Prague). This paper also benefited from insightful discussions and/or informations on stratigraphy and/or systematics with Joseph Botting, Yves Candela, Eric Monceret, Lucy Muir, Olga Obut,
Marika Polechová, Sergei Rozhnov, Nikolay Sennikov, Peter Van Roy, Muriel Vidal, Daniel Vizcaïno and Samuel Zamora. Finally, the authors also want to express their gratitude to Gilles Escarguel for his precious help with statistics, Sophie Passot, who made all necessary maps and publications available, and Vincent Perrier, for his invaluable assistance with photographs.

**Funding**

This research was supported by the Czech Science Foundation (GAČR) project no.18-14575S and is also an outcome of the European Synthesys projects GB-TAF-4565 (2008), SE-TAF-4765 (2009) and CZ-TAF-6049 (2016). The authors are grateful to the LABEX Lyon Institute of Origins (ANR-10-LABX-0066) of the Université de Lyon for its financial support within the program "Investissements d'Avenir" (ANR-11-IDEX-0007) of the French government operated by the National Research Agency (ANR). Field work in the Tafilalt area was funded by the CNRS-CNRST French-Moroccan cooperation project "Les faunes à conservation exceptionnelle de l'Ordovicien de l'Anti-Atlas (Maroc): implications évolutives et écologiques" (2009–2012). Field work in Maroc was also partly supported by project CGL2017-87631-P of the Spanish Ministry of Science and Innovation (to JCG-M).

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Figure captions

**Fig. 1.** Cornute morphology: (a,b) *Persiacarpos? fellinensis*, late Tremadocian, Montagne Noire, France; camera lucida drawings of holotype, UCBL-FSL.168715; (a) lower aspect of aulacophore and posteriorly incomplete theca; (b) upper view of aulacophore with cover plates in open position, and slightly disarticulated theca; (c,d) *Procothurnocystis owensi*, Dapingian, Wales, UK; camera lucida drawings of holotype, NMW.84.17G.119; (c) lower aspect of aulacophore and incomplete theca (left part missing); (d) upper view of aulacophore with cover plates in open position, and incomplete theca (right and posterior parts missing).

**Fig. 2.** Orientation in cornutes; *Phyllocystis blayaci*, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970): (a) aulacophore (single appendage along main axis) and theca (flattened body) in lower aspect; the lower thecal surface is generally divided into two unequal, polyplated infracentral areas by an oblique structure: the zygal bar; (b) aulacophore and theca in upper aspect; when present, respiratory structures generally occur in the right anterior corner of the upper thecal surface; (c) aulacophore and theca in left lateral view, showing proximal and distal regions, anterior and posterior directions, and upper and lower sides.

**Fig. 3.** Morphology of lower thecal surface in cornutes: (a) *Ceratocystis perneri*, Wuliuan–Drumian, Bohemia, Czech Republic; redrawn and modified from Ubaghs (1967); (b)
Amygdalotheca griffei, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970); (c) Cothurnocystis elizae, late Katian, Scotland, UK; redrawn and modified from Ubaghs (1968); (d) Galliaecystis lignieresi, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970); (e) Ampelocarpus landeyranensis, late Floian, Montagne Noire, France; modified from Lefebvre & Vizcaïno (1999); (f) Sokkaejaecystis serrata, late Tremadocian, Korea; modified from Lee et al. (2005).

Fig. 4. Morphology of upper thecal surface in cornutes: (a) Ceratocystis perneri, Wuliuan–Drumian, Bohemia, Czech Republic; redrawn and modified from Ubaghs (1967); (b) Scotiaecystis curvata, late Katian, Scotland, UK; redrawn and modified from Jefferies (1968); (c) Cothurnocystis elizae, late Katian, Scotland, UK; redrawn and modified from Ubaghs (1968); (d) Galliaecystis lignieresi, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970); (e) Ampelocarpus landeyranensis, late Floian, Montagne Noire, France; modified from Lefebvre & Vizcaïno (1999); (f) Sokkaejaecystis serrata, late Tremadocian, Korea; modified from Lee et al. (2005).

Fig. 5. Respiratory structures in cornutes: (a) cothurnopores, Procothurnocystis owensi, Dapingian, Wales, UK; holotype, NMW.84.176.119; (b) proto-lamellate organ, Proscotiaecystis melchiori, late Floian, Montagne Noire, France; holotype, UCBL-FSL.712807; (c) lamellate organ with high lamellae protruding within thecal cavity and above supracentral area, Bohemiaecystis bouceki, late Darriwilian, Bohemia, Czech Republic; holotype, NMP.L17728; (d) lamellate organ with low lamellae, not extending below supracentral membrane, Scotiaecystis curvata, late Katian, Scotland, UK; holotype, BMNHUK.E.23129. All scale bars: 1 mm.
Fig. 6. Morphology of thecal internal structures associated to aulacophore insertion in cornutes: (a) anterior view of the five thecal plates framing the aulacophore insertion in *Phyllocystis blayaci*: adorals A₁, A₀ and A'₁ (above, from left to right), and marginals M₁ (below, on the left) and M'₁ (below, on the right); late Tremadocian, Montagne Noire, France; composite reconstruction redrawn and modified from Ubaghs (1970); (b,c) posterior view of adaxial part of M₁ in *Thoralicarpus jefferiesi*, late Sandbian–early Katian, central Iberian Zone, Spain; paratype UCM.EO.036; (b) interpretative camera lucida drawing; (c) latex cast of actual specimen, same view as in (b).

Fig. 7. Morphology of aulacophore and aulacophore insertion in the cornute *Phyllocystis blayaci*, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970) and Lefebvre (2003): (a) lower aspect with the two most anterior marginals (M₁ on the left, and M'₁ on the right), proximal aulacophore and posterior portion of the distal appendage (more distal ossicles and associated cover plates not shown); (b) upper view, with adorals, proximal rings, and posterior part of distal aulacophore (cover plates represented in wide open, probably post-mortem, position).

Fig. 8. Mode of life and internal (soft) anatomy of the cornute *Domfrontia milnerorum*, Katian, Anti-Atlas, Morocco: (a) presumed epibenthic mode of life on soft substrates, with aulacophore spikes providing temporary anchorage to the sea floor, and theca downstream; modified and redrawn from Ruta (1999a) and Lefebvre (2003); (b) reconstruction of presumed ambulacral and digestive systems, based on observations made on exceptionally preserved soft parts in cornutes from the Fezouata Shale, late Tremadocian, Anti-Atlas, Morocco (Lefebvre et al. 2019a).
Fig. 9. Three-dimensional reconstruction of the skeletal morphology and associated soft tissue anatomy in the distal aulacophore of the early cornute Ceratocystis perneri, Wuliuan–Drumian, Bohemia, Czech Republic; modified from Lefebvre et al. (2019a). The ambulacral system is reconstructed based on exceptionally preserved soft parts described in cornutes from the Fezouata Shale, late Tremadocian, Anti-Atlas, Morocco. Transverse channels are absent in Ceratocystis perneri (Ubaghs 1967; Jefferies 1969).

Fig. 10. Thecal plate homologies in cornutes. Persiacarpos? fellinensis, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970) and Lefebvre & Vizcaïno (1999): (a) skeletal plate homologies, lower thecal surface; (b) skeletal plate homologies, upper thecal surface. Abbreviations: A, adoral; D, digital; G, glossal; M, marginal; Z, zygal plate. Plates bearing the same name are considered as homologous in all other figures.

Fig. 11. Thecal plate homologies in scotiaecystid cornutes (lower thecal surface): (a) Proscotiaecystis melchiori, late Floian, Montagne Noire, France; redrawn and modified from Ubaghs (1983) and Lefebvre & Vizcaïno (1999); (b) Bohemiaecystis bouceki, late Darriwilian, Bohemia, Czech Republic; (c) Thoralicarpus bounemrouensis gen. et sp. nov., early Sandbian, Anti-Atlas, Morocco; (d) Scotiaecystis curvata, late Katian, Scotland, UK; redrawn and modified from Jefferies (1968) and Lefebvre & Vizcaïno (1999).

Fig. 12. Thecal plate homologies in Cambrian cornutes: (a–c) Ceratocystis perneri, Wuliuan–Drumian, Bohemia, Czech Republic; redrawn and modified from Ubaghs (1967) and Lefebvre & Vizcaïno (1999); (a,c) two alternative interpretations of skeletal homologies on lower thecal surface; (a) first interpretation with two isolated infracentral elements and M'5 in
posterior position (Lefebvre & Vizcaïno 1999; Lefebvre 2001); (c) second interpretation with one left infracentral element, and both $M'_4$ and $M'_5$ posteriorly sutured to $M'_3$; (b) skeletal plate homologies, upper thecal surface; (d,e) Protocystites menevensis, Drumian, Wales, UK; redrawn and modified from Jefferies et al. (1987) and Lefebvre & Vizcaïno (1999); (d) skeletal homologies, lower thecal surface; (e) skeletal homologies, upper thecal surface.

*Fig. 13.* Thecal plate homologies in Cambrian cornutes: (a,b) Ponticulocarpus robisoni, Wuliuan, Utah, USA; redrawn and modified from Sumrall & Sprinkle (1999) and Lefebvre & Ausich (2021); (a) skeletal homologies, lower thecal surface; (b) skeletal homologies, upper thecal surface; (c,d) Persiacarpos jefferesi, late Guzhangian, Iran; new reconstruction of theca, based on specimens figured in Rozhnov & Parsley (2017); (c) tentative reinterpretation of skeletal homologies on lower thecal surface; (d) tentative reinterpretation of skeletal homologies on upper thecal surface; the occurrence of $A_0$ and $A_1$ is not documented in specimens figured in Rozhnov & Parsley (2017).

*Fig. 14.* Thecal plate homologies in hanusiid cornutes: (a,b) Drepanocarpos australis, Furongian, Queensland, Australia; new reconstruction of theca, based on specimens figured in Smith & Jell (1999); (a) tentative reinterpretation of skeletal homologies on lower thecal surface; (b) tentative reinterpretation of skeletal homologies on upper thecal surface; (c,d) Galliaecystis lignieresi, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970) and Lefebvre & Vizcaïno (1999); (c) skeletal homologies, lower thecal surface; (d) skeletal homologies, upper thecal surface.

