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New Peri-Gondwanan occurrences of the Ordovician genus *Diamphidiocystis* (Echinodermata, Stylophora) – Implications for mitrocystitid palaeobiogeography and diversity

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Abbreviated title: Ordovician mitrate stylophorans

Abstract

Anomalocystitid mitrates represent one of the most diverse and long ranging clade of stylophorans (Early Ordovician–Middle Devonian). Although they probably originated from a peri-Gondwanan stock of early mitrocystitids during the Floian, the fossil record of anomalocystitids in the Middle–Upper Ordovician of the Mediterranean Province remains extremely scarce and largely underestimated. The unusually shaped anomalocystitid genus *Diamphidiocystis* was originally described in the latest Katian–Hirnantian of North America (Illinois). However, earlier occurrences of this genus in the late Darriwilian of western France (Brittany) suggest a probable peri-Gondwanan origin. Based on new Middle to Late Ordovician material from the Anti-Atlas (Morocco), Bohemia (Czech Republic) and Brittany (France), all occurrences of Mediterranean *Diamphidiocystis* are considered as conspecific and formally described as *D. regnaulti* sp. nov.. The palaeobiogeographic significance of Ordovician anomalocystitid mitrates is discussed.

Keywords: Anomalocystitida, Echinodermata, Mitrata, Ordovician, Mediterranean Province, Stylophora

Anomalocystitids (two-spined mitrocystitid mitrates) are a well-defined, long-ranging and taxonomically diverse clade of stylophoran echinoderms (Ubaghs 1968; Kolata & Jollie 1982; Craske & Jefferies 1989; Ruta 1999; Lefebvre & Ausich 2021). New fossil evidence from the Floian of the Anti-Atlas (Morocco) suggests that, in Early Ordovician times, anomalocystitids probably originated from a stock of spineless, *Mitrocystites*-like early mitrocystitids by the modification of two posterior marginal thecal plates into a pair of movable spine-shaped elements (Lefebvre 2007*a*; Noailles & Lefebvre 2012; Lefebvre *et al*. 2016; Lefebvre & Ausich 2—021). In Middle Ordovician times, the fossil record of anomalocystitids is extremely scarce, and long remained restricted to a single occurrence (*Diamphidiocystis* sp.) in the late Darriwilian of the Armorican Massif (France) (Chauvel 1981; Lefebvre 2000*a*, 2003; Lefebvre & Ausich 2021). In marked contrast, Late Ordovician anomalocystitids are geographically widespread (Avalonia, Baltica, Gondwana and Laurentia) and taxonomically diverse, with the earliest known representatives of the two main subfamilies

Allanicytidiinae and Anomalocystitinae (e.g. Billings 1858; Barrande 1887; Caster 1952; Chauvel 1971; Kolata & Guensburg 1979; Ubaghs 1979; Kolata & Jollie 1982; Parsley 1982, 1991; Craske & Jefferies 1989; Ruta 1997*a*, 1999; Ruta & Jell 1999*a*; Lefebvre 2007*a*; Lefebvre *et al.* 2013; McDermott & Paul 2017; Lefebvre & Ausich 2021). Anomalocystitids were not severely affected by the Late Ordovician mass extinction, with Siluro-Devonian allanicytidiines and anomalocystitines diversifying worldwide in response to environmental conditions (e.g. Hall 1859; Dehm 1932; Caster 1954, 1983; Gill & Caster 1960; Ubaghs 1968; Jefferies & Lewis 1978; Philip 1981; Régnault & Chauvel 1987; Rozhnov 1990; Haude 1995; Ruta, 1997*b*, 1999; Ruta & Theron 1997; Ruta & Bartels 1998; Ruta & Jell 1999*b*; Scheffler *et al*. 2019; Lefebvre & Ausich 2021). The allanicytidiine mitrate *Placocystella langei* (late Emsian–early Givetian; Paraná Basin, Brazil) represents the youngest known occurrence of anomalocystitids (Scheffler *et al*. 2019).

This paper is part of a broader analysis dedicated to investigate the poorly documented early diversification of anomalocystitids in high latitude peri-Gondwanan regions of the Mediterranean Province in Middle Ordovician times. This study focuses on *Diamphidiocystis*, the single anomalocystitid documented so far in this time interval. Although the presence of this genus has been long reported in several Middle–Upper Ordovician localities from Brittany, France (Chauvel, 1981; Lefebvre 2000*a*, 2003), the Anti-Atlas, Morocco (Lefebvre *et al*. 2008, 2010*a*; Lebrun 2018) and Bohemia, Czech Republic (Noailles *et al*. 2014), this mitrate had never been formally described. Consequently, the morphology of peri-Gondwanan diamphidiocystines is reconstructed here for the first time, based on the reevaluation of Chauvel's (1981) original specimens from Brittany, coupled with the description of abundant new material from several late Darriwilian–late Katian localities from the Czech Republic, France and Morocco.

Geological setting

The genus *Diamphidiocystis* was originally described in Laurentia based on over thirty specimens collected in the Orchard Creek Shale (latest Katian–early Hirnantian; Fig. 1.10) and the overlying Girardeau Limestone (early Hirnantian; Fig. 1.11) in southern Illinois, USA (*D. drepanon*; Kolata and

Guensburg 1979; Guensburg 1988). Unpublished well-preserved remains of *D. drepanon* are also possibly present in the Maquoketa Shale (latest Katian; Fig. 1.12) near Dubuque, Iowa (T. Guensburg, pers. comm., July 2021).

The situation is different in peri-Gondwanan Europe and North Africa. There, *Diamphidiocystis* was first reported by Chauvel (1981) in the Traveusot Formation (late Darriwilian) of Brittany, France (Fig. 1.2). However, the incomplete preservation of the three Armorican specimens prompted Chauvel (1981) to leave this material in open nomenclature (*Diamphidiocystis* sp.). In the last 40 years, at least 14 additional specimens of *Diamphidiocystis* sp. were collected in the late Darriwilian of the Armorican Massif, adding substantial new data on its morphology (see below; Lefebvre *in* Ruta 1999; Lefebvre 2000*a*, 2003). In the last two decades, additional remains of diamphidiocystine mitrates were also reported in the Izegguirene Formation (early Sandbian; Fig. 1.9) of Morocco (see below; Lefebvre *et al*. 2008, 2010*a*; Lebrun 2018) and the Vinice Formation (latest Sandbian–early Katian; Fig. 1.5) of Bohemia (Noailles *et al*. 2014). More recently, new specimens of *Diamphidiocystis* were collected from several other localities and stratigraphic levels in the Prague Basin, Czech Republic (see below; Fig. 1.3–4,6–8). The geological context of all known occurrences of peri-Gondwanan diamphidiocystines is discussed below. *Diamphidiocystis* often co-occurs with cornute stylophorans and added information on these sites is already provided by Lefebvre *et al*. (this volume).

Anti-Atlas, Morocco

In the western Tafilalt area (eastern Anti-Atlas), the purple to reddish coarse, micaceous sandstones of the Izegguirene Formation (early Sandbian, uppermost unit of the First Bani Group, Fig. 1.9; see Destombes *et al*. 1985; Álvaro *et al*. this volume) yielded two well-preserved, fully articulated specimens of *Diamphidiocystis*. They were both collected in the deep quarries excavated at Bou Nemrou, within the Jbel Tijarfaïouine Massif, about 30 km SW of Erfoud (see Lefebvre *et al*. this volume). This locality also yielded abundant remains of exceptionally preserved taxa typical of the Tafilalt Biota (e.g. aglaspidid and cheloniellid arthropods, paropsonemid eldonioids, hydrozoans, palaeoscolecids; Van Roy 2006, 2011; Lefebvre *et al*. 2008; Gutiérrez-Marco & García-Bellido 2015;

MacGabhann *et al*. 2019; Gutiérrez-Marco *et al*. 2020 *b*, this volume), trilobites with soft parts (gut; Van Roy 2006; Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al*. 2020 *a*, this volume) and the taxonomically most diverse starfish bed (echinoderm Lagerstätte *sensu* Smith 1988) in the Upper Ordovician of Morocco (Lefebvre *et al*. 2007, 2008, 2010*a*; Hunter *et al*. 2010). The Bou Nemrou echinoderm assemblage is dominated by asterozoans (protasterid ophiuroids; Hunter *et al.* 2010), eocrinoids (*Ascocystites*; Régnault 2007; Nardin & Régnault 2015) and mitrate stylophorans (mostly *Anatifopsis*, *Aspidocarpus* and *Eumitrocystella*; Lefebvre *et al.* 2008, 2010*a*). *Diamphidiocystis* is a rare element of the assemblage, although the existence of a possible sampling bias due to its particularly small size (theca about 5 mm wide) and unusual morphology cannot be entirely ruled out. Other echinoderms occurring in Bou Nemrou include diverse crinoids (Botting this volume), edrioasteroids (Sumrall & Zamora 2011), the enigmatic genus *Hexedriocystis* (Sumrall & Zamora 2011, this volume), as well as several cornute stylophorans (Lefebvre *et al*. 2007, 2008, 2010*a*, this volume). Taphonomic features of the Bou Nemrou assemblage indicate that its preservation results from the sudden burial of autochthonous to para-autochthonous, fully marine, relatively shallow communities living at or slightly above storm-wave base by obrution, probably storm-generated, deposits (Lefebvre *et al*. 2008, 2010*a*; Hunter *et al*. 2010; Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al. a*, this volume). In specimens of *Diamphidiocystis* from Bou Nemrou, the preservation of long, fully articulated portions of their particularly fragile feeding appendage (aulacophore) is unique and supports the view that these individuals were very likely buried alive and *in situ*. However, minute morphological details (e.g. internal structures of the aulacophore, plate boudaries) of the *Diamphidiocystis* material from Bou Nermou are often obscured by the coarse lithology.

Armorican Massif, France

All diamphidiocystines from the Armorican Massif (W. France) were collected in the same stratigraphic interval (late Darriwilian, *Hustedograptus teretiusculus* graptolite Zone). One of them was found in the micaceous shales of the upper part of the Postolonnec Formation (Fig. 1.1), in the abandoned slate quarry of Guernanic, Gourin (Châteaulin Basin, Morbihan; see Hunter *et al*. 2007 for locality details and map). The single Gourin specimen of *Diamphidiocystis* occurs within a well-defined, thin, starfish bed (echinoderm Lagerstätte *sensu* Smith 1988) dominated by the protasterid ophiuroid *Taeniaster armoricanus* and the mitrate *Mitrocystella incipiens miloni*, along with less common crinoids (*Heviacrinus melendezi*) and aristocystitid diploporites (*Calix* sp.) (Hunter *et al*. 2007; Lefebvre *et al*. 2015). Although they are strongly flattened and pyritized, echinoderms from the Guernanic starfish bed are remarkably preserved. For example, long, fully articulated portions of the delicate feeding structures (brachioles) can be observed in some specimens of *Calix*. Most mitrates are preserved with their appendage (aulacophore) in extended position, which is generally interpreted as the living (feeding) posture (Parsley 1988; Lefebvre 2003; Hunter *et al*. 2007; Lefebvre & Ausich 2021). These taphonomic features, along with the preservation of several fully articulated, complete specimens of ophiuroids, suggest that the Guernanic starfish bed results from the sudden burial of an autochthonous echinoderm assemblage, probably by distal storm deposits, in an otherwise quiet, moderately deep (shelf) environment (Hunter *et al.* 2007).

All other specimens of *Diamphidiocystis* from Brittany were collected in the upper part of the Traveusot Formation (Fig. 1.2) in three neighbouring localities (le Domaine, la Saudrais and Traveusot) occurring in a small geographic area within the Martigné-Ferchaud syncline (Guichen, Ille-et-Vilaine; see Lefebvre *et al*. this volume, for more details and map). The three sites have yielded similar, particularly diverse assemblages of late Darriwilian marine invertebrates (e.g. brachiopods, graptolites, hyolithids, molluscs, ostracods, trilobites; see e.g. Babin 1966; Mélou 1973, 1975; Henry 1980, 1989; Vannier 1986*a*, *b*). Echinoderms constitute a significant and diverse component of these assemblages, with aristocystitid and sphaeronitid diploporites, crinoids, stenuroid asterozoans and both cornute and mitrate stylophorans (e.g. Rouault 1851; Chauvel 1941, 1980, 1981, 1986; Jefferies 1968; Cripps & Daley 1994; Lefebvre & Vizcaïno 1999; Lefebvre *et al*. 2015, this volume; Blake *et al*. 2016). La Saudrais is the type locality of the scotiaecystid *Thoralicarpus guilloui*, and Traveusot, the type locality of the cornute *Milonicystis kerfornei* (see Chauvel 1986; Lefebvre & Vizcaïno 1999; Lefebvre *et al.* this volume). Independently of their occurrence in fine micaceous siltstones (la Saudrais) or in alumino-siliceous concretions (le Domaine, Traveusot), diamphidiocystines are displaying the same type of preservation as other co-occurring mitrates (kirkocystids, *Mitrocystella*; see Chauvel 1941, 1981; Jefferies 1968). Their theca is collapsed, slightly disarticulated and often incomplete posteriorly (anal area), with only the proximal part of the appendage and sometimes the stylocone present (more distal portions of the aulacophore are rarely preserved). These taphonomic features suggest that most specimens correspond to decaying carcasses probably buried by thin, occasional, distal storm-generated deposits in an otherwise very quiet, well-oxygenated and moderately deep setting (Lefebvre 2007*a*; Lefebvre *et al.* this volume). A similar palaeoenvironmental interpretation was proposed based on the preservation of associated trilobites (see e.g. Henry 1980, 1989).

Bohemia, Czech Republic

The occurrence of diamphidiocystines in the Ordovician of the Prague Basin was first briefly reported by Noailles *et al*. (2014), who mentioned their presence in the Vinice Formation (latest Sandbian–early Katian). In recent years, intensive field work in the Barrandian area yielded additional specimens, which were collected in several new localities (Figs 2–3) and five more stratigraphic units (Dobrotivá, Libeň, Zahořany, Bohdalec and Králův Dvůr formations; see below). As a result, *Diamphidiocystis* now appears as a largely overlooked, particularly long-ranging stylophoran genus in the Ordovician of Bohemia (Fig. 1.3–8). In this area, the fossil record of diamphidiocystines is almost continuous from the late Darriwilian to the late Katian with, so far, no reported occurrence in the Letná Formation.