*Fig. 15.* Thecal plate homologies in cornutes: (a,b) Archaeocothurnus goshutensis, Paibian, Nevada, USA; redrawn and modified from Sumrall et al. (1997) and Lefebvre & Vizcaïno
(1999); (a) skeletal homologies on lower thecal surface, based on camera lucida drawing of paratype 1794TX2 (Sumrall et al. 1997, fig. 6.3); (b) skeletal homologies on upper thecal surface, based on camera lucida drawing of holotype 1794TX1 (Sumrall et al. 1997 fig. 6.2); (c) skeletal homologies on lower thecal surface of Cornuta gen. et sp. nov. (informally designated here as 'Tigzagiaouine cornute'), late Tremadocian, Anti-Atlas, Morocco; redrawn and modified from Ware & Lefebvre (2007); (d) skeletal homologies on lower thecal surface of *Flabellicarpus rushtoni*, late Tremadocian, Shropshire, UK; redrawn and modified from Martí Mus (2002).

**Fig. 16.** Thecal plate homologies in cornutes (lower thecal surface): (a) *Phyllocystis jingxiensis*, Furongian, Guangxi Province, China; new reconstruction, based on specimens figured in Han & Chen (2008); (b) *Phyllocystis blayaci*, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970) and Ware & Lefebvre (2007); (c) *Amygdalotheca griffei*, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1970); (d) *Chauvelicystis vizcainoi*, late Tremadocian, Montagne Noire, France; redrawn and modified from Ubaghs (1983) and Lefebvre & Vizcaíno (1999).

**Fig. 17.** Location of main Middle–Upper Ordovician localities yielding cornute stylophorans in the Anti-Atlas, Morocco. Numbers refer to localities: 1, Jbel Ouazemine (Destombes' locality 2410), Tiznit area, western Anti-Atlas: *Bohemiaecystis* sp. (Tachilla Formation); 2, Jbel Bou Isidane (Destombes' locality 1826), Alnif area, western Maïder: *Bohemiaecystis chouberti* (upper part of the Guezzart Formation); 3, Jbel Bou Isidane (locality TA-F5), Alnif area, western Maïder: *Bohemiaecystis chouberti* (upper part of the Guezzart Formation); 4, Jbel Izegguirene (Destombes' localities 755 and 2479), Tazarine area, central Anti-Atlas: *Destombesicarpus izegguirenensis*, *Thoralicarpus bounemrouensis* (Izegguirene Formation);
5, Bou Nemrou (locality ECR-F4), Jbel Tijarfaïouine Massif, western Tafilalt: Arauricystis clariondi, Milonicystis reboulorum, Thoralicarpus bounemrouensis (Izegguirene Formation); 6, Khabt-el-Hejar (Van Roy's locality E2), Erfoud area, eastern Tafilalt: Domfrontia milnerorum (Upper Tiouririne Formation); 7, Tizi n’Takrit (Destombes' locality 756), Tazarine area, central Anti-Atlas: Domfrontia milnerorum (base of the Lower Second Bani Formation).

Fig. 18. Preservation of Middle–Late Ordovician cornutes from the Anti-Atlas, Morocco: (a) fully articulated individual of the cornute stylophoran Thoralicarpus bounemrouensis (theca, aulacophore) preserved along well-preserved, unprepared specimen of the eocrinoid Ascocystites sp. (theca, brachioles and part of stem); MHNM.15690.009, Bou Nemrou (Izegguirene Formation, early Sandbian), western Tafilalt; (b) cluster of 11 specimens of the cornute Bohemiaecystis chouberti; most individuals are fully articulated (aulacophore intact, connected to the theca, with ambulacral cover plates still attached to underlying ossicles); UCBL-FSL.173120 (holotype and paratypes), Jbel Bou Isidane (Guezzart Formation, late Darriwilian), Alnif area; (c) accumulation of over 22 fully articulated to slightly disarticulated individuals of the cornute Bohemiaecystis chouberti (almost complete thecae, proximal aulacophores and more or less extensive portions of distal appendages); original slab described by Chauvel (1971), IGR.PAL.16685, Jbel Bou Isidane (Guezzart Formation, late Darriwilian), Alnif area; (d) complete, slightly disarticulated theca of the cornute Destombesicarpus izegguirenensis, with fragments of distal aulacophore (stylocone, four ossicles); IGR.PAL.16691 (holotype), Jbel Izegguirene (Izegguirene Formation, early Sandbian), Tazarine area, central Anti-Atlas; (e) cluster of six different-sized specimens of the cornute Domfrontia milnerorum, probably preserved in life position, all with the same orientation and the aulacophore probably facing the current; AA-KEH.OS.36, Khabt-el-Hejar
(Upper Tiouririne Formation, early Katian), Erfoud area, eastern Tafilalt. All scale bars: 10 mm.

**Fig. 19.** Frequency distribution of thecal length (TL) in *Domfrontia milnerorum*, based on 114 measured individuals collected within the same horizon and in the same locality (Khabt-el-Hejar, eastern Tafilalt, Morocco), Upper Tiouririne Formation (early Katian). Although size distribution is normal, a clear sampling bias can be evidenced towards larger and best preserved individuals selectively chosen for museum purposes (MHNMM samples, red). The range of thecal sizes in the more extensive collections made for research purposes is much wider and includes smaller individuals (AA.KEH samples, blue). The table summarises statistics and normality tests for all 114 measured individuals and two sub-samples corresponding to specimens registered in the collections of Marrakesh University (AA.KEH) and the Natural History Museum of Marseille (MHNM).

**Fig. 20.** Location of main Ordovician localities yielding cornute stylophorans in the Armorican Massif, France. Numbers refer to localities: 1, côte 85, Laillé, Ille-et-Vilaine: *Domfrontia?* sp. (lower part of the Traveusot Formation); 2, le Domaine, Guichen, Ille-et-Vilaine: *Milonicystis kerfornei* (upper part of the Traveusot Formation); 3, la Saudrais, Guichen, Ille-et-Vilaine: *Thoralicarpus guillouii* (upper part of the Traveusot Formation); 4, Traveusot, Guichen, Ille-et-Vilaine: *Milonicystis kerfornei* (upper part of the Traveusot Formation); 5, Beauséjour, Bain-de-Bretagne, Ille-et-Vilaine: *Domfrontia pissotensis* (uppermost part of the Traveusot Formation); 6, le Pissot, Domfront, Orne: *Domfrontia pissotensis* (Le Pissot Formation). Abbreviations: MNAD, Medio-North Armorican Domain; SAD, South Armorican Domain; SASZ: South Armorican Shear Zone.
Fig. 21. Preservation of Middle–Late Ordovician cornutes from the Armorican Massif (France) and the Barrandian area (Czech Republic): (a) slightly disarticulated theca (upper surface) and partial aulacophore of *Milonicystis kerfornei* preserved in a concretion; IGR.PAL.15640, Traveusot, Guichen (Brittany, France), Traveusot Formation (late Darriwilian); (b) large, slightly disarticulated theca (in upper view) of the scotiaecystid *Thoralicarpus guilloui* with associated proximal aulacophore, stylocone and posterior-most ossicles preserved in micaceous siltstones; UCBL-FSL.170875 (holotype), la Saudrais, Guichen (Brittany, France), Traveusot Formation (late Darriwilian); (c) cluster of two partly overlapping individuals of *Domfrontia pissotensis* preserved in shales, next to portions of crinoid stems; GR/PC.1795, Beauséjour, Bain-de-Bretagne (Brittany, France), uppermost part of the Traveusot Formation (early Sandbian); (d) complete, slightly disarticulated theca of *Destombesicarpus budili* (upper surface) with articulated series of marginal spines (aulacophore missing); CGS.OZ.152 (holotype), Levín, Zahořany Formation (early Katian); (e–g) *Domfrontia* aff. *milnerorum*, Prague Basin (Czech Republic); (e) slightly collapsed, complete theca (lower surface) and partial aulacophore; CGS.OZ.123, Nová Vráž - Černošice, Králův Dvůr Formation (late Katian); (f) almost complete, slightly disarticulated theca in lower aspect, and associated proximal rings, stylocone and first ossicles; CGS.OZ.153, Levín, Zahořany Formation (early Katian); (g) weakly disarticulated theca and proximal rings, in upper aspect; CGS.OZ.154, Levín, Zahořany Formation (early Katian). All scale bars: 2 mm.

Fig. 22. Location of main Ordovician localities yielding non-hanusiid cornute stylophorans in the Barrandian area, Czech Republic. Numbers refer to localities: 1, Praha Šárka: *Thoralicarpus* cf. *prokopi* (Šárka Formation), *Bohemiaecystis bouceki* (Dobrotivá Formation); 2, Šárka field near Hammernikova villa: *Bohemiaecystis bouceki* (Dobrotivá Formation); 3, Malé Přílepy: *Bohemiaecystis bouceki* (Dobrotivá Formation); 4, Zbiroh, mine 'Veronika':
Arauricystis clariondi (Dobrotivá Formation); 5, Zahořany, Borová Street: Thoralicarpus jefferiesi, T. prokopi (upper part of the Letná Formation), T. prokopi (base of the Vinice Formation); 6, Chrustenice: Thoralicarpus prokopi (upper part of the Letná Formation); 7, Levín: Destombesicarpus budili, Domfrontia aff. milnerorum (Zahořany Formation); 8, Černošice, Nová Vráž: Domfrontia aff. milnerorum (Králův Dvůr Formation); 9, Zdice: Domfrontia aff. milnerorum (upper part of Bohdalec Formation); 10, Lejškov: Destombesicarpus budili (Králův Dvůr Formation).

Fig. 23. Preservation of the Late Ordovician scotiaecystid cornute Thoralicarpus prokopi, Letná Formation (late Sandbian), Barrandian area (Czech Republic): (a) fully articulated, nearly complete theca (in upper aspect) and long portion of associated aulacophore, with cover plates in closed position; CGS.OZ.150, Chrustenice; (b) fully articulated, almost complete theca in lower aspect, with proximal rings and part of distal aulacophore; CGS.OZ.205, Chrustenice; (c) slightly disarticulated, incomplete theca (white arrow) in upper aspect, with proximal rings, stylocone and two ossicles, occurring with strophomenid brachiopods in a Dendrocystites dense bed; CGS.LK.16, Borová Street, Zahořany. All scale bars: 10 mm.

Fig. 24. Schematic placement of Ordovician localities with cornute echinoderms in Iberia: (a) Ordovician succession in the southern Central Iberian Zone with indication of the Cantera Shale and the position of the Viso del Marqués fossil locality (VM, arrowed), which yielded Thoralicarpus jefferiesi; (b) Ordovician succession in the Valle syncline of the Ossa Morena Zone, showing the position of the Las Cañas locality west of Cazalla de la Sierra (CS, arrowed), where two specimens of Domfrontia? sp. were found; (c) Geological sketch map of the Iberian Peninsula showing the distribution of Ordovician rocks (in black) with reference
to the main Precambrian and Palaeozoic exposures (stippled), and the approximate location of cited localities VM and CS. For stratigraphical columns symbols are: Lithofacies: 1, glaciomarine diamicrites; 2, sandstones and quartzites; 3, alternating sandstones, siltstones and shales; 4, siltstones and shales; 5, marls and calcareous shales; 6, dark shales; 7, black shales; 8, limestones. Fossils: a, trilobites; b, bivalves; c, ostracods; d, brachiopods; e, Ordovician (left) and Silurian (right) graptolites; f, bryozoans; g, echinoderms; h, conodonts; i, chitinozoans; j, acritarchs; k, ichnofossils. Figure partially adapted from Gutiérrez-Marcó et al. (2002, © The Geological Society, London).