The stratigraphically earliest specimens of *Diamphidiocystis* in the Prague Basin were found in both siliceous concretions and black shales of the Dobrotivá Formation (late Darriwilian–early Sandbian; Fig. 1.3) at Malé Přílepy (late Darriwilian; about 6 km NE of Beroun, Fig. 2.1). This locality is well-known for having yielded the most diverse assemblage of marine invertebrates observed in the Dobrotivá Formation (e.g. brachiopods, chelicerates, conulariids, echinoderms, graptolites, hyolithids, machaeridians, molluscs, ostracods, palaeoscolecids, phyllocarids, sponges and trilobites; see Lefebvre *et al*. this volume). However, it is possible that this high diversity results from the mixing of several, originally distinct concretion-bearing fossiliferous levels. Kirkocystid mitrates are the most common echinoderms of the Malé Přílepy assemblage. Other echinoderm taxa are rare and include cheirocrinid rhombiferans, cornute and mitrate stylophorans (see Lefebvre *et al.* this volume). Diamphidiocystine remains were also found in other localities yielding assemblages from different stratigraphic horizons within the Dobrotivá Formation. At Chrustenice (latest Darriwilian–early Sandbian; upper part of the Dobrotivá Formation; Fig. 2.2), *Diamphidiocystis* is associated to relatively common kirkocystids and rare crinoids. Taphonomic features of *Diamphidiocystis* from Chrustenice (Fig. 3a–b) and Malé Přílepy (Fig. 3c) are very similar to those of specimens from the Traveusot Formation (see above): nearly complete, slightly disarticulated, collapsed thecae, with proximal rings and stylocone often present and more distal portions of the aulacophore generally absent. It is thus very likely that the preservation of most diamphidiocystines from the Dobrotivá Formation results from the occasional burial of *in situ* decayed carcasses by thin distal storm deposits in a quiet and relatively deep environment.

The Libeň Formation (early Sandbian; Fig. 1.4) overlies the Dobrotivá Formation with a thick sequence of quartz sandstones followed by a relatively thin succession of black shales, which are themselves overlain by quartz sandstones of the Letná Formation. Although the black shales are lithologically not very distinct from those of the underlying Dobrotivá Formation, they have been historically less intensively investigated and yielded less diverse fossil assemblages (see e.g. Havlíček & Vaněk 1996). At Lhotka, about 2 km N of Beroun (Fig. 2.3), five poorly preserved specimens of *Diamphidiocystis* were found together with common kirkocystids, rare *Lagynocystis* and disarticulated remains of solutans (*Dendrocystites*). In this locality, other faunal elements occurring in the black shales of the Libeň Formation comprise relatively common brachiopods (*Paterula*), as well as small conulariids, ostracods, and trilobites (*Ormathops*, *Selenopeltis*, and rare *Girvanopyge*).

Four specimens of *Diamphidiocystis* were also found in the micaceous shales of the lower part of the Vinice Formation (latest Sandbian–early Katian; Fig. 1.5). The two best preserved ones are from the village of Zahořany (W of Beroun; Fig. 2.5). This locality yielded a relatively low-diversity invertebrate fauna (e.g. molluscs, trilobites) comprising few echinoderm taxa: mostly kirkocystid mitrates, along with rare solutans, scotiaecystid cornutes and mitrocystitids (see Lefebvre *et al*. this volume). Two poorly preserved specimens of diamphidiocystines were also found at Hředle (Fig. 2.4). All known specimens of *Diamphidiocystis* from the Vinice Formation consist of a collapsed, more or less disarticulated theca, with the aulacophore entirely missing or restricted to disarticulated proximal rings. This preservation is suggestive of the prolonged exposure of decayed carcasses on the sea floor in a very quiet, probably distal environment, below storm wave base (see Lefebvre *et al*. this volume).

One specimen was collected in the Zahořany Formation (early Katian; Fig. 1.6) at Levín (Fig. 2.6), where it occurs with rare cornutes (*Destombesicarpus budili*, *Domfrontia* aff. *milnerorum*; see Lefebvre *et al*. this volume), and relatively common diploporites (*Aristocystites*, *Codiacystis*), edrioasteroids, rhombiferans (*Echinosphaerites*, *Homocystites*), solutans (*Dendrocystites*), and mitrate stylophorans (*Barrandeocarpus*, kirkocystids). Other faunal elements consist of bivalves, bryozoans, gastropods, brachiopods, graptolites, hyolithids and trilobites (*Dalmanitina*, *Prionocheilus*, *Cekovia*, *Eccoptochile*, *Selenopeltis*).

In the Bohdalec Formation (early Katian; Fig. 1.7), two specimens of *Diamphidiocystis* were found in two distinct localities: a temporary excavation at Praha - Harfa (Fig. 2.7) and a former brickyard near Neumětely (Fig. 2.8). Praha-Harfa yielded a very scarce fauna consisting of bivalves often preserved in 'butterfly position', brachiopods (*Aegiromena*, *Paterula*), cephalopods, small conulariids, hyolithids, mitrate stylophorans (*Anatifopsis*, anomalocystitids), and trilobites (*Onnia*). The Neumětely (lower part of the Bohdalec Formation) assemblage is typical of the cyclopygid facies, with very common *Cyclopyge* and scarcer *Onnia* and *Declivolithus* trilobites, common brachiopods, graptolites and hyolithids (Röhlich 1957). As in Praha-Harfa, echinoderms consist mainly of anomalocystitids and kirkocystids. The two known specimens of diamphidiocystines from the Bohdalec Formation correspond to incomplete, more or less disarticulated, collapsed thecae and their associated, disrupted proximal aulacophore (Fig. 3d). Taphonomic features of these two specimens are in good agreement with the composition of the associated fauna and the more general geological context all pointing out to relatively quiet and distal environmental conditions, well below storm wave base (see Havlíček 1982; Havlíček & Vaněk 1990; Lefebvre *et al*. this volume).

Finally, several specimens of *Diamphidiocystis* were collected in the soft grey shales of the Králův Dvůr Formation (*Dicellograptus laticeps* Zone, late Katian; Fig. 1.8). One was found in Nová Vráž - Černošice (about 15 km E of Beroun; Fig. 2.9). This locality yielded a relatively diverse invertebrate assemblage (e.g. brachiopods, echinoderms, hyolithids, machaeridians, molluscs, ostracods, trilobites). Most echinoderms are disarticulated and consist of crinoid columnals and rare cornutes (*Domfrontia*) (Lefebvre *et al*. this volume). The single specimen of *Diamphidiocystis* from Nová Vráž is relatively well preserved, with an almost complete, slightly disarticulated theca and the proximal part of the appendage (distal aulacophore missing; Fig. 3f). Another specimen was collected in the outskirts of Králův Dvůr, near the base of the Kosov hill (Fig. 2.10) in similarly aged levels (*Dicellograptus laticeps* Zone) yielding the same faunal assemblage as in Nová Vráž - Černošice. The Kosov hill specimen corresponds to an incomplete, slightly disarticulated theca with the aulacophore not visible, but likely present, at least proximally. *Diamphidiocystis* seems to be a relatively constant element in the lower to middle parts of the Králův Dvůr Formation, where several other specimens were found e.g. at Lejškov (see Lefebvre *et al*. this volume for locality details; Figs 2.11, 3e), in a metro excavation at Praha - Pankrác (Fig. 2.12) and also in a temporary exposure at Praha - Dolní Počernice (Fig. 2.13).

Material and methods

Material and institutional abbreviations

All known material of peri-Gondwanan diamphidiocystines from the Ordovician of the Czech Republic (Prague Basin), France (Brittany) and Morocco (Tafilalt) deposited in public collections was examined for this study. This material includes the three specimens of *Diamphidiocystis* sp. originally described by Chauvel (1981) from the Traveusot Formation (IGR.PAL.15216–15217, coll. Chauvel; IGR.PAL.15218, coll. Nion) and the fourth individual (MHNN.P.025931, coll. Lefebvre) from the same stratigraphic unit figured by Lefebvre (2003). However, most of the investigated material is new and has never been formally described and/or figured. New specimens of diamphidiocystines are the product of over 40 years of relatively intensive and careful field work in the Anti-Atlas (coll. Reboul), the Armorican Massif (coll. Catto, Chauvel, Claverie, Courville, Gaudu, Guillou) and the Barrandian area (coll. Kašička, Zicha). For comparison purposes, plaster casts of the holotype (SIU.4308) and two paratypes (SIU.4210 and UI.X5672) of *Diamphidiocystis drepanon* were also examined. This series of casts was originally belonging to the late Pr. G. Ubaghs (Liège University, Belgium). In 2006, these casts were donated by E. Poty (Liège University) to the palaeontological collections of Lyon 1 University (UCBL-FSL.424895–424897). Studied material is deposited in the following public collections: Czech Geological Survey, Prague, Czech Republic (CGS); Géosciences Rennes, Rennes, France (GR); Institut de Géologie de Rennes, Rennes, France (IGR); Muséum d'Histoire Naturelle, Marseille, France (MHNM); Muséum d'Histoire Naturelle, Nantes, France (MHNN); Prairie Research Institute at the University of Illinois, Urbana, USA (SIU and UI); and Collections de Paléontologie, Université Lyon 1, Villeurbanne, France (UCBL-FSL).

Methods

As all studied specimens are preserved as moulds, they were cast with latex. Latex casts were coated with ammonium chloride (NH_4Cl), so as to enhance contrast for camera lucida drawings and/or photographs. Observations and camera lucida drawings were made with a Zeiss SteREO Discovery.V8 stereomicroscope binocular. A Canon 5DSR camera equipped with a MP-E 100 mm macro lens was used for photographs.

Measurements were made directly on specimens and/or latex casts using the software AxioVision 4.8.2 running on a computer connected to the Zeiss AxioCam MRc5 digital camera mounted on the same Zeiss SteREO Discovery.V8 stereomicroscope binocular used for observation and drawings. Thecal width (TW) and thecal length (TL) were estimated following a protocol very similar to that used for *D. drepanon* (see Kolata & Guensburg 1979). TL was measured between the anterior-most portion of the theca (digital omitted), left of the aulacophore insertion, and the posterior thecal margin, along a line running parallel to the main body axis (i.e. symmetry axis of the appendage) and following the M'_1-M'_2 suture (Fig. 4). TW was estimated perpendicularly to TL, between the M_1-M_2 suture (right thecal edge) and the posterior-most extremity of M_7 (left thecal margin). Alternatively, when M_7 was not preserved, TL could be also measured perpendicularly to TW, between the M_1-M_2 suture (on the right) and the left extremity of M'_4.

Orientation and terminology

The terms used to describe the orientation and the main morphological features of the specimens follow those used by Ubaghs (1968) for mitrates and more specifically by Kolata & Guensburg (1979) for diamphidiocystines (Fig. 5). Consequently, as in all other stylophorans, the feeding appendage (aulacophore) is anterior and the anal opening, posterior (Fig. 5). However, because of the sinistral torsion of the theca in *Diamphidiocystis*, the anterior and posterior extremities of the organism are almost perpendicular to each other, instead of being more or less aligned along the main body axis, as this is the case in other anomalocystitids (Kolata & Guensburg 1979; Ruta 1999; Lefebvre 2003). Along the main body axis, the insertion of the aulacophore into the theca represents a landmark used to define the relative position of a structure next to it (proximal) or away from it (distal). In diamphidiocystines, the curved thecal margin opposite the aulacophore insertion is thus distal, but not posterior (Fig. 5). In stylophorans, the relative position of structures can be also defined perpendicularly to the main body axis (Ubaghs 1968): those situated away from it are abaxial, and those next to it, adaxial (Fig. 5). Similarly to the situation in other stylophorans, the theca of *Diamphidiocystis* is flattened, with two opposite and morphologically distinct surfaces (Fig. 5). The lower surface (originally in contact with the substrate) consists of few, large, tightly sutured, relatively thick skeletal elements: marginals and infracentrals (Kolata & Guensburg 1979; Lefebvre 2001, 2003). The opposite, upper thecal side (away from the substrate) is characterized by two large anterior plates (adorals) and numerous imbricate platelets (supracentrals) forming a relatively flexible and thin membrane (Lefebvre 2000*a*, 2003). As in other stylophorans, the presence of an anterior appendage and two distinct opposite thecal surfaces makes it possible to identify left and right sides in *Diamphidiocystis* (Fig. 5). However, contrary to the situation in all other stylophorans, the left thecal side of diamphidiocystines is also posterior (Kolata & Guensburg 1979). The identification of major skeletal elements in diamphidiocystines follows the revised scheme of thecal plate homologies proposed by Lefebvre & Ausich (2021) for mitrates and more specifically for anomalocystitids (Fig.

6). Abbreviations used below for designating skeletal elements are: A (adoral plate), D (digital, longest posterior spine), G (glossal, shortest posterior spine), M (marginal plate) and Z (zygal plate).

Systematic Palaeontology

Phylum **Echinodermata** Bruguière, 1791 (ex Klein, 1734)

Remarks. Stylophorans are considered derived echinoderms characterized by a single feeding appendage (aulacophore) bearing an ambulacral ray protected by two opposite (left and right) series of movable cover plates, and leading proximally to the mouth (see e.g. Ubaghs 1968; Kolata & Guensburg 1979; Chauvel 1981; Parsley 1988; Haude 1995; David *et al*. 2000; Lefebvre 2003; Scheffler *et al*. 2019; but see e.g. Dehm 1932; Jefferies 1968; Philip 1981; Kolata & Jollie 1982; Ruta & Bartels 1998 for alternative views). This interpretation is supported by the recent description of exceptionally preserved pyritized soft parts (ambulacral ray and podia, gut) in cornute stylophorans from the Lower Ordovician of Morocco (Lefebvre *et al*. 2019).

Class **Stylophora** Gill & Caster, 1960

Order **Mitrata** Jaekel, 1918

Suborder **Mitrocystitida** Caster, 1952

Family **Anomalocystitidae** Bassler, 1938

Subfamily **Diamphidiocystinae** Kolata & Guensburg, 1979

Diagnosis. A subfamily of anomalocystitid mitrates, with asymmetrical, reniform theca, oro-anal axis perpendicular to main axis; anterior thecal margin deeply encased at aulacophore insertion; very large scimitar-shaped digital recurved towards aulacophore; glossal small and slightly bent; A_0? inserted posteriorly to A_1 and A'_1; no placocystid plate; no ratchet sculpture on theca; numerous spike-shaped platelets along anal opening; proximal aulacophore consisting of 6–8 telescopic rings; lower surface of stylocone and ossicles bearing low median longitudinal keel and short blunt distal protuberance.

Remarks. In its original description, *Diamphidiocystis drepanon* was assigned to its own family (Diamphidiocystidae) and suborder (Diamphidiocystida) within the order Mitrata (Kolata & Guensburg 1979; see also Chauvel 1981). One of the main arguments supporting its placement in a distinct suborder was the possession of a single massive posterior sickle-shaped spine (see Kolata & Guensburg 1979; Chauvel 1981). However, peri-Gondwanan specimens of *Diamphidiocystis* possess two spines (D and G) (see below; Lefebvre *in* Ruta 1999; Lefebvre 2000*a*, 2003), and the reinterpretation of *D. drepanon*, suggests that what was interpreted as a small 'vestigial' glossal by Kolata & Guensburg (1979) could be considered a second spine, bringing this taxon's morphology more in line with typical anomalocystitids. Examination of plaster casts of *D. drepanon* paratypes indicates that the glossal spine is present, although small (e.g. paratype UI.X5672; see also Kolata & Guensburg 1979, pl. 1 fig. 4). Moreover, as already pointed out by several authors, the thecal plate patterns of *Diamphidiocystis* and 'regular' anomalocystitids are identical (e.g. Kolata & Guensburg 1979; Craske & Jefferies 1989; Ruta 1999; Lefebvre 2001). Following Lefebvre & Ausich (2021), *Diamphidiocystis* is thus considered as an anomalocystitid characterized by highly distinct, autapomorphic reniform thecal outlines resulting from the sinistral flexion of the distal (posterior) portion of a 'regular' anomalocystitid theca. *Diamphidiocystis* shares with anomalocystitids the possession of two posterior spines (D and G), resulting from the modification of two marginals. Consequently, *Diamphidiocystis* is here assigned to a small, distinct subfamily (Diamphidiocystinae) within the family Anomalocystitidae. The original diagnosis of this monogeneric clade is modified so as to accommodate morphological features of the two herein included species: *D. drepanon* Kolata & Guensburg, 1979 (Fig. 6a–b) and *D. regnaulti* sp. nov. (see below; Figs 6c–d, 7). The most obvious apomorphy of diamphidiocystines is the sinistral flexion of their theca. Diamphidiocystines also differ from allanicytidiines by the absence of a robust, ploughshare-like stylocone, and from anomalocystitines by the absence of a distinct, rounded placocystid plate on their upper thecal surface (see Lefebvre & Ausich 2021). Comparison with the earliest known, yet undescribed anomalocystitid from the Floian of Morocco (see Noailles & Lefebvre 2012; Lefebvre & Ausich 2021) indicates that several morphological features of peri-Gondwanan diamphidiocystines are plesiomorphic. For example, the presence of a vestigial right infracentral area, the unorganized plating of the left infracentral area and the possession of imbricate supracentrals (see below) are characters shared with early mitrocystitids and the Floian anomalocystitid but generally lost in both allanicytidiines and anomalocystitines. Although a phylogenetic analysis of anomalocystitids is far beyond the scope of this study, it is very likely that, based on character distribution, diamphidiocystines form a small clade of early, highly autapomorphic anomalocystitids, and could represent the sister-group to the two other subfamilies (see Ruta 1999).

Genus *Diamphidiocystis* Kolata & Guensburg, 1979

Type species. *Diamphidiocystis drepanon* Kolata & Guensburg, 1979

Diagnosis. as for the family

Remarks. Two species are assigned here to the genus *Diamphidiocystis*: *D. drepanon* (latest Katian–early Hirnantian, USA; Fig. 6a–b) and D. *regnaulti* sp. nov. (late Darriwilian–late Katian; Czech Republic, France, Morocco; Figs 6c–d, 7). In many respects, the stratigraphically earlier peri-Gondwanan form is morphologically more plesiomorphic than the younger Laurentian one. For example, the occurrence of a vestigial right infracentral area, the presence of several left infracentrals and the imbricate plating of supracentrals are characters shared by *D. regnaulti* sp. nov. with early mitrocystitids and the Floian anomalocystitid. The imbricate plating of (at least part of) the supracentral area is also occurring in early anomalocystitines (e.g. *Ateleocystites*, *Barrandeocarpus*; see Ubaghs 1979; Kolata & Jollie 1982; Ruta 1997*a*, 1999; McDermott & Paul 2017; Lefebvre & Ausich 2021). Consequently, it is very likely that the loss of the right infracentral area, the reduction of the number of left infracentrals, and the acquisition of a supracentral area made of few, tesselate elements represent features acquired independently within diamphidiocystines (*D. drepanon*) and other anomalocystitids (see Lefebvre & Ausich 2021). Morphological features and stratigraphic ranges of the two species of diamphidiocystines are in good agreement with each other and are supporting the view that the North American form very likely derived from a peri-Gondwanan ancestor.

Diamphidiocystis regnaulti sp. nov.

Figures 3–5, 6c–d, 7–14

1981 *Diamphidiocystis* sp. – Chauvel, p. 85, text-fig. 5, pl. 3 figs 11–13

1986 *Diamphidiocystis* sp. – Chauvel, p. 79

1999 *Diamphidiocystis* sp. – Ruta, p. 360

2000*a* *Diamphidiocystis* sp. – Lefebvre, p. 116, fig. 6.5

2001 *Diamphidiocystis* sp. – Lefebvre, p. 611

2003 *Diamphidiocystis* sp. – Lefebvre, p. 548, text-fig. 24C

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

2006 *Diamphidiocystis* sp. – Lefebvre *et al.*, p. 496, fig. 6.30

2007 *Diamphidiocystis* sp. – Hunter *et al.*, p. 78, table 1

2007*a* *Diamphidiocystis* sp. – Lefebvre, p. 186

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

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

2010*b* *Diamphidiocystis* sp. – Lefebvre *et al.*, p. 38

2014 *Diamphidiocystis* sp. – Noailles *et al.*, p. 458

2015 *Diamphidiocystis* sp. – Lefebvre *et al.*, p. 303

2018 *Diamphidiocystis* sp. – Lebrun, p. 122

Derivation of name. This species is dedicated to Serge Régnault for his contribution to the knowledge of Palaeozoic echinoderms from the Armorican Massif (France) and Morocco.

Holotype. IGR.PAL.15217 (coll. Chauvel; Figs 8a–b, 12a, 14a): original specimen described by Chauvel (1981, text-fig. 5a, pl. 3 figs 11-12), preserved in a small concretion (part and counterpart). Almost complete, partly disarticulated lower thecal surface (M_7 and probably M'_6 missing), with distally incomplete glossal and slightly displaced digital and M'_4. Almost complete, slightly collapsed upper thecal surface with paired adorals (A'_1, A_1), large fan-shaped A_0?, over 20 imbricate supracentrals, part of marginal frame, and posterior spines. At least six slightly disarticulated proximal rings preserved in both part and counterpart. Stylocone and more distal portion of aulacophore missing.

Paratypes. Ten additional specimens from the same stratigraphic unit as the holotype (Traveusot Formation) are designated as paratypes. GR/PC.1796 (coll. Courville) corresponds to a small concretion (part and counterpart) containing a nearly complete, slightly disarticulated theca (left infracentral area and posterior region poorly preserved, distal half of digital and A'_1 missing), as well as proximal rings and part of stylocone (Figs 8e–f, 12e, 14b). IGR.PAL.15204 (coll. Chauvel) is an almost complete lower thecal surface (digital missing, only proximal-most extremity of G present) preserved both in external (part) and internal (counterpart) aspects in a concretion containing also trilobite fragments. Aulacophore is missing, but internal structures (e.g. anterior transverse groove, apophyses, left scutula, septum) are well preserved (Fig. 10c–d). IGR.PAL.15216 (coll. Chauvel) corresponds to the second specimen originally figured by Chauvel (1981, text-fig. 5b, pl. 3 fig. 13). It exposes a remarkably preserved, complete, only slightly disarticulated lower thecal surface (no counterpart), with no appendage (Figs 10b, 12f). IGR.PAL.15218 (coll. Nion) is the third specimen illustrated by Chauvel (1981, text-fig. 5c). It consists of some scattered aulacophore remains and a relatively complete upper thecal surface preserved both in upper (external) and lower (internal) aspects. IGR.PAL.15842 (coll. Chauvel) is associated to strophomenid brachiopods in a relatively large concretion (part and counterpart). It corresponds to an almost complete upper thecal surface (most of D missing) exposed in upper (external) and lower (internal) views, associated to disarticulated appendage elements (proximal rings and stylocone) (Figs 11f, 14d). IGR.PAL.15910 (coll. Chauvel) is a small, elongate concretion broken into four pieces and containing two side by side, slightly disarticulated, incomplete diamphidiocystine thecae. An isolated, fully articulated portion of distal aulacophore (cover plates and ossicles) is remarkably preserved on two pieces (part and counterpart) of the concretion. MHNN.P.025931 (coll. Lefebvre) is a small concretion (part and counterpart) yielding a slightly disarticulated, nearly complete lower thecal surface (G and posterior part missing), with well exposed aulacophore apophyses due to the absence of proximal rings (Fig. 11e; see also Lefebvre 2003, text-fig. 24C). The opposite (upper) thecal surface is very poorly preserved. UCBL-FSL.170938 (coll. Guillou) corresponds to a small concretion (part and counterpart) containing articulated proximal rings and a partly disarticulated, almost complete theca with well-preserved posterior area (small anal platelets) on upper surface (Figs 8c–d, 12c, 14c). UCBL-FSL.712498 (coll. Gaudu) exposes a slightly disarticulated, nearly complete lower thecal surface (no counterpart), with stylocone and dissociated proximal rings (Figs 10a, 12d). UCBL-FSL.713377 (coll. Catto) is an almost complete theca (part and counterpart) with well-preserved, fully articulated proximal aulacophore and stylocone (Figs 11c–d, 12b, 14e).

Other material. Additional material from the Middle Ordovician of Brittany includes seven specimens corresponding to incomplete and/or poorly preserved thecae (IGR.PAL.15805, 809, coll. Chauvel; MHNN.P.035224, coll. Claverie; UCBL-FSL.170937, 170951, coll. Guillou) and isolated thecal plates (IGR.PAL.15908, 15909, coll. Chauvel). Two fully articulated individuals (aulacophore and theca) from the Upper Ordovician of Morocco are also included: MHNM.15690.28 and 37 (coll. Reboul). Both specimens are preserved on isolated slabs (no counterpart). One of them (MHNM.15690.28) is exposed in lower aspect (Figs 9a, 13a) and the other one (MHNM.15690.37) in upper view (Figs 9b, 13b). Nine individuals from the late Darriwilian (CGS.OZ.151, 291–292, coll. Zicha) and the Upper Ordovician (CGS.LK.18–19, coll. Kašička; CGS.OZ.120–121, 293–294, coll. Zicha) of Bohemia were also studied. CGS.LK.18 (Figs 11b, 14f) is a partly disarticulated lower thecal surface in upper (internal) aspect (no counterpart), exposing well preserved internal structures (e.g. left scutula, septum). CGS.LK.19 corresponds to a sligthly disarticulated, incomplete theca (part and counterpart). CGS.OZ.120 exposes a large portion of lower thecal surface in upper (internal) aspect, with only D preserved on the counterpart. CGS.OZ.121 (Fig. 3f) is a better preserved specimen, with proximal rings and almost complete (G missing) theca (part and counterpart). CGS.OZ.151 (Figs 3c, 10e–f, 13c–d) is a small concretion (part and conterpart) containing a slightly disarticulated, nearly complete theca (D missing), with proximal rings, stylocone and scattered more distal elements (ossicles, cover plates). CGS.OZ.291 (Fig. 3a), 292 (Fig. 3b) and 293 (Fig. 3d) are preserved in shales (all with part and counterpart). They consist of a nearly complete, more or less slightly disarticulated theca, with proximal rings (CGS.OZ.291, 293), stylocone and at least five ossicles and associated cover plates (CGS.OZ.292). Finally, CGS.OZ.294 (Fig. 3e) corresponds to a complete, fully articulated theca (with both D and G), proximal rings and stylocone (part and counterpart). However, precise plate boundaries are not clearly distinct.