**Fig. 25.** Measurement of thecal length (TL) and thecal width (TW) in Middle–Late Ordovician cornutes from the Mediterranean Province (Czech Republic, France, Morocco); all reconstructions in lower aspect; arrows indicate landmark points for measurements: (a) *Milonicystis kerfornei*, Traveusot Formation, Brittany (France); TW measured between M'_3-M'_4 suture (on the left) and M_2-Mc suture (on the right); TL estimated perpendicularly to TW, between anterior extremity of M_2 and D-G suture; (b) *Milonicystis reboulorum*, Izegguirene Formation, Anti-Atlas (Morocco); TW measured between M'_3-M'_4 suture (on the left) and M_2-Mc suture (on the right); TL measured perpendicularly to TW between M_1-M_2 suture (anteriorly) and posterior extremity of infracentral area (anal pyramid); (c) *Domfrontia milnerorum*, Upper Tiouririne and Lower Second Bani formations, Anti-Atlas (Morocco); TL measured between M'_1-M'_2 suture (anteriorly) and distal extremity of subanal plate (posteriorly); TW estimated perpendicularly to TL, between abaxial edges of M'_3 and Mc; (d) *Domfrontia pissotensis*, Le Pissot Formation, Normandy (France) and Traveusot Formation, Brittany (France); TL measured between M'_1-M'_2 suture (anteriorly) and distal extremity of subanal plate (posteriorly); TW estimated perpendicularly to TL, between abaxial edges of M'_3 and Mc; (e) *Destombesicarpus izegguirensis*, Izegguirene Formation, Anti-Atlas
Arauricystis clariondi, Izegguirene Formation, Anti-Atlas (Morocco) and Dobrotivá Formation, Bohemia (Czech Republic); TW measured between M′2-M′3 suture (on the left) and M2-M3 suture (on the right); TL estimated perpendicularly to TW between anterior extremity of M′2 and posterior extremity of M5 (digital, glossal, spinal and other protuberances omitted for measurements).

Fig. 26. Measurement of thecal length (TL) and thecal width (TW) in Middle–Late Ordovician scotiaecystid cornutes from the Mediterranean Province (Czech Republic, France, Morocco, Spain); all reconstructions in lower aspect; arrows indicate landmark points for measurements: (a) Bohemiaecystis bouceki, Dobrotivá Formation, Bohemia (Czech Republic); TW measured between M′3-M′4 suture (on the left) and M2-M3 suture (on the right); TL estimated perpendicularly to TW, between anterior margin of M′2 and posterior extremity of Z; (b) Bohemiaecystis chouberti, Guezzart Formation, Anti-Atlas (Morocco); TW measured between M′3-M′4 suture (on the left) and M2-M3 suture (on the right); TL estimated perpendicularly to TW, between anterior margin of M′2 and posterior extremity of M5; (c) Thoralicarpus bounemrouensis, Izegguirene Formation, Anti-Atlas (Morocco); TW measured between M′4-M5 suture (on the left) and M2-M3 suture (on the right); TL estimated perpendicularly to TW, between anterior margin of M′2 and posterior extremity of Z; (d) Thoralicarpus guilloui, Traveusot Formation, Brittany (France); TW measured between median part of M′4 (on the left) and M2-M3 suture (on the right); TL estimated perpendicularly to TW, between anterior margin of M′2 and posterior extremity of Z; (e) Thoralicarpus jefferiesi, Cantera Shale, Central Iberian Zone (Spain) and Letná Formation, Bohemia (Czech Republic); TW measured between M′3-M′4 suture (on the left) and M2-M3 suture (on the...
right); TL estimated perpendicularly to TW, between anterior margin of M'\textsubscript{2} (or M\textsubscript{1}) and posterior extremity of Z (or M\textsubscript{5}); (f) *Thoralicarpus prokopi*, Letná and Vinice formations, Bohemia (Czech Republic); TW measured between M'\textsubscript{3}-M'\textsubscript{4} suture (on the left) and M\textsubscript{2}-M\textsubscript{3} suture (on the right); TL estimated perpendicularly to TW, between anterior margin of M'\textsubscript{2} and posterior extremity of Z.

**Fig. 27.** Reconstruction of *Milonicystis kerfornei*, Traveusot Formation (late Darriwilian), Brittany (France); (a) lower thecal surface and proximal aulacophore; (b) upper thecal surface and proximal aulacophore.

**Fig. 28.** Camera lucida drawings of *Milonicystis kerfornei*, Traveusot Formation (late Darriwilian), Brittany (France); (a) nearly complete lower thecal surface, with few large infracentrals; IGR.PAL.15774.2 (individual in same concretion as the holotype), Traveusot (Guichen); (b) well-preserved lower thecal surface, with D and G posteriorly sutured to each other; IGR.PAL.15167 (paratype), Traveusot (Guichen); (c) well-preserved, posteriorly incomplete lower thecal surface; IGR.PAL.15774.1 (holotype), Traveusot (Guichen); (d) well-preserved upper thecal surface, with peripheral flange, and supracentrals bearing a central 'mushroom-like' spike; IGR.PAL.15774.1 (holotype), Traveusot (Guichen); (e) proximal aulacophore and slightly disarticulated theca in upper aspect, with wide peripheral flange along marginals; IGR.PAL.15640, Traveusot (Guichen); (f) proximal aulacophore and almost complete, fully articulated theca in upper aspect; UCBL-FSL.170939.1, le Domaine (Guichen).

**Fig. 29.** *Milonicystis*; (a–g) *Milonicystis kerfornei*, Traveusot Formation, Brittany (France); (a,b) IGR.PAL.15774.1 (holotype), Traveusot (Guichen); (a) fully articulated theca (lower
aspect) with proximal aulacophore, stylocone and next two ossicles; (b) aulacophore and fully articulated theca (upper aspect) with supracentrals bearing typical 'mushroom-like' spikes; (c) IGR.PAL.15774.2 (individual in same concretion as holotype), Traveusot (Guichen); fully articulated theca (in lower aspect), proximal rings, stylocone and next two ossicles; (d) IGR.PAL.15640, Traveusot (Guichen); proximal aulacophore and slightly disarticulated theca (in upper view) with wide peripheral flange; (e) UCBL-FSL.170939.1, le Domaine (Guichen); theca (in upper aspect) and proximal rings; (f,g) IGR.PAL.15167 (paratype), Traveusot (Guichen); (f) fully articulated lower thecal surface and some proximal rings; (g) incomplete theca (in upper aspect) with proximal rings, stylocone and six next ossicles; (h) *Milonicystis reboulorum*, Izegguirene Formation, Bou Nemrou (western Tafilalt), Anti-Atlas (Morocco); fully articulated theca (in upper aspect), proximal and distal aulacophore (cover plates in closed position); MHNM.15690.77 (holotype). All scale bars: 5 mm.

**Fig. 30.** *Milonicystis reboulorum*, Izegguirene Formation, Bou Nemrou (western Tafilalt), Anti-Atlas (Morocco); (a) camera lucida drawing of holotype (MHNM.15690.77); articulated aulacophore and theca in upper aspect; (b) reconstruction of lower thecal surface.

**Fig. 31.** Reconstruction of the theca of *Nanocarpus dolambii*, Landeyran Formation (late Floian), Montagne Noire (France); (a) lower thecal surface; (b) upper thecal surface.

**Fig. 32.** Camera lucida drawings of the amygdalothe cid cornute *Nanocarpus dolambii*, Landeyran Formation, Pont supérieur (Saint-Nazaire-de-Ladarez), Montagne Noire (France); (a,b) UCBL-FSL.712529 (holotype); (a) slightly disarticulated lower thecal surface, proximal aulacophore, stylocone and next two ossicles; (b) aulacophore and slightly disarticulated upper thecal surface; (c) slightly disarticulated theca (in lower aspect), with proximal rings,
stylocone and next two ossicles; UCBL-FSL.712530.3; (d) slightly disarticulated theca (in lower aspect) with proximal aulacophore, stylocone and next ossicle; UCBL-FSL.712530.1; (e) slightly disarticulated theca (in lower view) with proximal aulacophore, stylocone and next three ossicles; UCBL-FSL.712522; (f) slightly disarticulated lower thecal surface with proximal aulacophore and stylocone; UCBL-FSL.712580.

**Fig. 33.** Ordovician amygdalothecids: (a) *Nanocarpus dolambii*, Landeyran Formation (late Floian), Pont supérieur (Saint-Nazaire-de-Ladarez), Montagne Noire (France); UCBL-FSL.712529 (holotype); slightly disarticulated theca (in lower aspect), poorly-preserved proximal aulacophore, and spike-bearing stylocone and ossicles; (b,c) *Domfrontia milnerorum*, Lower Second Bani Formation (late Katian), Tizi n'Takrit (Destombes’ locality 756), central Anti-Atlas (Morocco); IGR.PAL.16697, Chauvel's (1971) original material of 'gen. indet. AVII'; (b) strongly disarticulated theca (in upper aspect, with zygal crest), proximal rings and stylocone; (c) aulacophore and strongly disarticulated lower thecal surface. All scale bars: 1 mm.

**Fig. 34.** *Domfrontia milnerorum*, Upper Tiouririne Formation (early Katian), Khabt-el-Hejar, eastern Tafilalt (Morocco); (a) almost complete lower thecal surface and proximal aulacophore; AA.KEH.OS.22; (b) aulacophore and fully articulated theca in upper aspect, with outlines of underlying zygal crest and subanal plate; AA.KEH.OS.27; (c) well-preserved aulacophore, fully articulated lower thecal surface with large distal subanal plate; AA.KEH.OS.20; (d) aulacophore and fully articulated upper thecal surface, with course of underlying zygal crest; AA.KEH.OS.20; (e) aulacophore and well-preserved theca in upper aspect, with clearly distinct underlying zygal crest and outlines of subanal plate; AA.KEH.OS.8; (f) disarticulated aulacophore, and well-preserved upper thecal surface, with
course of underlying zygal crest and outlines of subanal plate; MHN.15690.132; (g) fully articulated upper thecal surface, with outlines of underlying zygal crest and subanal plate; MHN.15690.129; (h) fully articulated upper thecal surface with course of underlying zygal crest; AA.KEH.OS.14a; (i) theca in upper aspect, with course of underlying zygal crest; AA.KEH.OS.14b. All scale bars: 2 mm.

**Fig. 35.** Reconstruction of *Domfrontia milnerorum*, Upper Tiouririne and Lower Second Bani formations (early–late Katian), Anti-Atlas, Morocco; (a) aulacophore and theca in lower aspect; (b) upper thecal surface and aulacophore (cover plates omitted).

**Fig. 36.** Camera lucida drawings of *Domfrontia milnerorum*; (a–c) specimens from the Lower Second Bani Formation (late Katian), Tizi n'Takrit (Destombes’ locality 756), central Anti-Atlas (Morocco); (a) strongly disarticulated theca (in upper aspect) and aulacophore; IGR.PAL.16697, Chauvel’s (1971) original material of ‘gen. indet. AVII’; (b) well-preserved upper thecal surface, with large supracentrals, several of them overlying the subanal plate; BMNHUK.EE.3119; (e) very large theca in upper aspect, with serrations along abaxial edges of M’ and M; BMNHUK.EE.3072; (d–f) large specimens from the Upper Tiouririne Formation (early Katian), Khabt-el-Hejar, eastern Tafilalt (Morocco); (d,e) AA.KEH.OS.20; (d) fully articulated lower thecal surface, with associated proximal aulacophore and stylocone; (e) proximal aulacophore and upper thecal surface with course of underlying zygal crest; (f) well-preserved upper thecal surface with adorals and imprint of underlying structures (zygal crest, subanal plate); AA.KEH.OS.27.

**Fig. 37.** Camera lucida drawings of *Domfrontia milnerorum*, Upper Tiouririne Formation (early Katian), Khabt-el-Hejar, eastern Tafilalt (Morocco); all specimens in upper aspect; (a)
fully articulated theca, with proximal aulacophore, stylocone and first ossicle; AA.KEH.OS.8;
(b) well-preserved aulacophore, with proximal rings, stylocone and next three ossicles, theca
with imprint of subanal plate; MHNM.15690.132; (c) stylocone, proximal rings and upper
thecal surface with imprint of underlying zygal crest; AA.KEH.15d; (d) stylocone, proximal
aulacophore and incomplete, fully articulated theca; AA.KEH.OS.6a; (e) fully articulated
upper thecal surface with imprint of underlying structures (zygal crest, subanal plate);
AA.KEH.OS.36e; (f) proximal aulacophore and upper thecal surface with imprint of
underlying structures (zygal crest, subanal plate); AA.KEH.OS.32r.

Fig. 38. Camera lucida drawings of Domfrontia aff. milnerorum, Upper Ordovician (early–
late Katian), Prague Basin (Czech Republic); (a,b) CGS.OZ.123, Nová Vráž - Černošice,
Králův Dvůr Formation (late Katian); slightly collapsed theca; (a) lower surface; (b) upper
surface; (c,d) specimens from Levín, Zahořany Formation (early Katian); (e) slightly
disarticulated theca in lower aspect, proximal aulacophore, stylocone, ossicle and isolated
cover plate; CGS.OZ.153; (d) well-preserved theca in upper aspect and proximal
aulacophore; CGS.OZ.154.

Fig. 39. Middle–Late Ordovician amygdalothecid cornutes from Bohemia (Czech Republic)
and the Ossa Morena Zone (Spain); (a–d) Domfrontia aff. milnerorum, Upper Ordovician
(early–late Katian), Prague basin (Czech Republic); (a,b) CGS.OZ.123, Nová Vráž -
Černošice, Králův Dvůr Formation (late Katian); poorly preserved aulacophore and slightly
collapsed theca; (a) lower surface; (b) upper surface; (c,d) specimens from Levín, Zahofany
Formation (early Katian); (e) slightly disarticulated theca in lower aspect, proximal
aulacophore, stylocone, ossicle and isolated cover plate; CGS.OZ.153; (d) well-preserved
theca in upper aspect and proximal aulacophore; CGS.OZ.154; (e,f) Domfrontia? sp., yet
unnamed formation of dark mudstones (middle Darriwilian), Cazalla de la Sierra, Ossa Morena Zone (Spain); (e) poorly preserved, disarticulated portion of lower thecal surface, with part of left margin (M_3', M_4'), posterior zygal plate (Z) and possibly M_3(?); MGM-6444O; (f) portion of disarticulated upper thecal surface, with part of left margin (M_2', M_3'), zygal bar (M_1', Z) and probably a portion of Mc; MGM-6445O. All scale bars: 1 mm.

Fig. 40. Reconstruction of *Domfrontia pissotensis*, Le Pissot and Traveusot formations (late Darriwilian–early Sandbian), Bain-de-Bretagne (Brittany) and Domfront (Normandy), France; (a) lower thecal surface and aulacophore; (b) upper thecal surface (appendage omitted).

Fig. 41. Camera lucida drawings of *Domfrontia pissotensis*, Armorican Massif (France); (a–b,d–f) specimens from le Pissot (Domfront, Normandy), Le Pissot Formation, Middle Ordovician (late Darriwilian); (a) aulacophore with cover plates and slightly disarticulated, collapsed, posteriorly incomplete upper thecal surface with large supracentrals and two adorals; IGR.PAL.15702.1 (holotype), original specimen of Chauvel & Nion (1977); (b) proximal aulacophore and slightly disarticulated lower thecal surface; IGR.PAL.15702.2 (individual occurring on same slab as holotype); (d,e) BMNHUK.E.63496.1, specimen originally designated as holotype of *Beryllia miranda* by Cripps & Daley (1994); (d) aulacophore and fully articulated, posteriorly incomplete lower thecal surface; (e) aulacophore and upper thecal surface, with two adorals and large supracentrals; (f) fully articulated, complete lower thecal surface, with posterior zygal plate and distinct subanal plate; BMNHUK.E.63499; (e) poorly preserved proximal aulacophore and theca (in lower aspect); GR/PC.1795, Beauséjour (Bain-de-Bretagne, Brittany), uppermost part of the Traveusot Formation, Upper Ordovician (early Sandbian).
**Fig. 42.** *Domfrontia pissotensis*, Le Pissot and Traveusot formations, Bain-de-Bretagne (Brittany) and Domfront (Normandy), France; (a–e) specimens from le Pissot (Domfront, Normandy), Le Pissot Formation (late Darriwilian); (a) well-preserved aulacophore and slightly disarticulated, collapsed theca (in upper view); IGR.PAL.15702.1 (holotype); (b) aulacophore and fully articulated theca in lower aspect with large, distinct subanal plate, at posterior extremity of left infracentral area, against posterior zygal plate (Z), on lower thecal surface; BMNHUK.E.63499; (c,d) BMNHUK.E.63496.1, specimen originally designated as holotype of *Beryllia miranda* by Cripps & Daley (1994); (e) aulacophore and fully articulated, posteriorly incomplete lower thecal surface; (d) aulacophore and fully articulated, posteriorly incomplete theca (in upper view); (e) two relatively well-preserved individuals side by side, in upper view, on same slab as holotype of *B. miranda* (here all reinterpreted as belonging to *D. pissotensis*); BMNHUK.EE.63496.2–3; (f) aulacophore and poorly preserved theca (in lower aspect); GR/PC.1795, Beauséjour (Bain-de-Bretagne, Brittany), uppermost part of the Traveusot Formation (early Sandbian). All scale bars: 2 mm.

**Fig. 43.** Camera lucida drawings of *Domfrontia?* sp., unnamed formation of dark mudstones (middle Darriwilian), Cazalla de la Sierra, Ossa Morena Zone (Spain); (a,b) MGM-64440, strongly disarticulated portion of theca; (a) lower thecal surface, with some marginals and posterior zygal plate in central (non marginal) position; (b) upper thecal surface, with disrupted marginal frame and imprint of underlying zygal crest; (c,d) MGM-64450, disarticulated, incomplete theca; (c) part of lower thecal surface with zygal bar (M'1, Z) and some marginals; (d) portion of upper thecal surface, with internal aspect of zygal bar.
**Fig. 44.** Camera lucida drawings of *Lyricocarpus courtessolei*, Landeyran Formation (late Floian), Montagne Noire (France); (a,b) UCBL-FSL.712550, les Rocs Nègres (Causses-et-Veyran); original specimen figured by Ubaghs (1991); (a) aulacophore and partly disarticulated lower thecal surface with at least one spine articulated to M'2/3; (b) aulacophore and disarticulated theca (upper aspect) with several spines along left margin; (c) stylocone, proximal aulacophore and posteriorly disarticulated lower thecal surface, with both digital and glossal; UCBL-FSL.711697, les Sources du Foulon (Cessenon); (d,e) UCBL-FSL.712546 (holotype), les Rocs Nègres (Causses-et-Veyran); original specimen figured by Ubaghs (1991); (d) aulacophore and partly disarticulated lower thecal surface with at least two spines articulated along M'2/3; (e) aulacophore and disarticulated theca in upper aspect (digital missing); (f) part of proximal aulacophore and slightly disarticulated, complete lower thecal surface, with both digital and glossal (spines missing); UCBL-FSL.712699, les Sources du Foulon (Cessenon).

**Fig. 45.** Early–Late Ordovician chauvelicystids from Czech Republic, France and Morocco; (a–c) *Lyricocarpus courtessolei*, Landeyran Formation (late Floian), Montagne Noire (France); the arrows indicate thecal spines; (a) aulacophore and partly disarticulated theca in lower view; UCBL-FSL.712546 (holotype), les Rocs Nègres (Causses-et-Veyran); (b,c) UCBL-FSL.712550, aulacophore and slightly disarticulated theca; (b) upper aspect; (c) lower surface; (d) *Destombesicarpus izegguirenensis*, Izegguirene Formation (early Sandbian), Jbel Izegguirene (Destombes locality 755), central Anti-Atlas (Morocco); complete, slightly disarticulated upper thecal surface with articulated spines; IGR.PAL.16691 (holotype), specimen originally described as 'genus indet. AVIII' by Chauvel (1971); (e,f) *Destombesicarpus budili*, Zahořany Formation (early Katian), Levín, Prague Basin (Czech
Republic); complete, slightly disarticulated theca with lateral spines articulated to it; (e) upper thecal surface; (f) lower thecal surface; CGS.OZ.152 (holotype). All scale bars: 1 mm.