Horizon and locality. The holotype was collected in the upper part of the Traveusot Formation, late Darriwilian (Dw3, *H. teretiusculus* graptolite Zone, Middle Ordovician; Fig. 1.2) at Traveusot (main field, between the farm and S of the D39 road between Guichen and Laillé), Guichen (Ille-et-Vilaine, Brittany, France; see Lefebvre *et al.* this volume). The type locality yielded also six paratypes (IGR.PAL.15204, 15216, 15218, 15842, 15910, and UCBL-FSL.712498) and four other specimens (IGR.PAL.15805, 15809, 15908, 15909). On the opposite (north) side of the D39 road, additional material was collected in the same stratigraphic horizons at the two nearby localities of le Domaine, Guichen (paratypes GR/PC.1796, MHNN.P.025931, UCBL-FSL.170938, and specimens UCBL-FSL.170937, 170951) and la Saudrais, Guichen (paratype UCBL-FSL.713377). In the Armorican Massif, another specimen (MHNN.P.035224) was found in the upper member (Guernanic unit) of the Postolonnec Formation, late Darriwilian (Dw3, Middle Ordovician; Fig. 1.1), in the abandoned slate quarry of Guernanic, Gourin, Morbihan, Brittany, France (see Hunter *et al*. 2007). The two Moroccan specimens (MHNM.15690.28, 37) were sampled in the Izegguirene Formation, early Sandbian (Sa1, Upper Ordovician; Fig. 1.9) at Bou Nemrou, 4 km NE of the small village of Ksar Tamarna, about 30 km SW of Erfoud, Jbel Tijarfaïouine, western Tafilalt, eastern Anti-Atlas, Morocco (see Lefebvre *et al*. this volume). In the Prague Basin (Czech Republic), CGS.OZ.151 was collected at Chyňaya, Malé Přílepy, about 6 km NE of Beroun (Fig. 2.1), in late Darriwilian levels (Dw3, Middle Ordovician) of the Dobrotivá Formation (Fig. 1.3; see Lefebvre *et al.* this volume). Two other specimens (CGS.OZ.291–292) were found in the upper part of the same stratigraphic unit (Dobrotivá Formation, next to the Darriwilian–Sandbian boundary; Fig. 1.3) at Chrustenice, about 7 km NE of Beroun (Fig. 2.2). Five poorly preserved unregistered specimens of *Diamphidiocystis* were observed in the overlying Libeň Formation, early Sandbian (Sa1, Upper Ordovician; Fig. 1.4), at Lhotka (Fig. 2.3), about 2 km N of Beroun (O. Zicha, pers. obs.). Two other individuals from Bohemia (CGS.LK.18–19) were sampled in the lowermost part of the Vinice Formation, latest Sandbian–earliest Katian (Sa2–Ka1, Upper Ordovician; Fig. 1.5) in a temporary excavation made at the extremity of Borová street, along the slope of Děd Hill, Zahořany, W of Beroun, Prague Basin, Czech Republic (Fig. 2.5; see Lefebvre *et al.* this volume). Recently, two additional poorly preserved specimens of *Diamphidiocystis* were collected in the same stratigraphic unit (Vinice Formation), but in a distinct locality of the Barrandian area (Hředle; Fig. 2.4) (O. Zicha, pers. obs.). One unregistered specimen was collected in the Zahořany Formation, early Katian (Ka1, Upper Ordovician; Fig. 1.6) at Levín (Fig. 2.6; O. Zicha, pers. obs.). The Bohdalec Formation, early Katian (Ka2, Upper Ordovician; Fig. 1.7), yielded at least two individuals: CGS.OZ.293 was found in a former brickyard near Neumětely, about 13 km SW of Beroun (Fig. 2.8), and the other, unregistered specimen, at Praha-Harfa (Fig. 2.7). In the Prague Basin (Czech Republic), the Králův Dvůr Formation, late Katian (Ka3–4, Upper Ordovician; Fig. 1.8), yielded several individuals of *Diamphidiocystis*: CGS.OZ.120 is from Kosov hill, Králův Dvůr (Fig. 2.10), CGS.OZ.121, from Nová Vráž, Černošice (Fig. 2.9; see Lefebvre *et al*. this volume), CGS.0Z.294, from Lejškov (Fig. 2.11; Lefebvre *et al*. this volume), and additional, unregistered material from Praha - Pankrác (Fig. 2.12) and Praha-Dolní Počernice (Fig. 2.13) (O. Zicha, pers. obs.).

Diagnosis. A species of *Diamphidiocystis* with strongly concave posterior margin encased between two 'horns' formed by M_7 (distally) and both M'_3 and M'_4 (proximally); vestigial right infracentral area; polyplated left infracentral area; strong anterior crest on lower surface of M’$_1$ and M’$_2$; no serrations on digital; supracentrals numerous and imbricate.

Description. Small-sized (5 < TW < 12 mm), strongly asymmetrical, reniform to 'bagpipe-shaped' (*sensu* Chauvel 1981) theca bearing two movable, unequal, elongate, recurved posterior spines (D and G) (Fig. 7). Theca transversely elongate (TW/TL ≈ 1.4), flattened, consisting of two opposite convex surfaces. Anterior thecal margin sinuous, W-shaped, with two distinct concavities separated by three well-defined, anteriorly protruding areas. Along anterior edges of M'$_2$, M'$_3$ and M'$_4$, left concavity forming relatively wide and shallow embayment, with similar extension on both thecal surfaces. Left anterior embayment abaxially in continuity with regularly curved, concave adaxial edge of digital. On lower thecal side, right anterior concavity corresponding to narrow, relatively deep gulf for aulacophore insertion delimited by M$_1$ and M'$_1$. On opposite (upper) surface, right anterior concavity shallower and partly roofed by adorals. Thecal height maximal between left and right anterior concavities, between anterior portions of M'$_1$ and M'$_2$ (below) and A'$_1$ (above), immediately left of aulacophore insertion. Away from this region, theca regularly decreasing in height both abaxially and distally. Right portion of distal thecal margin strongly convex, regularly curved along distal edges of M$_2$, Mc and M$_3$. Left part of distal thecal margin shorter, slightly concave, forming wide, shallow embayment from glossal insertion on M$_3$ (on the right) to posterior extremity of horn-like protuberance produced by M$_7$ (on the left). Posterior (left) thecal margin concave, corresponding to wide, shallow embayment delimited by M$_7$ horn-like protuberance (distally) and digital-bearing narrow, straight, delicate process produced by M'$_3$ and M'$_4$ (anteriorly) (e.g. CGS.OZ.151, 294, GR/PC.1796, IGR.PAL.15842, MHNM.15690.37, UCBL-FSL.713377). Lower thecal side rigid, made of few, thick, relatively large, tesselate skeletal elements forming well-defined marginal frame (M'$_{1–4}$, M'$_6$, M$_{1–2}$, Mc, M$_{3–4}$, M$_{6–7}$) and more irregularly plated central area (Z, infracentrals). Lower thecal surface delimited by relatively wide peripheral flange extending from right of aulacophore insertion (anteriorly), around right thecal lobe (along M$_1$ and M$_2$) to distal thecal margin and glossal insertion (along Mc and M$_3$). Glossal almost flat, extending horizontally at same level as, and in continuity with, peripheral flange (e.g. CGS.OZ.294, IGR.PAL.15216, 15842, UCBL-FSL.713377).

Peripheral flange delimiting relatively inflated, markedly convex portions of lower thecal surface (e.g. CGS.OZ.151, 294, GR/PC.1796, IGR.PAL.15216, 15842, UCBL-FSL.170938). On both M'$_1$ and M$_1$, narrow, depressed, elongate U-shaped area extending around aulacophore insertion on lower thecal surface. Well-defined sharp anterior transverse crest running along transition between raised vertical anterior edges of left anterior marginals (M'$_{1-4}$) and their almost perpendicular, flat to inflated portions on lower thecal surface (e.g. holotype, GR/PC.1796, IGR.PAL.15216, UCBL-FSL.170938, 713377). Upper thecal surface gently convex, consisting of two large, thick, almost symmetrical anterior adorals on both sides (left and right) of aulacophore insertion, and numerous, fan-shaped, imbricate, unorganized, thin skeletal elements (supracentrals) decreasing in size both distally and posteriorly (e.g. holotype, IGR.PAL.15842, MHNM.15690.37, UCBL-FSL.713377).

M$_1$ large, elongate, morphologically complex anterior marginal, extending obliquely from right anterior thecal corner (antero-abaxially) to aulacophore insertion (postero-adaxially) (see e.g. GR/PC.1796, UCBL-FSL.170938; Figs 8a, c, e, 9a, 10a–b, e, 12a, c–f, 13a, c). Distal margin of M$_1$ long, almost straight to slightly sinuous along suture with M$_2$. Adaxially, M$_1$ in contact with M'$_1$ along short, straight suture, and forming with it deeply concave gulf for aulacophore insertion. Right anterior margin of M$_1$ rounded and modified into wide, delicate anterior portion of peripheral flange (see e.g. CGS.OZ.294, GR/PC.1796, UCBL-FSL.170938). Along aulacophore insertion and in continuity with peripheral flange, lower surface of M$_1$ strongly depressed. Distally to peripheral flange and aulacophore insertion, lower side of M$_1$ relatively convex, and regularly increasing in height postero-adaxially along suture with M$_2$. Distally to aulacophore insertion, anterior margin of M$_1$ forming relatively high, strongly concave vertical wall (right aulacophore apophysis). Right apophysis separated from lower thecal surface by sharp, thin, delicate crest (e.g. holotype, GR/PC.1796, MHNN.P.025931, UCBL-FSL.170938). Right apophysis transversely elongate, subtriangular in shape, with vertical contact (adaxially) along symmetrical left apophysis (borne by M'$_1$), almost straight upper edge and longer, regularly curved lower margin (e.g. MHNN.P.025931). Upper abaxial portion of right apophysis very likely bearing delicate process (apophysis horn). Adaxial tip of right apophysis horn not observed, but abaxial base of it preserved in some specimens (e.g. IGR.PAL.15204). Abaxially to apophysis horn, right scutula corresponding to well-defined, small, transversely elongate cup-shaped structure along anterior margin of M_1 (e.g. IGR.PAL.15204, UCBL-FSL.713377). Posteriorly to upper margin of right apophysis, transverse anterior groove corresponding to well-defined, narrow, transversely elongate depression extending from right scutula (abaxially) to right anterior extremity of septum (on the left, on M'_1) (e.g. IGR.PAL.15204). Internal (upper) surface of M_1 flat to slightly concave, with the exception of its strongly raised, convex antero-adaxial margin along right apophysis (e.g. CGS.LK.18, IGR.PAL.15204).

M_2 very large, elongate, subtriangular skeletal element forming posterior half of right anterior thecal lobe (with M_1) (e.g. GR/PC.1796, UCBL-FSL.170938; Figs 8a, c–f, 9a, 10, 12a, c–f, 13a, c–d, 14b–c). Anterior margin of M_2 particularly long, oblique to main body axis, almost straight to slightly sinuous along contact with M_1. Adaxial (left) margin of M_2 much shorter, straight, along suture with Mc. Distal edge of M_2 elongate, gently curved, regularly convex, contributing to about one third of distal thecal margin. On lower thecal side, distal margin of M_2 forming delicate, wide peripheral flange (e.g. CGS.OZ.294, GR/PC.1796, UCBL-FSL.170938). Anterior portion of lower surface of M_2 more strongly concave, regularly increasing in height adaxially, along contact with M_1 (e.g. GR/PC.1796, MHNN.P.025931, UCBL-FSL.170938). Internal (upper) aspect of M_2 conversely deeply concave antero-adaxially, with raised, nearly vertical walls leading to flat peripheral flange (e.g. holotype, GR/PC.1796, UCBL-FSL.170938).

Next distal marginal, Mc, much shorter than M_2, relatively broad, almost as wide as long, quadrangular to subpentagonal in shape (e.g. GR/PC.1796, IGR.PAL.15216, UCBL-FSL.170938; Figs 8a, c, e–f, 9a, 10–11, 12a, c–f, 13a, c–d, 14). Lateral edges of Mc almost straight, with right one (along M_2) longer than left one (along M_3). Distal and anterior margins of Mc both slightly convex, with proximal one (in contact with Z) shorter than distal one. On lower thecal surface, distal half of Mc particularly flat, contributing to delicate peripheral flange (e.g. CGS.OZ.151, 294, GR/PC.1796, IGR.PAL.15216, 15842, UCBL-FSL.170938). In contrast, anterior portion of Mc convex, domed, strongly increasing in height proximally. In internal (upper) aspect, anterior part of Mc conversely markedly concave and separated from distal peripheral flange by nearly vertical wall (e.g. GR/PC.1796, UCBL-FSL.170938).

M_3 small, broad, pentagonal, almost in median position along distal thecal margin (e.g. GR/PC.1796, IGR.PAL.15216, UCBL-FSL.170938; Figs 8, 9a, 10–11, 12a, c–f, 13a, c–d, 14). M_3 sutured to three neighbouring plates by relatively short and straight sutures: Mc (on the right), Z (antero-adaxially) and M_6 (antero-abaxially). Distal (outer) margin of M_3 straight to slightly convex, along flattened, delicate, left extremity of peripheral flange (e.g. CGS.OZ.151, 294, GR/PC.1796, IGR.PAL.15216, 15842, UCBL-FSL.170938). Abaxial (left) edge of M_3 short, bearing well-defined socket for glossal articulation. On lower thecal surface, anterior portion of M_3 slightly raised along M_6 and Z sutures, though decreasing in height abaxially. Internal (upper) surface of M_3 slightly concave anteriorly, with low vertical walls leading to flat peripheral flange (e.g. GR/PC.1796, UCBL-FSL.170938).

Glossal gently curved, elongate, narrow, flattened, blade-shaped element adaxially articulated to M_3 by a small process (ball) (e.g. CGS.LK.18, CGS.OZ.294, IGR.PAL.15216, 15842; Fig. 3c, e, 8–9, 10a–b, e–f, 11a–c, f, 12, 14). Glossal slightly oblique to main body axis, extending in continuity to peripheral flange along, and more or less parallel to, left distal thecal margin. Anterior edge of G slightly raised, regularly curved, slightly concave. Opposite, distal margin of G flattened, gently curved, convex, with sharp outer edge. Abaxial extremity of G blunt, extending more posteriorly than M_7 and anal opening.

M_6, relatively elongate, small, pentagonal, slightly oblique to main axis, forming most of left portion of distal thecal margin (e.g. CGS.OZ.151, GR/PC.1796, IGR.PAL.15216, UCBL-FSL.713377; Figs 8a, c–f, 9, 10a–b, e–f, 11b–f, 12–13). M_6 tightly sutured to four skeletal elements along straight, relatively short sutures: M_3 (on the right), Z (antero-adaxially), one infracentral plate (anteriorly), and M_7 (antero-abaxially). Distal margin of M_6 almost straigth. Lower surface of M_6 flat to very slightly convex. Upper (internal) surface of M_6 nearly flat, with very sligthtly raised distal edge.

M_7, small, massive, broad, sub-quadrangular, forming short, blunt, horn-like process at left distal extremity of theca (see e.g. CGS.OZ.151, GR/PC.1796, IGR.PAL.15216, 15842, UCBL-FSL.713377; Figs 8c, e–f, 9, 10a–c, e, 11b–d, f, 12b–f, 13b–c, 14b, e). M_7 adaxially in contact with both M_6 (distally) and M'_6 (anteriorly), along relatively straight, short sutures. Outer (abaxial) edge of M_7 strongly convex, rounded, forming short, blunt outgrowth. M_7 with slightly convex lower surface and, conversely, slightly concave internal (upper) surface.

M'_6, small, elongate, narrow, polygonal, forming most of posterior thecal margin, below periproct (Figs 8c–f, 11c, 12b–c). M'_6 distally in contact with M_7, and adaxially sutured to several infracentrals (e.g. UCBL-FSL.713377). Lower surface of M'_6 slightly convex. Upper (internal) surface of M'_6 almost flat, with slightly raised left (outer) margin.