Fig. 46. Reconstructions of Early Ordovician chauvelicystids; (a,b) *Lyricocarpus courtessolei*, Landeyran Formation (late Floian), Montagne Noire (France); the colour of spines indicates whether they have been observed (white spines) or not (dark ones); (a) lower thecal surface; (b) upper thecal surface; (c,d) *Prochauvelicystis semispinosa*, Shineton Shale (late Tremadocian), Shropshire (UK); redrawn and modified from Daley (1992) and Lefebvre (2001); (e) lower thecal surface; (d) upper thecal surface.

Fig. 47. Reconstruction of *Destombesicarpus izegguirenensis*, Izegguirene Formation (early Sandbian), Jbel Izegguire, Tazarine area, central Anti-Atlas (Morocco); the colour of spines indicates whether they have been observed (white spines) or not (dark ones); (a) lower thecal surface; (b) upper thecal surface.

Fig. 48. Camera lucida drawing of *Destombesicarpus izegguirenensis*, Izegguirene Formation (early Sandbian), Jbel Izegguire, Tazarine area, central Anti-Atlas (Morocco); IGR.PAL.16691 (holotype), slightly disarticulated theca in upper aspect.

Fig. 49. Reconstruction of *Destombesicarpus budili*, Zahořany and Králův Dvůr formations (early–late Katian), Barrandian area (Czech Republic); the colour of spines indicates whether they have been observed (white spines) or not (dark ones); (a) lower thecal surface; (b) upper thecal surface.
Fig. 50. Camera lucida drawings of *Destombesicarpus budili*, Zahořany Formation (early Katian), Levrn, Prague Basin (Czech Republic); (a,b) CGS.OZ.152 (holotype); (a) lower thecal surface; (b) upper thecal surface.

Fig. 51. Composite reconstruction of *Procothurnocystis courtessolei*, Saint-Chinian Formation (late Tremadocian), Montagne Noire, France, based on MNHN.R.09421 (holotype), Villerambert (Caunes-Minervois), Montagne Noire (France), Saint-Chinian Formation (late Tremadocian); (a) aulacophore and theca in lower aspect; (b) aulacophore and upper thecal surface. Unknown (not preserved) parts are stippled.

Fig. 52. Camera lucida drawings of *Procothurnocystis courtessolei*; (a,b) MNHN.R.09421 (holotype), original specimen described by Ubaghs (1970), Villerambert (Caunes-Minervois), Montagne Noire (France), Saint-Chinian Formation (late Tremadocian); (a) part of aulacophore and slightly disarticulated, incomplete (stippled area) theca in lower aspect; (b) aulacophore and slightly disarticulated, incomplete (stippled area) upper thecal surface.

Fig. 53. Early–Middle Ordovician cothurnocystids from the Montagne Noire (France) and Wales (UK); (a,b) *Procothurnocystis owensi*, Pontyfenny Formation (Dapingian), Llwyn-crwn, Whitland (UK); NMW.84.17G.119 (holotype), original specimen described by Jefferies (1987) and Woods & Jefferies (1992); (a) fully articulated aulacophore and incomplete theca in lower aspect; (b) fully articulated aulacophore and upper thecal surface (posterior parts missing); (c,d) *Procothurnocystis courtessolei*, Saint-Chinian Formation (late Tremadocian), Villerambert, Caunes-Minervois (France); MNHN.R.09421 (holotype), original specimen described by Ubaghs (1970); (c) proximal aulacophore and slightly disarticulated theca; the arrow indicates the occurrence of the elongate knob borne on Mc (thus indicating the presence
of this marginal, between M$_2$ and M$_3$; (d) part of aulacophore and slightly disarticulated upper thecal surface. All scale bars: 5 mm.

Fig. 54. Reconstructions of Furongian–Early Ordovician cothurnocystids from Nevada (USA) and the Montagne Noire (France); (a,b) *Procothunocystis prolixora*, Whipple Cave Formation (late Furongian), Nevada (USA); new reconstruction, based on specimens figured in Sumrall *et al.* (2009); (a) lower thecal surface; (b) upper thecal surface; (c,d) *Arauricystis primaeva*, Saint-Chinian Formation (late Tremadocian), Montagne Noire (France); redrawn and modified from Thoral (1935), Ubaghs (1970) and Lefebvre (2001); (c) lower thecal surface; (d) upper thecal surface; (e,f) *Arauricystis occitana*, Saint-Chinian Formation (late Tremadocian), Montagne Noire (France); redrawn and modified from Ubaghs (1994); the posterior part of the theca is unknown (posterior infracentral area, digital, glossal and M'$_4$), but was certainly present and possibly bent towards the right; (e) lower thecal surface (posterior part not represented); (f) upper thecal surface (posterior part not represented).

Fig. 55. Ordovician cothurnocystids from the Anti-Atlas (Morocco) and the Montagne Noire (France); (a) *Arauricystis clariondi*, Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); aulacophore and slightly disarticulated lower thecal surface; MHNM.15690.67 (holotype); (b) *Arauricystis primaeva*, Saint-Chinian Formation (late Tremadocian), Saint-Chinian, Montagne Noire (France); proximal aulacophore and fully articulated theca in lower aspect; UM.ACI.642 (holotype). All scale bars: 5 mm.

Fig. 56. Reconstruction of *Arauricystis clariondi*, Izegguirene Formation (early Sandbian), eastern Anti-Atlas (Morocco) and Dobrotivá Formation (late Darriwilian–early Sandbian),
Prague Basin (Czech Republic); (a) aulacophore and theca in lower aspect; (b) aulacophore and theca (upper surface).

Fig. 57. Camera lucida drawings of Arauricystis clariondi, Izegguirene Formation (early Sandbian), Bou Nemrou, eastern Anti-Atlas (Morocco); (a) aulacophore and slightly disarticulated, posteriorly incomplete theca in upper aspect; MHNM.15690.103 (paratype); (b) aulacophore and almost complete, articulated upper thecal surface; MHNM.15690.4 (paratype); (c) aulacophore and slightly disarticulated, almost complete (D missing) theca in lower aspect; MHNM.15690.67 (holotype). All scale bars: 5 mm.

Fig. 58. Camera lucida drawings of Arauricystis clariondi, Dobrotivá Formation (late Darriwilian–early Sandbian), Zbiroh, Prague Basin (Czech Republic); NMP.L13230; (a) aulacophore and slightly disarticulated upper thecal surface; (b) slightly disarticulated proximal aulacophore, stylocone and cover plates.

Fig. 59. Arauricystis clariondi (late Darriwilian–early Sandbian), Anti-Atlas (Morocco) and Bohemia (Czech Republic); (a) aulacophore and slightly disarticulated, well-preserved upper thecal surface, with spine-shaped supracentrals; NMP.L13230, Dobrotivá Formation (late Darriwilian–early Sandbian), Zbiroh, Prague Basin (Czech Republic); (b,c) paratypes, Izegguirene Formation (early Sandbian), Bou Nemrou, eastern Anti-Atlas (Morocco); (b) aulacophore and fully articulated theca in upper aspect; MHNM.15690.4; (c) long portion of distal aulacophore, proximal rings and incomplete upper thecal surface (left posterior part missing); MHNM.15690.103. All scale bars: 5 mm.
Fig. 60. Reconstruction of *Bohemiaecystis bouceki*, Dobrotivá Formation (late Darriwilian), Barrandian area (Czech Republic); some parts of the original morphology are unknown (e.g. number of distal ossicles, size and shape of D and G); (a) lower aspect of theca, proximal aulacophore and stylocone; (b) theca, proximal rings and stylocone (cover plates omitted) in upper view.

Fig. 61. Camera lucida of *Bohemiaecystis bouceki*, Dobrotivá Formation (late Darriwilian), Barrandian area (Czech Republic); (a,b) NMP.L17728 (holotype), Praha-Šárka; original specimen figured in Ubaghs (1968); (a) proximal aulacophore and almost complete (D and G missing), fully articulated lower thecal surface; (b) stylocone, proximal rings and incomplete upper thecal surface, with well-preserved lamellate organ; (c,d) NMP.L32304 (paratype), Šárka field, near Hammernikova villa; (c) almost complete theca in lower aspect, with apophyses and digital; (d) right part of upper thecal surface, with lamellate organ.

Fig. 62. *Bohemiaecystis bouceki*, Dobrotivá Formation (late Darriwilian), Bohemia (Czech Republic); (a,b) NMP.L17728 (holotype), Praha-Šárka; original specimen figured in Ubaghs (1968); (a) proximal aulacophore and fully articulated, almost complete lower thecal surface (D and G missing); (b) stylocone, proximal aulacophore and upper thecal surface, with lamellate organ; (c,d) NMP.L32304 (paratype), Šárka field, near Hammernikova villa; (c) almost complete, fully articulated lower thecal surface; the arrow indicates the digital; (d) right part of the upper thecal surface, with lamellate organ. All scale bars: 10 mm.

Fig. 63. Reconstruction of *Bohemiaecystis chouberti*, Guezzart Formation (late Darriwilian), Jbel Bou Isidane, Anti-Atlas (Morocco); (a) lower thecal surface; (b) stylocone, proximal aulacophore and upper thecal surface.
Fig. 64. Camera lucida drawings of *Bohemiaecystis chouberti*, Guezzart Formation (late Darriwilian), locality TA-F5, Jbel Bou Isidane, Anti-Atlas (Morocco); UCBL-FSL.173120; (a,b) specimen A (holotype); (a) proximal aulacophore and almost complete, slightly disarticulated lower thecal surface (D missing); (b) almost complete theca in upper aspect (D and M₃ missing) with lamellipores; (c,d) specimen B (paratype); (c) stylocone, proximal aulacophore and slightly disarticulated, incomplete lower thecal surface (left posterior part missing), with well-preserved spinal blade; (d) proximal rings and almost complete upper thecal surface (D missing) with lamellipores and well-preserved spinal; (e,f) specimen C (paratype); (e) slightly disarticulated, incomplete theca in lower aspect (right part missing) with small digital articulated to M₄; (f) stylocone, proximal aulacophore and slightly disarticulated, incomplete upper thecal surface.

Fig. 65. Camera lucida drawings of *Bohemiaecystis chouberti*, Guezzart Formation (late Darriwilian), Destombes' locality 1826, Jbel Bou Isidane, Anti-Atlas (Morocco); IGR.PAL.16685, specimens originally described as "Cornuta gen. indet. AVI" by Chauvel (1971); (a) stylocone, proximal aulacophore and disarticulated, incomplete theca in upper aspect (D and G missing), with lamellate organ and long spinal blade; specimen A; (b) proximal aulacophore and slightly disarticulated, incomplete theca (D, G, M₃ missing); specimen E; (c) disarticulated proximal rings and anterior part of theca (in lower aspect), with strong protuberance on M₂; specimen D; (d) incomplete upper thecal surface (D, G, M₃ and M₅ missing); specimen B.

Fig. 66. *Bohemiaecystis chouberti*, Guezzart Formation (late Darriwilian), locality TA-F5, Jbel Bou Isidane, Anti-Atlas (Morocco); UCBL-FSL.173120; (a,b) specimen A (holotype);
(a) part of distal aulacophore, proximal rings and slightly disarticulated, almost complete lower thecal surface (D missing); (b) partial distal aulacophore and slightly disarticulated, almost complete upper thecal surface (adorals, D and M₃ missing) with lamellate organ; (c) general view of the slab with four distinct specimens; two individuals are in upper aspect: A (holotype) and C (paratype); paratypes B and E are in lower aspect. All scale bars: 10 mm.

**Fig. 67. Bohemiaecystis chouberti**, Guezzart Formation (late Darriwilian), locality TA-F5, Jbel Bou Isidane, Anti-Atlas (Morocco); UCBL-FSL.173120; (a,b) specimen C (paratype); (a) left part of slightly disarticulated lower thecal surface, with small digital (arrow) articulated to M₄; (b) stylocone, proximal aulacophore and slightly disarticulated upper thecal surface (right part missing); (c) general view of the slab with eleven distinct specimens; two individuals are in lower aspect: A (holotype) and C (paratype); paratypes B and D–K are in upper view. All scale bars: 10 mm.

**Fig. 68. Bohemiaecystis chouberti**, Guezzart Formation (late Darriwilian), Jbel Bou Isidane, Anti-Atlas (Morocco); (a–c) UCBL-FSL.173120, locality TA-F5; (a) specimen C (paratype), left part of the lower thecal surface with G, M₃, M₄, M₅ and Z; the arrow indicates the occurrence of a small digital articulated to M₄; (b,c) specimen B (paratype); (b) part of distal aulacophore (ossicles, stylocone), disarticulated proximal rings and well-preserved, incomplete lower thecal surface (left posterior part missing) with elongate spinal blade; (c) long portion of distal aulacophore, proximal rings and almost complete theca in upper aspect with lamellate organ and adorals (D, G and supracentrals not preserved); (d) three juxtaposed, partly overlapping, more or less disarticulated, incomplete individuals; IGR.PAL.16685, Destombes' locality 1826; two specimens in upper aspect (A and V), one in lower view (D);
specimen A with elongate spinal blade and distinct lamellate organ; individual D with elongate spike-shaped protuberance on M’2. All scale bars: 5 mm.

**Fig. 69.** Bohemiaecystis chouberti, Guezzart Formation (late Darriwilian), Destombes’ locality 1826, Jbel Bou Isidane, Anti-Atlas (Morocco); IGR.PAL.16685, accumulation of 22 specimens originally described as "Cornuta gen. indet. AVI" by Chauvel (1971); all individuals except one (D) in upper aspect. Scale bar: 10 mm.

**Fig. 70.** Camera lucida drawings of Bohemiaecystis? sp., Tachilla Formation (early–middle Darriwilian), Jbel Ouarzemine, western Anti-Atlas (Morocco); IGR.PAL.16698; (a) slightly disarticulated, incomplete lower thecal surface (right part missing), proximal aulacophore and stylocone; specimen A; (b) stylocone, proximal rings and strongly disarticulated, incomplete theca in upper aspect, with fragments of a lamellate organ, spinal-bearing M3 and scotiaecystid marginal Mc; specimen B.

**Fig. 71.** Bohemiaecystis? sp., Tachilla Formation (early–middle Darriwilian), Jbel Ouarzemine, western Anti-Atlas (Morocco); IGR.PAL.16698; (a) aulacophore and theca in lower aspect; specimen A; (b) aulacophore, slightly disarticulated, incomplete theca (right part missing) in lower aspect; specimen A; (b) stylocone, proximal aulacophore and strongly disarticulated and incomplete upper thecal surface, with fragments of the lamellate organ (arrow). All scale bars: 5 mm.

**Fig. 72.** Reconstruction of Thoralicarpus bounemrouensis, Izegguirene Formation (early Sandbian), Anti-Atlas (Morocco); (a) aulacophore and theca in lower aspect; (b) aulacophore and theca in upper view.
Fig. 73. Frequency distribution of thecal width (TW) in *Thoralicarpus bounemrouensis*, based on 23 measured individuals collected within the same horizon and in the same locality (Bou Nemrou, western Tafilalt, Morocco), Izegguirene Formation (early Sanbian).

Fig. 74. Camera lucida drawings of *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sanbian), Bou Nemrou, Anti-Atlas (Morocco); all specimens in lower aspect; (a) part of distal aulacophore, proximal rings and almost complete, slightly disarticulated theca (M₃ missing); MHNM.15690.86 (paratype); (b) stylocone, proximal rings and fully articulated theca (M₃ and left posterior part missing); MHNM.15690.81 (paratype); (c) distal aulacophore, disarticulated proximal rings and incomplete theca (G and M₃ missing); MHNM.15690.106 (paratype); (d) well-preserved, fully articulated aulacophore and incomplete theca (M₃ and left posterior extremity missing); MHNM.15690.76 (paratype); (e) stylocone, proximal rings and complete theca with elongate spinal blade; UCBL-FSL.713378 (paratype); (f) proximal rings and fully articulated, incomplete theca (left posterior part missing) with well-preserved, elongate spinal blade; MHNM.15690.56 (paratype).

Fig. 75. Camera lucida drawings of *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sanbian), Bou Nemrou, Anti-Atlas (Morocco); all specimens in upper aspect; (a) long portion of distal aulacophore, proximal rings and fully articulated, complete theca with lamellate organ, glossal and spinal; UCBL-FSL.425000 (holotype); (b) well-preserved aulacophore and almost complete, articulated theca (G missing), with lamellate organ; MHNM.15690.80 (paratype); (c) aulacophore and fully articulated, almost complete theca (G and M₃ missing); MHNM.15690.55 (paratype), smallest observed specimen; (d) stylocone, proximal aulacophore and fully articulated, incomplete theca (G and M₃ missing); MHNM.102 (paratype); (e) long portion of well-preserved aulacophore and slightly
disarticulated, incomplete theca with lamellate organ (G and M₃ missing); UCBL-FSL.424999 (paratype); (f) well-preserved distal and proximal aulacophore, fully articulated, incomplete theca with lamellate organ (left and right margins missing); MHNM.15690.85 (paratype).

Fig. 76. Camera lucida drawings of *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); all specimens in upper aspect; (a) proximal aulacophore and fully articulated, incomplete theca (M₃ and M₅ missing) with lamellate organ; MHNM.15690.49 (paratype); (b) proximal aulacophore and well-preserved, incomplete theca (G, M₃ and M₅ missing); UCBL-FSL.424997 (paratype); (c) aulacophore (in lateral view) and articulated, almost complete theca (G and M₃ missing); MHNM.15690.15 (paratype); (d) long portion of distal aulacophore (over 30 ossicles and associated pairs of cover plates), proximal rings and slightly disarticulated, incomplete theca (left part and M₃ missing); MHNM.15690.70 (paratype); (e) distal aulacophore with closed, indistinct cover plates, proximal rings, and fully articulated, incomplete theca (G, M₃ and M₅ missing); MHNM.15690.68 (paratype).

Fig. 77. *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); (a) long portion of distal aulacophore (at least 31 ossicles and associated pairs of closed to ajar cover plates), proximal rings and fully articulated theca in upper aspect, with lamellate organ; UCBL-FSL.425000 (holotype); (b) partial distal aulacophore (at least 9 ossicles) in lateral view, proximal rings and fully articulated, incomplete theca in upper aspect (G and M₃ missing); MHNM.15690.15 (paratype); (c) stylocone, proximal aulacophore and fully articulated, incomplete upper thecal surface (G and
M₃ missing) with adorals and lamellate organ; MHNM.15690.102 (paratype). All scale bars: 10 mm.

Fig. 78. *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); (a) fully articulated proximal aulacophore and posteriorly incomplete upper thecal surface, with well-preserved adorals; MHNM.15690.82 (paratype); (b) proximal aulacophore and fully articulated, incomplete theca in upper aspect (M₃ missing); MHNM.15690.49 (paratype); (c) stylocone, proximal rings and fully articulated, incomplete theca in lower aspect (G and M₃ missing); MHNM.15690.68 (paratype); (d) small portion of distal appendage (with stylocone), proximal rings and incomplete, fully articulated lower thecal surface (G and right part missing); MHNM.15690.49 (paratype); (e) part of distal aulacophore (with stylocone), proximal rings and slightly disarticulated, incomplete theca in lower aspect (M₃ missing); MHNM.15690.86 (paratype); (f) fully articulated, posteriorly incomplete theca in lower aspect, with well-preserved, elongate spinal blade; MHNM.15690.56 (paratype). All scale bars: 10 mm.

Fig. 79. *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); (a) aulacophore and fully articulated, incomplete lower thecal surface (M₃ and left posterior part missing); MHNM.15690.80; (b) long portion of distal aulacophore (at least 13 ossicles and associated pairs of closed to ajar cover plates), proximal rings and fully articulated, almost complete upper thecal surface; MHNM.15690.80 (paratype); (c) distal aulacophore (with closed to slightly ajar cover plates), proximal rings and fully articulated, incomplete upper thecal surface (M₃ and M₅ missing); MHNM.15690.68 (paratype); (d) long portion of distal aulacophore (with closed to ajar cover plates), proximal rings and fully articulated, incomplete upper thecal surface (M₅ and left part missing);
MHNM.15690.85 (paratype) ; (e) long portion of distal aulacophore (with closed to slightly
ajar cover plates), proximal rings and posteriorly incomplete upper thecal surface with well-
preserved adorals and lamellate organ; MHNM.15690.101 (paratype); (f) part of distal
aulacophore, proximal rings and fully articulated, incomplete theca in upper aspect (G and M₃
missing); MHNM.15690.55 (paratype). All scale bars: 5 mm.

Fig. 80. *Thoralicarpus bounemrouensis*, Izegguirene Formation (early Sandbian), Bou
Nemrou, Anti-Atlas (Morocco); (a) long portion of distal aulacophore (at least 28 ossicles and
associated pairs of closed to ajar cover plates), proximal rings and slightly disarticulated,
incomplete upper thecal surface (G and M₃ missing); UCBL-FSL.424999 (paratype); (b) long
portion of distal aulacophore (over 40 ossicles and associated pairs of cover plates) with fully
articulated proximal rings and theca in lower aspect (G, M',₄, M₃ and M₅ missing);
MHNM.15690.76 (paratype). All scale bars: 10 mm.