M'_1, large, wide, antero-distally elongate, sub-triangular in shape, wider distally, and tapering anteriorly (e.g. IGR.PAL.15216, 15805, MHNN.P.025931, UCBL-FSL.170938; Figs 8a–c, 9a, 10a–e, 11a–c, e, 12, 13a, c, 14f). M'_1 distally in contact with three skeletal elements along relatively short, straight sutures: M_1 (adaxially), right infracentral (distally) and Z (distalo-abaxially). Right anterior margin of M'_1 long, sinuous, curved, distally concave along aulacophore insertion, and more convex anteriorly. Left anterior margin of M'_1 elongate, straight to slightly concave along suture with M'_2. Left of aulacophore insertion, M'_1 contributing with adjacent marginal M'_2 to strong, anteriorly protruding thecal re-entrant. Anterior-most portion of M'_1 forming short, semi-circular, vertical wall, slightly oblique to main body axis, delimited abaxially by suture with M'_2, below and adaxially by sharp anterior crest forming delicate anterior collar extending abaxially into M'_2 (e.g. holotype, IGR.PAL.15216, MHNN.P.025931, UCBL-FSL.170938, 713377). On the right, distal portion of collar giving rise to sharp anterior edge of M'_1 on lower thecal surface and, more adaxially, delicate crest below left aulacophore apophysis. Left apophysis corresponding to relatively high, transversely elongate, anteriorly concave cup-shaped vertical wall borne by M'_1, distally to aulacophore insertion (e.g. MHNN.P.025931). External morphology of left apophysis identical, although mirror-inverted, to that of right apophysis (see above). Lower surface of M'_1 depressed along aulacophore insertion, but strongly convex, domed along M'_2 suture and distally. On upper thecal surface, sharp, delicate, straight upper margin of left apophysis probably bearing, abaxially, delicate horn-like transwerse process (base of left apophysis horn preserved in IGR.PAL.15204). Left scutula corresponding to small rounded, cup-shaped structure at anterior margin of M'$_1$ in contact with, and abaxial to, base of left apophysis horn (CGS.LK.18, IGR.PAL.15204). On upper (internal) surface of M'$_1$, septum corresponding to strong, sharp, asymmetrical ridge inserted anteriorly in between left scutula and left apophysis horn (CGS.LK.18, IGR.PAL.15204). Course of septum almost straight, more or less parallel to M'$_1$-M$_1$ suture, across internal surface of M'$_1$. Left flank of septum almost vertical, whereas right wall wider and more gently sloping. Posteriorly to upper anterior edge of left apophysis, internal surface of M'$_1$ bearing left portion of transverse anterior groove extending from M$_1$ (on the right) to antero-adaxial extremity of septum (see above; IGR.PAL.15204). Most of internal (upper) surface of M'$_1$ strongly depressed, with the exception of raised anterior margin (next to M'$_2$ suture; see above), left apophysis, and septum.

M'$_2$ wide, broad, abaxially tapering, sub-pentagonal, largely contributing to anterior thecal margin (e.g. GR/PC.1796, IGR.PAL.15216, MHNN.P.025931, UCBL-FSL.170938, 713377; Figs 8a, c, e, 9a, 10a–e, 11a–c, e, 12, 13a, c, 14f). Adaxial edge of M'$_2$ elongate, slightly convex along suture with M'$_1$. Distal portion of M'$_2$ in contact with both Z (adaxially) and left infracentral area (abaxiallly) along relatively straight sutures. Left margin of M'$_2$ particularly short along contact with M'$_3$. Lower surface of M'$_2$ flat to slightly convex, delimited anterioly by sharp crest (e.g. GR/PC.1796, IGR.PAL.15216, MHNN.P.025931, UCBL-FSL.170938). Anterior side of M'$_2$ forming markedly concave, almost vertical wall, particularly high along suture with M'$_1$ and regularly decreasing in height abaxially (e.g. holotype). Conversely, internal (upper) surface of M'$_2$ strongly depressed, distally to high, anterior, vertical edge (e.g. CGS.LK.18, CGS.OZ.121, UCBL-FSL.713377).

M'$_3$ small, broad, almost as long and wide, quadrangular to sub-pentagonal, forming base of left anterior digital-bearing process, oblique to main body axis (e.g. holotype, GR/PC.1796, IGR.PAL.15216, 15842, UCBL-FSL.170938, 713377; Figs 8a, c, e–f, 9a, 10a–c, e, 11a–c, e, 12, 13a, c, 14a–b, f). M'$_3$ sutured to both M'$_2$ (adaxially) and M'$_4$ (antero-abaxially) along relatively short, straight sutures. Distal margin of M'$_3$ separated from M'$_6$ by small intercalated infracentral (e.g.

UCBL-FSL.170938, 713377). Postero-abaxial edge of M'$_3$ particularly short, straight, contributing to posterior thecal margin. Lower surface of M'$_3$ flat to slightly convex, separated from low, vertical anterior side by particulatly sharp edge. Internal (upper) surface of M'$_3$ with wide, oblique, elongate, slightly depressed area delimited by low vertical walls along anterior and posterior edges (e.g. CGS.LK.18, CGS.OZ.121, GR/PC.1796, IGR.PAL.15842).

M'$_4$ slightly shorter than M'$_3$, quadrangular, forming posterior extremity of delicate digital-bearing process (e.g. holotype, GR/PC.1796, UCBL-FSL.170938, 713377; Figs 8a–c, e–f, 9a, 10a–c, e, 11b–c, e–f, 12, 13a, 14a–b, d–f). M'$_4$ contributing to both anterior and posterior thecal margins. Adaxial edge of M'$_4$ in contact with M'$_3$ along short suture. Left margin of M'$_4$ short, almost straight, bearing socket for digital insertion. Lower surface of M'$_4$ nearly flat. M'$_4$ semi-cylindrical in upper aspect, with narrow, elongate, central groove delimited by low, raised anterior and posterior margins (e.g. CGS.LK.18, GR/PC.1796, IGR.PAL.15842).

Digital corresponding to relatively wide, elongate, flattened, blade-like, anterior spine recurved towards distal aulacophore (antero-adaxially) (e.g. holotype, CGS.LK.18, CGS.OZ.120, 121, 291, 294, IGR.PAL.15216, MHNM.15690.37, MHNN.P.025931, UCBL-FSL.170938; Figs 3a–b, d–f, 8, 9b, 10a–b, 11a–b, d–e, 12a, c–d, f, 13a–b, 14a–c, e–f). Adaxial (right) margin of D slightly raised, markedly concave, more strongly curved posteriorly, almost straight anteriorly. Opposite (left) portion of D flattened, with sharp, outer cutting edge, clearly convex, more strongly curved posteriorly than anteriorly. Width of D almost constant, except at anterior, rounded tip. Opposite (posterior) extremity of digital with well-defined ball for articulation with M'$_4$ socket (e.g. holotype).

Zygal plate (Z) relatively small, broad, polygonal, in central position on lower thecal surface (Figs 8a, c, e, 9a, 10a–e, 11a–c, e, 12, 13a, c, 14f). Z in contact with M'$_1$ (antero-adaxially), Mc (distalo-adaxially), M$_3$ (distally), M$_6$ (distalo-abaxially) and infracentrals (e.g. CGS.OZ.151, IGR.PAL.15216, UCBL-FSL.170938, 713377). Lower surface of Z almost flat. Upper (internal) side of Z bearing straight, distal portion of asymmetrical septum, with nearly vertical adaxial (rigth) flank and more gently sloping abaxial side (CGS.LK.18, IGR.PAL.204). Septum rapidly decreasing in height across internal surface of Z.

Right infracentral area particularly reduced, possibly absent in some individuals (e.g. IGR.PAL.15216, UCBL-FSL.170938; Figs 8c, 10b, 12c, f), sometimes corresponding to very small (e.g. IGR.PAL.15805; Figs 11a, e, 12d) or larger polygonal skeletal element inserted in between M'$_1$, M$_1$, M$_2$, Mc and Z (e.g. IGR.PAL.15204; Figs 9a, 10c, 13a). Left infracentral area more extensive, forming irregular tesselate pavement of small-sized polygonal plates framed by three anterior marginals (M'$_1$, M'$_2$, M'$_3$), Z, and three posterior marginals (M$_6$, M$_7$ and M'$_6$) (Figs 8a, c, e, 10c, e, 11c, 12). Left infracentrals variable in size, at least three (e.g. IGR.PAL.15216) and up to five in number (e.g. UCBL-FSL.713377). Left infracentral area extending posteriorly to left (outer) thecal margin, in between M'$_2$ and M'$_3$ (anteriorly) and M'$_6$ (posteriorly) (e.g. UCBL-FSL.170938, 713377). All infracentrals with flat lower (external) and upper (internal) surfaces.

Left and right adorals (A'$_1$, A$_1$) relatively broad, thick, almost symmetrical skeletal elements framing aulacophore insertion on both anterior thecal margin and upper surface (see e.g. holotype, CGS.OZ.151, MHNM.15690.37, UCBL-FSL.713377; Figs 8b, d, f, 9b, 10f, 11f, 13b, d, 14a–e). Anterior portion of each adoral, forming low, nearly vertical, sub-triangular wall, strongly tapering adaxially, with short straigth suture along contact with underlying anterior marginal, and elongate concave adaxial edge along proximal rings (tectals). Particularly sharp anterior transverse crest at junction between anterior vertical part of adorals and their much wider distal portion on upper thecal surface (e.g. holotype, GR/PC.1796, MHNM.15690.37). Upper (external) surface of distal part of adorals sub-quadrangular, transversely elongate, smooth, flat to slightly domed, with relatively straight to slightly concave sharp anterior edge and more gently curved, convex, opposite (distal) margin. On upper thecal surface, A'$_1$ and A$_1$ in contact with each other, anteriorly, along very short adaxial suture along main body axis (e.g. holotype, MHNM.15690.37). On internal (lower) surface of left adoral, small anterior, cup-shaped structure delimited by well-defined rim probably corresponding to left co-operculum (e.g. IGR.PAL.15842, 15910). Left co-operculum in close contact with underlying left scutula borne by M'$_1$. Lower (internal) surface of A'$_1$ slightly concave, bearing at least two, possibly three shallow grooves (putative 'palmar system' *sensu* Chauvel 1941) converging towards distal abaxial edge of left co-operculum (IGR.PAL.15842). Right co-operculum possibly present on internal surface of A_1 (above right scutula), but not observed in available material.

Distally and posteriorly to adorals, supracentral area consisting of several tens of slightly convex skeletal elements forming thin, imbricate pavement (e.g. holotype, CGS.OZ.291, GR/PC.1796, IGR.PAL.15218, 15842, MHNM.15690.37, UCBL-FSL.170938, 713377; Figs 8b, d, f, 9b, 10f, 11d, f, 13b, d, 14a–e). On left part of theca, outlines of supracentral area matching very closely those of underlying marginal frame along $M'_{2–4}$, M'_6, M_4, $M_{6–7}$. Along M_2, Mc and M_3, distal edge of supracentral area, regularly curved, strongly convex, running along anterior edge of peripheral flange. Supracentrals fan-shaped, with rounded, strongly convex free (outer) margin, strongly decreasing in size both distally and posteriorly (e.g. holotype, IGR.PAL.15218, 15842, UCBL-FSL.713377). Upper (external) surface of supracentals entirely smooth. Opposite (internal) side of each supracentral bearing small, rounded to elliptical, almost central pit (e.g. 1GR.PAL.15218, 15842). A_0? corresponding to largest, fan-shaped, delicate skeletal element on upper thecal surface, distally inserted along and in between adaxial edges of A'_1 and A_1, although anteriorly not in contact with aulacophore insertion. A_0? morphologically not distinct from neighbouring supracentrals: same small central pit on internal surface (e.g. IGR.PAL.15842) and comparable fan-shaped outlines (e.g. holotype, IGR.15218). At posterior extremity of supracentral area (above M'_6), anal opening roofed by a series of small, elongate, teeth-like supracentrals (e.g. CGS.OZ.294, MHNM.15690.37).

Proximal aulacophore relatively broad, slightly longer than wide, consisting of at least six or seven (e.g. holotype, CGS.OZ.151, MHNM.15690.28, UCBL-FSL.170938) and up to eight (e.g. UCBL-FSL.713377) bilaterally symmetrical telescopic rings (Figs 8a–b, d–f, 9, 10a, e, 11a, c, 12a–e, 13, 14a–e). Proximal aulacophore slightly wider than high, with proximal-most ring fitting within almost elliptical insertion zone on theca, delimited by adorals (above) and marginals M'_1 and M_1 (below), anteriorly and against outer (i.e. abaxial and lower) edges of aulacophore apophyses (e.g. holotype, CGS.OZ.151, GR/PC.1796, IGR.PAL.15842, MHNM.15690.28, 37; UCBL-FSL.713377). Communication between intrathecal cavity and hollow, tube-like structure formed by proximal rings strongly reduced, possible only through narrow, transversely elongate opening in between aulacophore apophyses (below) and adorals (above). Opening possibly reduced abaxially by occurrence of two small processes (i.e. putative apophyses horns, see above). Proximal-most rings entirely roofed by antero-adaxial portion of overlying adorals (e.g. holotype, MHNM.15690.37). Each ring made of two inferolaterals forming lower and most of lateral walls and, tightly sutured above them, a pair of tectals. Each ring forming a low truncated cone, with its proximal (posterior) margin narrower than distal (anterior) one. Each ring distally overlapping proximal portion of next, more anterior one or posterior portion of stylocone (e.g. holotype, MHNM.15690.28, 37, UCBL-FSL.713377).

Stylocone broad, with relatively short, straight distal portion and proximally widening, posterior part (e.g. IGR.PAL.15910, MHNM.15690.28, 37; Figs 9, 13a–b). Anterior portion of stylocone nearly sub-triangular in cross-section, with left and right lower sides oblique and meeting along low, median longitudinal keel (MHNM.15690.28). Keel relatively thin and narrow posteriorly, thickening distally into short, low, blunt, drop-shaped protuberance. Upper surface of distal part of stylocone nearly flat, bearing longitudinal median groove (e.g. IGR.PAL.15910, MHNM.15690.37). Lower (external) surface of proximal portion of stylocone markedly convex, rounded, smooth, more or less overlapped by interolaterals of distal-most proximal ring. Upper (internal) side of proximal part of stylocone containing deep, V-shaped cavity tapering distally towards proximal extremity of longitudinal median groove (IGR.PAL.15910, MHNM.15690.37). Stylocone cavity entirely roofed by tectals of distal-most proximal rings.

More anterior portions of distal aulacophore rarely preserved, but consisting of at least 12 (MHNM.15690.28), possibly 14 (MHNM.15690.37), ossicles and associated pairs of cover plates (Figs 3b, 9, 13a–b). Lower side of ossicles V-shaped, with opposite, oblique lateral sides converging into low, blunt median longitudinal keel (MHNM.1560.28). As in stylocone, anterior portion of keel widening anteriorly into low, blunt protuberance on lower surface of ossicles. Opposite (upper) side of ossicles not observed, hidden by overlying, ajar to nearly closed cover plates (e.g. IGR.PAL.15910, MHNM.15690.37). One pair of opposite (left and right), symmetrical, cover plates articulated to abaxial edges of upper surface of each ossicle (two pairs of cover plates inserted on stylocone). Cover plates low, longitudinally elongate, thin, with convex external (upper) surface and concave internal (lower) side (e.g. IGR.PAL.15910, MHNM.15690.37). Within each (left and right) lateral series, distal margin of each cover plate more or less overlapping posterior edge of its anterior neighbour. Proximal-most ossicles almost as long at wide. More distal elements (ossicles and associated cover plates) apparently longer than proximal ones (e.g. IGR.PAL.15910, MHNM.15690.28, 37).

Remarks. The occurrence of two posterior spines (digital and glossal) in the strongly asymmetrical mitrate stylophorans from the Traveusot Formation (France) supports their assignment to anomalocystitids (Ruta 1999; Lefebvre 2000*a*, 2001, 2003). Moreover, the possession of a reniform, sinistrally flexed theca and the scimitar-shaped morphology of the digital are both diagnostic characters of *Diamphidiocystis* (Kolata & Guensburg 1979). Consequently, their presence in Armorican anomalocystitids supports their assignment to this genus (Chauvel 1981; Ruta, 1999; Lefebvre 2000*a*, 2001, 2003). However, as already pointed out by Chauvel (1981), the Armorican material of *Diamphidiocystis* is morphologically distinct from the type species, *D. drepanon* (see also Lefebvre 2000*a*, 2003). Main differences concern (1) the plating of the supracentral area (imbricate in French specimens, tesselate in North American ones); (2) the higher number of left infracentrals and their posterior extension in between M'_4 and M'_6 (these two marginals are sutured in *D. drepanon*); (3) the possession of significantly distinct thecal outlines (more gently rounded distally, with no posterior M_7 'horn' in North American diamphidiocystines); (4) the aspect of the lower thecal surface (almost flat to slightly convex in *D. drepanon*, but with strongly convex portions delimited by a wide, flat peripheral flange in Armorican specimens); (5) the relative size of the right thecal lobe (more reduced in *D. drepanon*); and (6) the relative size, shape and extent of several major skeletal elements (e.g. the four largest marginals in Armorican specimens, $M'_{1–2}$ and $M_{1–2}$, are significantly reduced in the Laurentian material). Moreover the range of observed thecal sizes is significantly more reduced in diamphidiocystines from Brittany ($6.5 < TW < 12$ mm) compared to those from North America ($5 < TW < 40$ mm; see Kolata & Guensburg 1979, table 2). Other putative differences concern the presence of a vestigial right infracentral plate in at least some Armorican specimens (see above), and the morphology of the glossal, which is longer and curved in the French material, and much smaller, possibly vestigial in *D. drepanon* (see Kolata & Guensburg 1979; Chauvel 1981; Lefebvre *in* Ruta 1999; Lefebvre 2000*a*, 2001, 2003). The numerous morphological differences observed between French and North American diamphidiocystines are considered here as significant enough to assign the Armorican material to a distinct species, *D. regnaulti*.

The original report of diamphidiocystines in the late Darriwilian Traveusot Formation was based on three individuals (Chauvel 1981). In the last 40 years, the acquisition of several new specimens from the same area and horizons made it possible to better characterize the morphology of these mitrates and to compare them more accurately with *D. drepanon* (see above). However, this larger sample also made it also possible to better document the occurrence of putative inter-individual variations within *D. regnaulti*. The occurrence of a relatively significant, mostly ontogenetic, intraspecific variability was described in *D. drepanon*, based on a larger number of specimens (32) and a much wider range of sizes (Kolata & Guensburg 1979). The pattern of growth allometries evidenced in North American diamphidiocystines suggests that small (juvenile) individuals of *D. drepanon* are characterized by semi-circular thecal outlines with an almost straight anterior margin, whereas the largest (gerontic) specimens are more asymmetrical, with a W-shaped anterior edge resulting from a deeper embayment for aulacophore insertion (on the right) and a more protruding digital-bearing process (on the left) (Kolata & Guensburg 1979). Comparison with *D. regnaulti* indicates that thecal outlines of Armorican diamphidiocystines are closer to those of large North American individuals, than to those of small specimens of *D. drepanon*. This observation questions the possibility that Laurentian diamphidiocystines derived from *D. regnaulti*-like ancestors by peramorphosis. In the material from the Traveusot Formation, the reduced range of observed thecal sizes does not make it possible to evidence any clear ontogenetic pattern. However, several (minor) differences could be observed between Armorican individuals from the type horizon: (1) the right infracentral plate is apparently not present in all specimens; (2) the number and extent of left infracentrals are variable; (3) some major skeletal elements (e.g. Z) can display slightly distinct outlines and relative proportions; and (4) although it is often difficult to assess precisely, the number of proximal rings does not seem to be constant (varying from 6 to 8; see above).

In recent years, the successive reports of diamphidiocystines in other areas of the Armorican Massif (Hunter *et al*. 2007), in slightly younger levels (early Sandbian) of Morocco (Lefebvre *et al*. 2008, 2010*a*; Lebrun 2018) and within a much wider stratigraphic interval (late Darriwilian–late Katian) in the Prague Basin (see above; Noailles *et al*. 2014) questions their taxonomic assignment. In spite of a relatively wide palaeogeographic distribution (Anti-Atlas, Armorican Massif, Barrandian area) and an extensive stratigraphic range, the morphology of these new specimens is remarkably conservative and does not exhibit any significant difference with *D. regnaulti*. All diagnostic features of the Armorican species are also found in Czech and Moroccan individuals (see above; e.g. imbricate supracentral area, unorganized left infracentral area protruding posteriorly in between M'_4 and M'_6, peripheral flange around partly inflated lower thecal surface, horn-like M_7, delicate M'_3-M'_4 digital bearing process). Small morphological differences observed in some Bohemian and/or Moroccan individuals are falling within the range of variation occurring within Armorican specimens. Consequently, in the absence of any major significant difference with *D. regnaulti*, all late Darriwilian and Late Ordovician diamphidiocystines from the Anti-Atlas (Morocco) and the Prague Basin (Czech Republic) are considered here as conspecific with those from the late Darriwilian of Brittany (France). In stylophorans, such an extensive stratigraphic range and wide palaeobiogeographic distribution are not unique to *D. regnaulti*. The same situation occurs for example in the kirkocystid mitrate *Balanocystites primus*, which is known in the Floian of the Anti-Atlas (Morocco) and Montagne Noire (France) and also in the late Darriwilian of Brittany (France) and the Prague Basin (Czech Republic) (Barrande 1872, 1887; Chauvel 1941, 1981; Jefferies 1986; Lefebvre, 2000*a*, 2001; Lefebvre *et al*. 2016). Another example is the mitrate *Lagynocystis pyramidalis*, which is possibly present in the Furongian of Guangxi (China), and definitively occurring in the late Tremadocian of the Anti-Atlas (Morocco), the late Floian of the Montagne Noire (France), the Dapingian of Wales (UK), the Darriwilian of Bohemia (Czech Republic), Brittany (France) and Ossa Morena (Spain), and the Upper Ordovician of Anjou (France), the Barrandian area (Czech Republic) and the Saint-Petersburg region (Russia) (e.g. Barrande, 1887; Chauvel 1941; Jefferies 1973, 1987; Chauvel & Nion 1977; Ubaghs 1991; Henry *et al.* 1997; Prokop & Petr 1999; Lefebvre 2007*a*; Lefebvre & Gutiérrez-Marco 2007; Lefebvre *et al*. 2010*b*, 2016; Zamora *et al.* 2013; Rozhnov *et al*. 2019).

Discussion

Palaeoecology of diamphidiocystines

The very contrasted constructional characteristics of the two opposite thecal surfaces of *D. regnaulti* strongly suggest that, similarly to the situation in other mitrates (e.g. *Lagynocystis*, *Mitrocystites*, *Peltocystis*), the thickest and most rigid surface made of few, wide and robust skeletal elements (infracentrals, marginals) was in contact with the substrate, whereas the opposite side, comprising the delicate, thinly plated supracentral area was directed towards the water column (see e.g. Kolata & Guensburg 1979; Chauvel 1981; Parsley 1988; Lefebvre 2003). This orientation implies that ambulacral tube feet were directed away from the sea floor (Ubaghs 1968; Nichols 1972; Kolata & Guensburg 1979; Parsley 1988; David *et al*. 2000; Lefebvre 2003). Consequently, diamphidiocystines were probably either deposit and/or low-level suspension feeders (Kolata & Guensburg 1979; Parsley 1988; Lefebvre 2003).

In *D. regnaulti* and large individuals of *D. drepanon*, the aulacophore insertion is deeply encased within a narrow neck provided by M_1 and M'_1 (see above). This unusual morphology suggests that lateral flexion of the proximal part of the appendage was extremely limited (Kolata & Guensburg 1979; Parsley 1988; Lefebvre 2003). Moreover, leftward movements of the aulacophore were also limited by the strongly recurved digital. Interossicular articulations could not be observed in available material of *D. regnaulti*. However, in North American diamphidiocystines, distal and proximal ossicular facets are almost flat and 'cornute-like' (Kolata & Guensburg 1979). It is thus very likely that vertical flexion of the distal aulacophore was limited in diamphidiocystines (Parsley 1988; Lefebvre 2003). In *Diamphidiocystis*, the strongly reduced ornamentation on the lower surface of the stylocone and ossicles represents another 'cornute-like' feature and a significant difference with a 'standard' mitrate aulacophore. Consequently, morphological characteristics of their appendage indicate that diamphidiocystines could hardly use it for locomotion and/or for anchoring to the substrate. In these mitrates, the aulacophore was thus probably primarily used for feeding and/or respiration (Kolata & Guensburg 1979; Lefebvre 2003).

The sinistrally recurved, transversely elongate thecal morphology of *Diamphidiocystis* strongly departs from the almost bilaterally symmetrical, antero-posteriorly elongate thecae of other anomalocystitids (Kolata & Guensburg 1979; Chauvel 1981; Parsley 1988; Ruta 1999; Lefebvre 2003). In diamphidiocystines, the strong asymmetry and unequal development of the two posterior spines (with the digital much wider and longer than the glossal), as well as the absence of thecal sculpture (e.g. cuesta-shaped ribs, scale-like riblets, pustules) represent two additional major differences with other anomalocystitids (Kolata & Guensburg 1979; Ruta 1999; Lefebvre 2001, 2003). As already pointed out by Chauvel (1981), the unusual thecal morphology of diamphidiocystines is neither aberrant nor teratological. In many respects, it is remarkably convergent with the strongly asymmetrical, transversely elongate thecae of boot-shaped cornutes (e.g. *Cothurnocystis*, *Flabellicarpus*, *Galliaecystis*, *Scotiaecystis*, *Thoralicarpus*), also characterized by elongate, blade-like posterior spines (digital, glossal, spinal) (Kolata & Guensburg 1979; Parsley 1988; Lefebvre 2003; Lefebvre *et al*. 2006). As in *Diamphidiocystis*, boot-shaped cornutes are also characterized by relatively weakly ornamented, rigid distal appendages with flat interossicular facets (see e.g. Ubaghs 1968; Parsley 1988; Lefebvre 2003; Lefebvre *et al*. this volume). Consequently, it is very likely that the convergent acquisition of similar thecal and appendage morphologies in both boot-shaped cornutes and diamphidiocystines results from relatively comparable modes of life (Parsley 1988; Lefebvre 2003; Lefebvre *et al*. 2006).

In marine epibenthic invertebrates, the acquisition of wide, flattened morphologies with long, spine-shaped expansions are morphological features often observed in taxa living on soft substrates (e.g. raphiophorid trilobites, strophochonetid brachiopods; Fortey & Owens 1978; Racheboeuf & Thanh 2000). In *D. regnaulti*, it is very likely that the wide, flat peripheral flange running around the distal thecal margin contributed, along with the two posterior spines, to the stabilization of the organism on soft substrates. Consequently, the unusual morphology of *Diamphidiocystis* is well adapted to a relatively sessile, epibenthic mode of life on soft substrates, relatively comparable to that of boot-shaped cornutes (Frest 1988; Parsley 1988; Lefebvre 2003; Lefebvre *et al*. 2006). Diamphidiocystines thus possibly correspond to the colonization by early anomalocystitids of an ecological niche (almost sessile, epibenthic mode of life) clearly distinct from that of later, predominantly infaunal and mobile taxa (allanicytidiines and anomalocystitines) (e.g. Jefferies & Lewis 1978; Craske & Jefferies 1989; Ruta & Theron 1997; Ruta & Bartels 1998; Lefebvre 2003; Lefebvre & Ausich 2021).

Significant differences in thecal size were observed in North American diamphidiocystines, with individuals occurring in shales (Orchard Creek Shale; Fig. 1.10) much larger than those found in overlying limestones (Girardeau Limestone; Fig. 1.11) (see Kolata & Guensburg 1979). In southern Illinois, the Late Ordovician succession records the gradual transition from relatively deep, quiet environmental conditions (Orchard Creek Shale) to much shallower settings (Girardeau Limestone). This regressive trend was probably induced by the first pulse of the Hirnantian glaciation (Bergström *et al*. 2006). In both stratigraphic units, the preservation of fully articulated individuals makes the possible influence of current-induced size sorting improbable. The observed size pattern more likely reflects original differences in food availability, temperature, oxygenation, hydrodynamism and/or predation intensity. A relatively similar size pattern was described in several trilobite taxa from the Lower Ordovician of Morocco, with larger individuals consistently occurring in slightly deeper, more quiet and less stressful environmental conditions (Saleh *et al*. 2021). Although the range of observed thecal sizes is more reduced in *D. regnaulti*, the two Moroccan specimens (TW *ca* 5 mm) are significantly smaller than all known individuals from Brittany and the Prague Basin (6.5 < TW < 12 mm). Moroccan diamphidiocystines were found in relatively coarse sandstones, associated to relatively shallow environmental conditions, above storm-wave base (see above). Czech and French specimens are occurring in shales or fine silststones deposited in more distal settings, below storm wave base. Consequently, the same trend with larger individuals in more distal settings is apparently observed in both Laurentian and peri-Gondwanan *Diamphidiocystis*.