Fig. 81. Camera lucida drawing of the lamellate organ of *Thoralicarpus bounemrouensis*,
Izegguirene Formation (early Sandbian), Bou Nemrou, Anti-Atlas (Morocco); MHNM.15690.85 (the four distal-most lamellae are omitted). The table indicates the number
of lamellae (NL) observed in the four best preserved lamellate organs. The number of
lamellae, as well as the length (LOL) and the maximal width (LOW) of the lamellate organ
are regularly increasing with the size of the theca (expressed by its width, TW).

Fig. 82. Allometry in *Thoralicarpus bounemrouensis*, Izegguirene Formation (early
Sandbian), Bou Nemrou, Anti-Atlas (Morocco); all specimens in lower aspect and illustrated
at same scale. The absolute size of posterior processes (glossal and spinal) and anterior
protuberances (on M₂ and M'₂) remains almost equivalent during growth. As a result, their
relative size decreases during ontogeny, i.e. small individuals (a,b) are more strongly ornamented than large ones (c,d). Poorly and/or incompletely preserved portions of posterior processes are represented with dashed lines.

Fig. 83. Reconstruction of *Thoralicarpus guilloui*, Traveusot Formation (late Darriwilian), Brittany (France); lower thecal surface (aulacophore omitted).

Fig. 84. Camera lucida drawing of *Thoralicarpus guilloui*, Traveusot Formation (late Darriwilian), le Domaine, Guichen, Brittany (France); posterior part of distal aulacophore (ossicles, stylocone and isolated cover plates), proximal rings and slightly disarticulated, complete upper thecal surface with lamellate organ; UCBL-FSL.170875 (holotype).

Fig. 85. *Thoralicarpus guilloui*, Traveusot Formation (late Darriwilian), le Domaine, Guichen, Brittany (France); small part of distal aulacophore (including stylocone), proximal rings and slightly disarticulated upper thecal surface; UCBL-FSL.170875 (holotype); the arrow indicates the position of the short, pear-shaped glossal. Scale bar: 10 mm.

Fig. 86. Reconstruction of *Thoralicarpus jefferiesi*, Cantera Shale (late Sandbian–early Katian), Ciudad Real (Spain) and Letná Formation (late Sandbian), Barrandian area (Czech Republic); cover plates are represented in open position so as to illustrate the underlying ambulacral canal (longitudinal median groove); the distal aulacophore was originally certainly longer, but its precise length cannot be documented based on available material; (a) part of distal aulacophore, proximal rings and theca in lower aspect; (b) part of distal aulacophore, proximal rings and upper thecal surface with two adorals and lamellate organ.
Fig. 87. Camera lucida drawings of *Thoralicarpus jefferiesi*; (a,b) UCM.EO.035 (holotype), Cantera Shale (late Sandbian–early Katian), Central Iberian Zone (Spain); (a) isolated elements of distal aulacophore (cover plates, ossicles, stylocone), disrupted proximal rings and slightly disarticulated, incomplete lower thecal surface (*M*₃ and *M₃* missing); (b) isolated cover plate, proximal rings and slightly disarticulated, incomplete upper thecal surface (*M*₄ and *M₃* missing) with adorals and lamellate organ; (c,d) CGS.LK.17, Letná Formation (late Sandbian), Bohemia (Czech Republic); (c) proximal rings and almost complete, fully articulated theca in lower aspect (*G* missing); (d) incomplete upper thecal surface (left and anterior margins missing) with lamellate organ and well-preserved, wide, short spinal blade.

Fig. 88. Camera lucida drawings of *Thoralicarpus jefferiesi*, Cantera Shale (late Sandbian–early Katian), Central Iberian Zone (Spain); (a,c) UCM.EO.036 (paratype); (a) strongly disarticulated lower thecal surface, with scattered marginals; *M*₁ and *M₃* both in lateral view and showing internal structures; (c) poorly preserved, disarticulated, incomplete theca in upper aspect, with fragments of lamellate organ and proximal rings; (b,d) UCM.EO.037 (paratype); (b) isolated cover plates and scattered skeletal elements of the lower thecal surface (infracentrals, few marginals) (d) isolated plates belonging to the upper thecal surface (few marginals, supracentrals); (e) UCM.EO.038 (paratype); stylocone, proximal rings and slightly disarticulated, incomplete theca in upper aspect (left anterior corner, *M₃* and lamellate organ missing).

Fig. 89. *Thoralicarpus jefferiesi*, Cantera Shale (late Sandbian–early Katian), La Palomera, El Viso del Marqués, Ciudad Real (Spain); UCM.EO.035 (holotype); (a) fragments of distal aulacophore (cover plates, ossicles, stylocone), disrupted proximal rings and disarticulated, incomplete theca in lower aspect (*M₃* and *M*₃ missing); (b) isolated cover plates, disrupted
proximal aulacophore and disarticulated, incomplete theca in upper view (M₃ and M'₄ missing) with adorals and lamellate organ. All scale bars: 10 mm.

**Fig. 90.** *Thoralicarpus jefferiesi*, Cantera Shale (late Sandbian–early Katian), La Palomera, El Viso del Marqués, Ciudad Real (Spain); (a) stylocone, proximal rings and slightly disarticulated, incomplete upper thecal surface (left anterior thecal corner, lamellate organ and M₃ missing); UCM.EO.038 (paratype); (b,c) UCM.EO.036 (paratype); (b) strongly disarticulated, incomplete lower thecal surface, with both M'₁ and M₁ in lateral view; (c) strongly disarticulated upper thecal surface. All scale bars: 10 mm.

**Fig. 91.** *Thoralicarpus jefferiesi*, Letná Formation (late Sandbian), Děd Hill, Zahořany, Bohemia (Czech Republic); CGS.LK.17; (a) proximal rings and fully articulated, almost complete (G missing) theca in lower aspect; (b) fully articulated, incomplete upper thecal surface (anterior and left parts missing). All scale bars: 10 mm.

**Fig. 92.** Reconstruction of *Thoralicarpus prokopi*, Letná and Vinice formations (late Sandbian–early Katian), Prague Basin (Czech Republic); (a) aulacophore and theca in lower aspect; (b) aulacophore and theca in upper view.

**Fig. 93.** Camera lucida drawings of *Thoralicarpus prokopi*, Letná Formation (late Sandbian), Chrustenice, Prague Basin (Czech Republic); all specimens in lower aspect; (a) stylocone, proximal aulacophore and fully articulated theca; CGS.OZ.194 (holotype); (b) stylocone, proximal rings and fully articulated, incomplete theca (G, M₃ and M₅ missing); CGS.OZ.205 (paratype); (c) part of distal aulacophore, proximal rings and fully articulated, incomplete theca (G, M₅, and part of Ms and Z missing); CGS.OZ.201 (paratype); (d); fully articulated,
incomplete theca (Ms and part of Z missing); CGS.OZ.200 (paratype); (e) long portion of distal aulacophore (stylocone and over 20 ossicles), proximal rings and slightly disarticulated, almost complete theca (G missing); CGS.OZ.150 (paratype); (f) stylocone, proximal aulacophore and fully articulated, complete theca; CGS.OZ.189 (paratype).

**Fig. 94.** Camera lucida drawings of *Thoralicarpus prokopi*, Letná Formation (late Sandbian), Prague Basin (Czech Republic); all specimens in upper aspect; (a) almost complete, fully articulated theca (left anterior corner and part of right margin missing); CGS.OZ.194 (holotype), Chrustenice; (b) long portion of distal appendage (stylocone and over 20 ossicles), proximal rings and almost complete theca (G missing); CGS.OZ.150 (paratype), Chrustenice; (c) anterior part of largest observed, incomplete theca, with well-preserved lamellate organ, adorals and aulacophore apophyses; CGS.OZ.191 (paratype), Chrustenice; (d) fully articulated, almost complete theca (G missing); CGS/OZ.190 (paratype), Chrustenice; (e) slightly disarticulated, incomplete theca (left posterior part missing); CGS.OZ.199 (paratype), Chrustenice; (f) part of distal appendage (ossicles, stylocone), proximal aulacophore and well-preserved, slightly disarticulated, incomplete theca (left posterior part missing); CGS.LK.16, Děd Hill, Zahořany.

**Fig. 95.** Camera lucida drawings of *Thoralicarpus prokopi*, Vinice Formation (late Sandbian–early Katian), Děd Hill, Zahořany, Prague Basin (Czech Republic); (a) slightly disarticulated left part of lower thecal surface with short, subtriangular glossal; CGS.LK.10; (b) well-preserved, almost complete, fully articulated upper thecal surface (spinal blade missing) with fragments of lamellate organ; CGS.LK.14.
Fig. 96. *Thoralicarpus prokopi*, Letná Formation (late Sandbian), Chrustenice, Bohemia (Czech Republic); all specimens in lower aspect; (a) long portion of distal aulacophore (over 20 ossicles, stylocone), proximal rings and fully articulated, almost complete theca (left anterior corner missing); CGS.OZ.194 (holotype); (b) fully articulated, posteriorly incomplete theca, with well-preserved spinal (M3) and glossal; CGS.OZ.200 (paratype); (c) long portion of distal appendage (over 20 ossicles, stylocone), proximal aulacophore and fully articulated, incomplete theca (right anterior corner and left posterior extremity missing); CGS.OZ.195 (paratype); (d) distal aulacophore, proximal rings and posteriorly incomplete theca, with well-preserved, elongate spinal; CGS.OZ.201 (paratype); (e) proximal rings and anterior portion of large theca, with strong protuberance on M2; CGS.OZ.191 (paratype); (f) proximal rings and fully articulated, complete theca; CGS.OZ.189 (paratype). All scale bars: 5 mm.