Independently of possible depth-related variations in mean thecal size, North American diamphidiocystines can reach significantly much larger dimensions (maximal TW: 40 mm) than peri-Gondwanan ones (maximal TW: 11.5 mm). Strong variations in body size between mitrate assemblages occurring in distinct regions are frequently observed (see e.g. Lefebvre 2007*a*). For example, individuals of *Peltocystis cornuta* are significantly smaller in the lower part of the Fezouata Shale (late Tremadocian, Morocco) than those from the Saint-Chinian Formation (late Tremadocian, France) (Lefebvre & Botting 2007). Such differences in size can be related to various environmental conditions (e.g. nutrient availability, temperature, oxygenation). For example, many marine invertebrates are characterized by an increase in body size when water temperature decreases (Bergmann's rule; Hartnoll 1982; Fujita & Ohta 1990; Timofeev 2001; Lefebvre 2007*a*). However, the opposite pattern is observed in diamphidiocystines, with tropical forms (*D. drepanon*) larger than high-latitude ones (*D. regnaulti*). At this stage, it is thus difficult to interpret this difference in body size between Laurentian and peri-Gondwanan mitrates, and to decipher if it results from a macroevolutionary trend (e.g. Cope's rule) and/or from distinct environmental conditions.

Diversification and palaeobiogeography of Ordovician anomalocystitids

The occurrence of the same species of diamphidiocystines (*D. regnaulti*) in the Middle and Upper Ordovician of the Anti-Atlas (Morocco), Brittany (France) and the Prague Basin (Czech Republic) is in good accordance with the well-known strong faunal affinities between these three regions of the Mediterranean Province (e.g. Havlíček 1989; Gutiérrez-Marco *et al*. 2003; Lefebvre 2007*b*; Álvaro *et al.* this volume). Darriwilian–Katian deposits of the Anti-Atlas, the Armorican Massif and Bohemia have yielded very similar echinoderm faunas, with several other examples of taxa occurring in all three regions: e.g. aristocystitid (e.g. *Aristocystites*, *Calix*) and sphaeronitid diploporites (e.g. *Codiacystis*), eocrinoids (e.g. *Ascocystites*), and stylophorans (*Anatifopsis*, *Aspidocarpus*, *Domfrontia*, *Thoralicarpus*) (see e.g. Barrande 1887; Chauvel 1941, 1966, 1980; Chauvel & Nion 1977; Ubaghs 1979; Prokop & Petr 1999; Lefebvre & Fatka 2003; Hunter *et al*. 2010; Régnault 1990, 2007; Lefebvre *et al*. 2008, 2010*a*, *b*, this volume). Several other Middle–Late Ordovician echinoderm taxa are shared by two of these three regions, either the Anti-Atlas and the Prague Basin (e.g. *Arauricystis*, *Barrandeocarpus*, *Bohemiaecystis*, *Cardiocystites*, *Dendrocystites*, *Destombesicarpus*, *Echinosphaerites*, *Homocystites*, *Rhombifera*), the Anti-Atlas and Brittany (e.g. *Milonicystis*), or the Barrandian area and Brittany (e.g. *Lagynocystis*, *Mitrocystella*, *Mitrocystites*, *Taeniaster*) (see e.g. Barrande 1887; Chauvel 1941, 1971, 1981, 1986; Jefferies 1968, 1973; Prokop & Petr 1999; Hunter *et al*. 2007, 2010; Nardin 2007; Lefebvre *et al*. 2007*b*, 2010*a*, *b*, this volume; Noailles *et al*. 2014; Nohejlová & Lefebvre this volume; Zamora *et al*. this volume).

Diamphidiocystis regnaulti is the only anomalocystitid known so far in Middle Ordovician times. Although strongly autapomorphic, this mitrate is, in many respects, morphologically intermediate between the yet undescribed earliest anomalocystitid from the Floian of Morocco (Noailles & Lefebvre 2012; Lefebvre *et al*. 2013, 2016; Lefebvre & Ausich 2021) and Late Ordovician members of the two other subfamilies (see above). With the restrictions resulting from a very poor fossil record, available evidence suggests a probable Gondwanan origin for mitrocystitids and anomalocystitids (Lefebvre 2007*a*). Mitrocystitids very likely derived from a *'Nanocarpus' guoleensis*-like early mitrate, which is occurring in the late Cambrian of both South China and Korea (Zamora *et al*. 2013; Lefebvre & Ausich 2021). The earliest known occurrences of mitrocystitids are restricted to late Tremadocian–Floian deposits of high latitude peri-Gondwanan areas: e.g. in Morocco (e.g. *Aspidocarpus*?, *Vizcainocarpus*), the Montagne Noire, France (*Chinianocarpos*, *Ovocarpus*, *Vizcainocarpus*), and Shropshire, UK (*Vizcainocarpus*) (see e.g. Ubaghs 1961, 1970, 1994; Ruta 1997*c*; Lefebvre 2000*b*; Parsley & Gutiérrez-Marco 2005; Lefebvre *et al*. 2016). Available fossil evidence suggests that anomalocystitids originated from this stock of early mitrocystitids by the modification of two postero-lateral marginals into movable spines (see above; Lefebvre & Ausich 2021). In Early and Middle Ordovician times, the palaeobiogeographic distribution of mitrocystitids (including anomalocystitids) was restricted to high latitude peri-Gondwanan regions (Czech Republic, France, Morocco, Portugal, Spain) and Avalonia (Wales) (see Barrande 1887; Chauvel 1941, 1971, 1981; Ubaghs 1961, 1970, 1979, 1994; Jefferies 1968, 1987; Gutiérrez-Marco & Meléndez 1987; Cripps 1990; Beiswenger 1994; Ruta 1997*c*; Lefebvre 2000*b*, 2007*a*, *b*; Lefebvre & Fatka 2003; Lefebvre & Gutiérrez-Marco 2003; Lefebvre *et al*. 2010*b*, 2016). This pattern suggests a long, cryptic, yet largely unrecorded diversification of anomalocystitids between their earliest occurrence in the Floian and the first records of diamphidiocystines (late Darriwilian), anomalocystitines (Sandbian) and allanicytidiines (latest Sandbian).

In the latest Sandbian, the earliest occurrences of anomalocystitids in Laurentia (e.g. *Enoploura* in the Bromide Formation, Oklahoma, USA; Parsley 1982) are coinciding with a major regional faunal turnover (mid-Mohawkian invasion) and the onset of deeper, cooler environmental conditions, probably related to the Taconic orogeny (Patzkowsky & Holland 1993; Lefebvre 2007*a*, *b*; Ettensohn 2010; Wright & Stigall 2013). In mid-Mohawkian times (Turinian–Chatfieldian transition, i.e. around the Sanbdian–Katian boundary), this environmental change was matched by the sudden arrival of temperate, cool-adapted taxa formerly unrecorded on the shallow tropical shelves of eastern and central Laurentia (e.g. bivalves, cryptolithinid trilobites, anomalocystitid and kirkocystid mitrates, solutans; see Shaw 1991; Babin 1993; Cope & Babin 1999; Lefebvre 2007*a*, *b*). During the Katian, early allanicytidiines (e.g. *Enoploura*) and anomalocystitines (e.g. *Ateleocystites*) underwent a major diversification in Laurentia (see Billings 1858; Meek 1872, 1873; Bassler 1932; Caster 1952; Kolata & Jollie 1982; Parsley 1991). In contrast, diamphidiocystines have not been documented so far in Laurentia until the latest Katian–early Hirnantian time interval (Fig. 1; Kolata & Guensburg 1979; Guensburg 1988). The possibility that these anomalocystitids reached Laurentian shores earlier (e.g. during the mid-Mohawkian invasion) and that their late occurrence in the fossil record results from a sampling and/or taphonomic bias can not be ruled out. However, it is equally possible that diamphidiocystines migrated later into Laurentia. In southern Illinois, their sudden appearance in the upper part of the Orchard Creek Shale and the overlying Girardeau Limestone coincides with a strong faunal turnover and the onset of cool-adapted, *Hirnantia*-like assemblages (Bergström *et al*. 2006). This occurrence corresponds with the closure of the Iapetus Seaway and the Taconic Orogeny that facilitiated enhanced intercontinetal faunal exchange. Diamphidiocystines were fundamentally Gondwanan faunal elements whose final appearance was Laurentian.

In marked contrast with the situation in Laurentia, very little is known about Late Ordovician anomalocystitids in peri-Gondwanan areas, thus providing the misleading impression that most of their post-Darriwilian diversification occurred elsewhere. The example of diamphidiocystines demonstrates that this situation largely results from a strong sampling bias. Originally evidenced only in the late Darriwilian of eastern Brittany (Chauvel 1981), diamphidiocystines have been observed in the last 15 years in western Brittany (Hunter *et al*. 2007), but also in the early Sandbian of Morocco (Lefebvre *et al*. 2008, 2010*a*; Lebrun 2018) and, finally, in five distinct stratigraphic units of the Prague Basin (see above; Noailles *et al*. 2014), thus revealing an unexpectedly wide palaeobiogeographic distribution and a particularly extensive stratigraphic range (late Darriwilian–late Katian; Fig. 1).

The same situation probably also occurs for the two other clades of anomalocystitids. Within the Mediterranean Province, the spineless genus *Barrandeocarpus* is probably the most widespread and long ranging anomalocystitine (Sandbian–Hirnantian). Field observations and museum collections both suggest that this genus, originally described in the Letná Formation (Ubaghs 1979), is actually present in most Late Ordovician stratigraphic units of the Prague Basin. For example, reexamination of the type material of *Anomalocystites bohemicus* (Králův Dvůr Formation, late Katian; Barrande 1887) indicates that this mitrate should be assigned to *Barrandeocarpus* (B. Lefebvre, pers. obs. 2016). Similarly, observation of the Moroccan material from the lowermost part of the Lower Second Bani Formation (latest Katian) originally described as *Placocystites bohemicus* by Chauvel (1971) suggests that it should be assigned to *Barrandeocarpus*. In recent years, earlier, yet undescribed occurrences of *Barrandeocarpus* were observed in the Upper Ordovician of the eastern Anti-Atlas. This genus is also present in the Hirnantian of Spain (Lefebvre & Gutiérrez-Marco 2003). Consequently, the abundant new (mostly unpublished) data accumulated in the last 20 years in the Czech Republic, Morocco and Spain suggest that the stratigraphic range and palaeobiogeographic distribution of *Barrandeocarpus* in the Mediterranean Province are largely underestimated. So far, no spine-bearing anomalocystitines have been documented in peri-Gondwanan areas.

In marked contrast with anomalocystitines, the fossil record of allanicytidiines is almost inexistant in peri-Gondwanan areas, with the exception of *Protocytidium elliottae* from the Hirnantian of Victoria, Australia (Ruta and Jell 1999*a*). However, at least two other yet unpublished occurrences of

Late Ordovician *Enoploura*-like allanicytidiines from the Sandbian of the Barrandian area, Czech Republic (B. Lefebvre, pers. obs. 2008) and the Hirnantian of the Anti-Atlas, Morocco (B. Lefebvre, pers. obs. 2017) suggest that this clade was palaeogeographically more widespread than expected.

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Figure Captions

Fig. 1. Stratigraphic distribution of diamphidiocystine anomalocystitids in peri-Gondwanan regions (Brittany, France; Prague Basin, Czech Republic; Anti-Atlas, Morocco) and Laurentia (Illinois and Iowa, USA), with: 1: Postolonnec Formation; 2: Traveusot Formation; 3: Dobrotivá Formation; 4: Libeň Formation; 5: Vinice Formation; 6: Zahořany Formation; 7: Bohdalec Formation; 8: Králův Dvůr Formation; 9: Izegguirene Formation; 10: Orchard Creek Shale; 11: Girardeau Limestone; 12: Maquoketa Shale. Ages and correlations based on Bergström *et al*. (2006), Vidal *et al*. (2011), Gendry *et al*. (2013), Kraft *et al*. (2015), Álvaro *et al*. (this volume).

Fig. 2. Location of main Ordovician localities yielding diamphidiocystine mitrates in the Barrandian area, Czech Republic. Numbers refer to localities: 1, Malé Přílepy (Dobrotivá Formation); 2, Chrustenice (Dobrotivá Formation); 3, Lhotka (Libeň Formation); 4, Hředle (Vinice Formation); 5, Zahořany (Vinice Formation); 6, Levín (Zahořany Formation); 7, Praha - Harfa (Bohdalec Formation); 8, Neumětely (Bohdalec Formation); 9, Nová Vráž - Černošice (Králův Dvůr Formation); 10, Kosov hill (Králův Dvůr Formation); 11, Lejškov (Králův Dvůr Formation); 12, Praha - Pankrác (Králův Dvůr Formation); 13, Praha - Dolní Počernice (Králův Dvůr Formation).

Fig. 3. Preservation of *Diamphidiocystis regnaulti* from the Middle and Upper Ordovician of the Prague Basin, Czech Republic; (**a**–**b**) Specimens (in lower aspect) preserved in dark shales, upper part of the Dobrotivá Formation (latest Darriwilian–early Sandbian), Chrustenice, NE of Beroun; (**a**) CGS.OZ.291: proximal aulacophore and slightly disarticulated, incomplete theca (glossal missing); (**b**) CGS.OZ.292: long portion of distal aulacophore, proximal rings and slightly disarticulated, almost complete theca; (**c**) CGS.OZ.151: portion of distal aulacophore, proximal rings and slightly disarticulated, posteriorly incomplete theca (in upper aspect) preserved in a concretion, Dobrotivá Formation (late Darriwilian), Chyňaya, Malé Přílepy; (**d**) CGS.OZ.293: part of proximal aulacophore and collapsed, disarticulated lower thecal surface; Bohdalec Formation (early Katian), former brickyard near Neumětely, SW of Beroun; (**e**–**f**) Specimens (in lower aspect) preserved in soft grey shales of the Králův Dvůr Formation (late Katian); (**e**) CGS.OZ.294:

fully articulated, complete theca; Lejškov; (**f**) CGS.OZ.121, stylocone, proximal aulacophore and slightly disarticulated, incomplete theca; Nová Vráž, Černošice. All scale bars: 5 mm.