Fig. 97. *Thoralicarpus prokopi*, Letná Formation (late Sandbian), Chrustenice, Bohemia (Czech Republic); (a) fully articulated, incomplete upper thecal surface (left anterior corner and abaxial part of right margin missing); CGS.OZ.194 (holotype); (b) small portion of distal aulacophore (about 12 pairs of closed cover plates above ossicles and stylocone), proximal rings and almost complete theca (in upper aspect); CGS.OZ.196 (paratype); (c) small portion of distal appendage (including stylocone and few ossicles), flexed proximal aulacophore and well-preserved, incomplete lower thecal surface (G, M3 and M5 missing) with protuberances on M2 and M2; CGS.OZ.205 (paratype); (d) long portion of distal aulacophore (over 20 pairs of closed to slightly ajar cover plates above ossicles and stylocone), strongly flexed proximal rings and almost complete upper thecal surface (G missing); CGS.OZ.150 (paratype); (e) distal aulacophore (ossicles, stylocone), well-preserved proximal rings and anterior part of lower thecal surface; CGS.OZ.192 (paratype); (f) aulacophore and fully articulated, posteriorly incomplete theca in upper aspect; CGS.OZ.207 (paratype). All scale bars: 5 mm.
Fig. 98. *Thoralicarpus prokopi*, Letná Formation (late Sandbian), Chrustenice, Bohemia (Czech Republic); all specimens in upper aspect; (a) proximal rings and fully articulated, almost complete theca (part of left margin missing) with well-preserved posterior processes (glossal, spinal) and lamellate organ; CGS.OZ.200 (paratype); (b) small portion of distal aulacophore with closed cover plates (over stylocone and ossicles), proximal rings and almost complete theca (posterior processes missing); CGS.OZ.197 (paratype); (c) proximal rings and almost complete theca (G missing) with well-preserved spinal blade; CGS.OZ.190 (paratype); (d) proximal aulacophore and fully articulated, incomplete theca (left posterior part missing) with well-preserved spinal blade; CGS.OZ.199 (paratype); (e) stylocone, strongly flexed proximal rings and posteriorly incomplete theca; CGS.OZ.203 (paratype); (f) disrupted proximal rings and anterior portion of large theca, with well-preserved lamellate organ; CGS.OZ.191 (paratype). All scale bars: 5 mm.

Fig. 99. Middle and Late Ordovician scotiaecystids from Bohemia (Czech Republic); (a–d) *Thoralicarpus prokopi*; (a) part of distal aulacophore, fully articulated proximal rings and well-preserved, slightly disarticulated, incomplete theca in upper view (left and posterior parts missing); CGS.LK.16, Letná Formation (late Sandbian), Děd Hill (lower level), Zahořany; (b) fully articulated almost complete (spinal blade missing) upper thecal surface; CGS.LK.14, Vinice Formation (late Sandbian–early Katian), Děd Hill (upper level), Zahořany; (c,d) *Thoralicarpus cf. prokopi*, Šárka Formation (early–middle Darriwilian); NRS.Ec.19934; (c) proximal rings and disarticulated, incomplete lower thecal surface, with well-preserved triangular, spike-shaped spinal and protuberances on both M′2 and M2; (d) proximal rings and slightly disarticulated, incomplete upper thecal surface with well-preserved lamellate organ and spinal blade. All scale bars: 5 mm.
**Fig. 100.** Camera-lucida drawings of *Thoralicarpus* cf. prokopi, Šárka Formation (early-middle Darriwilian), Prague Basin (Czech Republic); NRS.Ec.19934, Praha-Šárka; (a) proximal aulacophore and disarticulated, incomplete lower thecal surface; (b) proximal rings and disarticulated, incomplete theca (in upper aspect) with lamellate organ.

**Table 1.** Classification adopted here, based on all described cornute genera. All families are considered as monophyletic. Unassigned genera embrace both well documented, relatively basal taxa (e.g. *Flabellicarpus*, *Persiacarpos*, *Ponticulocarpus*, *Protocystites*), and more problematic, incompletely known morphologies (e.g. *Acuticarpus*, *Babinocystis*, *Trigonocarpus*).
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Fig. 2

abaxial  <->  adaxial  <->  abaxial
right  <->  left

(a)
main axis
0  10 mm

(b)
main axis

(c)
aulacophore  <->  theca
proximal  <->  distal

(a) and (b) show the relationship between abaxial and adaxial regions, as well as the proximal and distal parts of the aulacophore and theca.

(c) illustrates the aulacophore and theca in a linear arrangement, with the aulacophore located distal to the theca.

(a) and (b) also highlight the anterior and posterior orientations, with anterior being left and posterior being right.

(c) shows the relationship between the aulacophore and theca in a linear arrangement, with the aulacophore located distal to the theca.
right adoral

right adoral orifice (hydropore)

median adoral

left adoral

left scutula

right scutula

apophysis crest

right aulacophore apophysis

left aulacophore apophysis

infundibulum

right scutula

anterior oblique groove

anterior transverse groove

posterior wall of right aulacophore apophysis

infundibulum
(a) soft substrate

(b) 1 mm

Fig. 8

- supracentra/ls
- proximal rings
- marginals
- cover plates
- ossicle
- intrathecal cavity
- proximal cavity
- esophagus
- gut
- mouth
- ambulacral ray
- tube feet
- aulacophore apophyses
- anus
Fig. 10

(a) Right infracentral area

(b) Left infracentral area

5 mm

(a) Right infracentral area

(b) Left infracentral area

Supracentral area

Digital

Glossal

Spinal

Integument

Z

Mc
new Fig. 14

(a) digital
glossal

(b) spinal
digital
glossal

(c) spinal
glossal
digital

(d) M'₄-M₄ bridge

Legend:
- M₁
- M₂
- M₃
- M₄
- Mc
- M'₁
- M'₂
- M'₃
- M'₄
- G
- D
- Z
- A'₁
- A₁
- integumentary areas
Fig. 15
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new Fig. 19

number of individuals

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Fig. 26

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proximal aulacophore

stylocone

ossicles

5 mm

longitudinal median groove

zygal crest

subanal
Fig. 41

(a) cover plates
(b) proximal rings
(c) left infracentral area
(d) left infracentral area
(e) subanal

ossicle
stylocone
proximal rings
M_1
M_2
M_3
M_4
Mc

G

Z

A_1
A_1'
M_1
M_1'
M_2
M_2'
M_3
M_3'
M_4
M_4'
Mc

D

1 mm
Fig. 43

(a) Right infracentral area

(b) Course of zygal crest

(c) Left infracentral area

(d) Supracentral area

M'2
M'3
M'4
M3
M'1
M'2
M'3
Mc
Z

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Fig. 47

(a) Left infracentral area

(b) Supracentral area

1 mm
Fig. 48

M'₁

M'₂/₃

M₁

M₂

Z

left infracentral area

spines

supracentrals

D

G

1 mm
Fig. 49

(a) Left infracentral area

(b) Supracentral area

M₁

M₂

Z

G

M'₁

M'₂/₃

A₁

A'₁

D

1 mm

spines

apophyses

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Fig. 52

proximal rings

M₁
M₂
Mc
Z
M₃

10 mm

(a)

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ossicles

stylocone

A₁

M₁
M₂
M₃
M₄
M₅
M'₁
M'₂
M'₃
M'₄
M'₅
M'₆
M'₇

supracentraals

(b)

D

G
Fig. 56

- distal aulacophore
- proximal aulacophore
- cover plates in closed position
- ossicles
- stylocone
- cothurnopores
- hydropore
- stylocone
- ossicles
- cover plates in closed position
- cothurnopores
- hydropore
- D
- M_2
- M_3
- M_5
- G
- Z

(a) 10 mm

(b)
Fig. 57
proximal rings

(a)

(b)

right infracentral area

stylocone
tectals

inferolaterals

A'₁
M'₁
M'₂
M'₃
M'₄
M'₅
M'₁'
M'₂'
M'₃'
M'₄'
M'₅'
M₁
M₂
M₃
M₄
M₅
A₁
G
D
Z

ossicles
cover plates
cothurnopores

supracentrals

(b)
Fig. 58

- stylocone
- cover plates
- longitudinal median groove
- transverse channels
- notch
- inferolaterals
- tectals
- supracentrals

(a) stylomegadonta

(b) stylomegadontine
Fig. 60

(a) stylcone
inferolaterals
M₁
M₂
M₃
Ms
Z

(b) longitudinal median groove
tectals
A₁
A'₁
M₁
M₂
M₃
M₄
M₅
D
G

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Fig. 61

(a) inferolaterals
M₁
M₂
M₃
Ms
Z

(b) tectals
M₁’
M₂’
M₃’
M₄’
M₅’
lamellipores

(c) lamellipores
M₁
M₂
M₃
Ms
Z

(d) stylocone
A₁
M₁
M₂
M₃
Ms
Z

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Fig. 63

10 mm

- inferolaterals
- stylocone
- tectals
- hydropore
- lamellipores

(a)

- M₁
- M₂
- M₃
- Ms

(b)

- M'₁
- M'₂
- M'₃
- M'₄
- M'₅
- Ms
- G
- D
- Z
- A'₁
- M₅
Fig. 64

(a) proximal rings

(b) lamellipores

(c) stylocone

(d) proximal rings

(e) proximal aulacophore

(f) stylocone

---

10 mm
Fig. 65

(a) stylolcone
(b) proximal rings
(c) lamellipores
(d) inferolaterals

M$_1$, M$_2$, M$_3$, M$_4$, M$_5$

Ms, Z

5 mm
Fig. 70

(a) styllocone
inferolaterals
proximal rings
lamellipores

M₁
M₂
M'₁
M'₂
M'₃

(b) tectals
lamellipores

M₃
Ms

5 mm
The number of individuals and their thecal width (TW in mm) are represented in the histogram. The histogram shows a peak at the thecal width of 20 mm, with a total sample size of N = 23.
new Fig. 75
proximal rings

M' 1
M' 2
M' 3
M' 4
M 5

M' 1
M' 2
M' 3
M' 4
M 5

Ms

G

Z

10 mm
closed/ajar cover plates

M 1
M 2
M 3
M 4
M 5

Ms

M' 2
M' 3
M' 4
M 5

Ms

M' 1
M' 2
M' 3
M' 4
M 5

Z

tectals

stylocone

inferolaterals

M 1
M 2
M 3
M 4
M 5

Ms

M' 2
M' 3
M' 4
M 5

Ms

M' 1
M' 2
M' 3
M' 4
M 5

Z

M 1
M 2
M 3
M 4
M 5

Ms

M' 1
M' 2
M' 3
M' 4
M 5

Z

M 1
M 2
M 3
M 4
M 5

Ms

M' 1
M' 2
M' 3
M' 4
M 5

Z

lamellipores

longitudinal median groove

closed/ajar cover plates

proximal rings

stylocone

lamellipores

longitudinal median groove

proximal rings

lamellipores
crest corresponding to suture between fused antero-abaxial and postero-adaxial U-shaped plates

new Fig. 81

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new Fig. 83

Click here to access/downloa
Fig. 86
longitudinal median groove
cover plates
ossicle
stylocone
tectals
inferolaterals
M'1
M'2
M'3
M'4
M'5
A'1
A1
M1
M2
M3
M5
Ms
G
Z
lamellipores
10 mm
Click here to access/download;figure;Lefebvre_et_al
new Fig. 92

distal aulacophore

proximal aulacophore

ossicles

longitudinal median groove

tectals

lamellipores

(a)

(b)