Fig. 4. Measurement of thecal length (TL) and thecal width (TW) in the anomalocystitid mitrate *Diamphidiocystis regnaulti* (digital and glossal spines omitted). TL is estimated along main body axis (longitudinal axis of symmetry running along the aulacophore) between M'_1-M'_2 suture (anteriorly) and outer margin of M_3 (distally). TW is measured perpendicularly to TL, between M_1-M_2 suture (on the right thecal side) and posterior extremity of M_7 (on the left thecal side).

Fig. 5. Orientation and terminology in the anomalocystitid mitrate *Diamphidiocystis regnaulti* (late Darriwilian–late Katian), Mediterranean Province (Anti-Atlas, Armorican Massif, Bohemia); (**a**) lower side; (**b**) upper side. Main morphological landmarks are the anus (posterior) and the mouth (anterior), the main body axis along the aulacophore (adaxial, abaxial), and the appendage insertion (proximal, distal); left and right are defined based on the presumed life orientation of the organism (upper, lower side).

Fig. 6. Thecal plate homologies in diamphidiocystine mitrates, based on model defined by Lefebvre & Ausich (2021); (**a–b**) *Diamphidiocystis drepanon* (latest Katian–early Hirnantian, USA), modified and redrawn from Kolata & Guensburg (1979); it is uncertain if the glossal was a small movable spine articulated to M_3 (as illustrated here) or if it was vestigial and part of the marginal frame along the distal margin of M_3 (see Kolata & Guensburg 1979, pl. 1 fig. 4); (**a**) lower thecal surface; (**b**) upper thecal surface; (**c–d**) *Diamphidiocystis regnaulti* (late Darriwilian–late Katian, Czech Republic, France, and Morocco); (**c**) lower thecal surface; (**d**) upper thecal surface.

Fig. 7. Reconstruction of *Diamphidiocystis regnaulti* (late Darriwilian–late Katian, Czech Republic, France, and Morocco); (**a**) aulacophore and theca in lower aspect; (**b**) aulacophore and theca in upper view.

Fig. 8. Camera lucida drawings of *Diamphidiocystis regnaulti*, Traveusot Formation (late Darriwilian), Martigné-Ferchaud syncline, Ille-et-Vilaine, Brittany, France; (**a–b**) IGR.PAL.15217 (holotype), Traveusot (Guichen); (**a**) proximal aulacophore and almost complete theca (in lower

view); (**b**) proximal rings and fully articulated, almost complete upper thecal surface; (**c–d**) UCBL-FSL.170938 (paratype), le Domaine (Guichen); (**c**) fully articulated, almost complete lower thecal surface, with well-preserved left infracentral area and posterior region; (**d**) partial proximal aulacophore and nearly complete upper thecal surface, with well-preserved supracentral area and periproct; (**e–f**) GR/PC.1796 (paratype), le Domaine (Guichen); (**e**) incomplete stylocone, proximal rings and almost complete lower thecal surface, with relatively well preserved posterior area; (**f**) proximal rings and slightly disarticulated articulated upper thecal surface with adorals, supracentrals and some internal structures (e.g. apophyses, left scutula) on upper surface of M'_1.

Fig. 9. Camera lucida drawings of *Diamphidiocystis regnaulti*, Izegguirene Formation (early Sandbian), Bou Nemrou, western Tafilalt, eastern Anti-Atlas, Morocco; (**a**) MHNM.15690.28, long portion of fully articulated aulacophore and almost complete theca in lower aspect (D missing and posterior region poorly preserved); (**b**) MHNM.15690.37, long portion of fully articulated aulacophore with slightly open cover plates, and fully articulated, nearly complete theca (in upper aspect) with well-preserved periproct.

Fig. 10. Camera lucida drawings of *Diamphidiocystis regnaulti* from the Armorican Massif (France) and Bohemia (Czech Republic); (**a–d**) Traveusot Formation (late Darriwilian), Martigné-Ferchaud syncline, eastern Brittany, France; (**a**) UCBL-FSL.712498 (paratype), le Domaine, Guichen; poorly preserved proximal aulacophore and nearly complete, slightly disarticulated lower thecal surface; (**b**) IGR.PAL.15216 (paratype), Traveusot, Guichen; complete, slightly disarticulated theca (in lower aspect); (**c–d**) IGR.PAL.15204 (paratype), Traveusot, Guichen; (**c**) incomplete, slightly disarticulated lower thecal surface with well-preserved right infracentral element; (d) internal aspect of lower thecal surface, with numerous internal structures (anterior transverse groove, apophyses, left scutula, septum); (**e–f**) CGS.OZ.151, Dobrotivá Formation (late Darriwilian), Chyňaya, Malé Přílepy, Prague Basin, Czech Republic; (**e**) part of aulacophore (stylocone and proximal rings) and slightly disarticulated, incomplete lower thecal surface; (**f**) proximal rings and well preserved, incomplete upper thecal surface, with adorals and numerous

imbricate supracentrals. Abbreviations: ant. tr. groove: anterior transverse groove; right infr.: right infracentral.

Fig. 11. Camera lucida drawings of *Diamphidiocystis regnaulti* from the Armorican Massif (France) and Bohemia (Czech Republic); (**a, c–f**) Traveusot Formation (late Darriwilian), Martigné-Ferchaud syncline, eastern Brittany, France; (**a**) IGR.PAL.15805 (paratype), Traveusot, Guichen; proximal rings and slightly disarticulated, incomplete lower thecal surface with reduced right infracentral area; (**c–d**) UCBL-FSL.713377 (paratype), la Saudrais, Guichen; (**c**) fully articulated proximal aulacophore consisting of eight rings, and incomplete lower thecal surface (right lobe missing), with well preserved posterior area; (**d**) slightly disarticulated, almost complete upper thecal surface with well preserved imbricate supracentral area; (**e**) MHNN.P.025931 (paratype), le Domaine, Guichen; slightly disarticulated, posteriorly incomplete lower thecal surface; (**f**) IGR.PAL.15842 (paratype), Traveusot, Guichen; slightly disarticulated, nearly complete upper thecal surface with adorals and imbricate supracentrals; (**b**) CGS.LK.18, lowermost part of Vinice Formation (latest Sandbian–earliest Katian), Děd Hill, Zahořany, Prague Basin, Czech Republic; upper (internal) aspect of lower thecal surface of largest observed specimen (estimated TW *ca* 12 mm), with well-preserved internal structures (e.g. apophyses, left scutula, septum). Abbreviations: r. infr.: right infracentral; sept.: septum.

Fig. 12. *Diamphidiocystis regnaulti*, all specimens in lower aspect; Traveusot Formation (late Darriwilian), Martigné-Ferchaud syncline, eastern Brittany, France; (**a**) IGR.PAL.15217 (holotype), proximal aulacophore and slightly disarticulated, posteriorly incomplete theca, with both digital and glossal; Traveusot, Guichen; (**b**) UCBL-FSL.713377 (paratype), fully articulated proximal aulacophore and incomplete theca (right lobe missing), with well preserved left infracentral area, M_6, M_7 and M'_6; la Saudrais, Guichen; (**c**) UCBL-FSL.170938 (paratype), slightly disarticulated theca with digital, glossal and well preserved posterior region (left infracentrals, M_6, M_7, M'_6); le Domaine, Guichen; (**d**) UCBL-FSL.712498 (paratype), aulacophore and slightly disarticulated, posteriorly incomplete theca with both digital, glossal, and small gap for right infracentral plate in between M'_1, M_1, M_2, Mc and Z; Traveusot, Guichen; (**e**)

GR/PC.1796 (paratype), proximal aulacophore and slightly disarticulated, posteriorly incomplete theca, with digital, glossal, M_6 and M_7; le Domaine, Guichen; (**f**) IGR.PAL.15216 (paratype), slightly disarticulated theca with digital, glossal and well preserved posterior region (infracentrals, M_6, M_7, M'_6); Traveusot, Guichen. All scale bars: 5 mm.

Fig. 13. *Diamphidiocystis regnaulti* from the Anti-Atlas (Morocco) and Bohemia (Czech Republic); (**a–b**) specimens from the Izegguirene Formation (early Sandbian), Bou Nemrou, western Tafilalt, eastern Anti-Atlas, Morocco; (**a**) MHNM.15690.28: long portion of fully articulated aulacophore and well preserved, posteriorly incomplete theca (in lower aspect); (**b**) MHNM.15690.37: long portion of fully articulated aulacophore with ajar cover plates, and almost complete upper thecal surface (part of glossal missing); (**c–d**) CGS.OZ.151, Dobrotivá Formation (late Darriwilian), Chyňaya, Malé Přílepy, Prague Basin, Czech Republic; (**c**) disarticulated aulacophore and posteriorly incomplete theca (in lower aspect); (**d**) proximal rings and relatively well preserved upper thecal surface with adorals, imbricate supracentrals and glossal. All scale bars: 5 mm.

Fig. 14. *Diamphidiocystis regnaulti* from the Armorican Massif (France) and Bohemia (Czech Republic), all specimens in upper aspect; (**a–e**) Specimens from the Traveusot Formation (late Darriwilian), Martigné-Ferchaud syncline, eastern Brittany, France; (**a**) IGR.PAL.15217 (holotype): proximal aulacophore and well preserved theca with adorals, imbricate supracentrals, digital and glossal; Traveusot, Guichen; (**b**) GR/PC.1796 (paratype): proximal rings and well preserved theca with digital, glossal, and collapsed adorals and imbricate supracentrals; le Domaine, Guichen; (**c**) UCBL-FSL.170938 (paratype): proximal aulacophore and slightly disarticulated theca with adorals, digital, glossal and imbricate supracentrals; le Domaine, Guichen; (**d**) IGR.PAL.15842 (paratype): portions of aulacophore and slightly disarticulated, incomplete theca with adorals, glossal, and imbricate supracentrals; Traveusot, Guichen; (**e**) UCBL-FSL.713377 (paratype): proximal rings and slightly disarticulated, incomplete theca with adorals, digital and imbricate supracentrals; la Saudrais, Guichen; (**f**) CGS.LK.18, lowermost part of Vinice Formation (latest Sandbian–earliest Katian), Děd Hill, Zahořany, Prague Basin, Czech Republic; disarticulated theca with adorals and most supracentrals missing, exposing upper

(internal) side of underlying marginals and their internal structures, e.g. apophyses (M_1 and M'_1), left scutula (M'_1) and septum (M'_1 and Z). All scale bars: 5 mm.

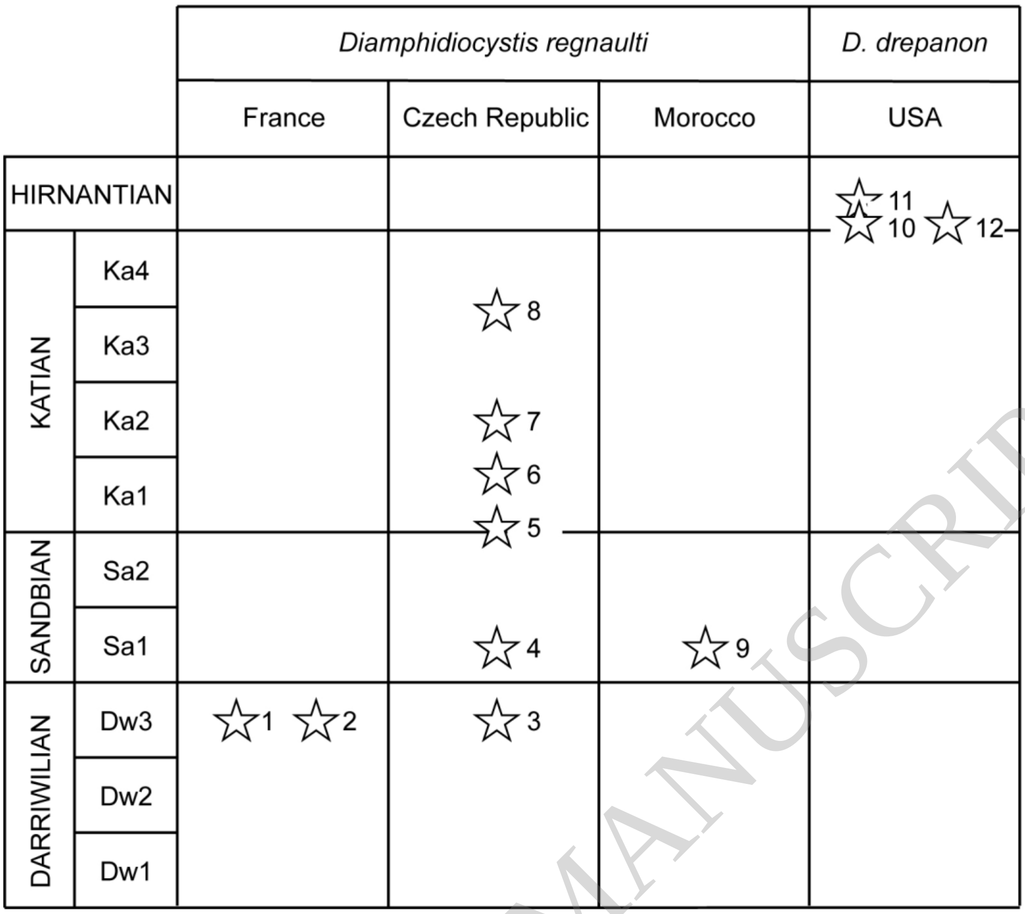
Diamphidiocystis regnaulti
D. drepanon
France
Czech Republic
Morocco
USA
HIRNANTIAN
KATIAN
Ka4
Ka3
Ka2
Ka1
SANDBIAN
Sa2
Sa1
DARRIWILIAN
Dw3
Dw2
Dw1
11
10
12
8
7
6
5
4
9
1
2
3

Figure 1

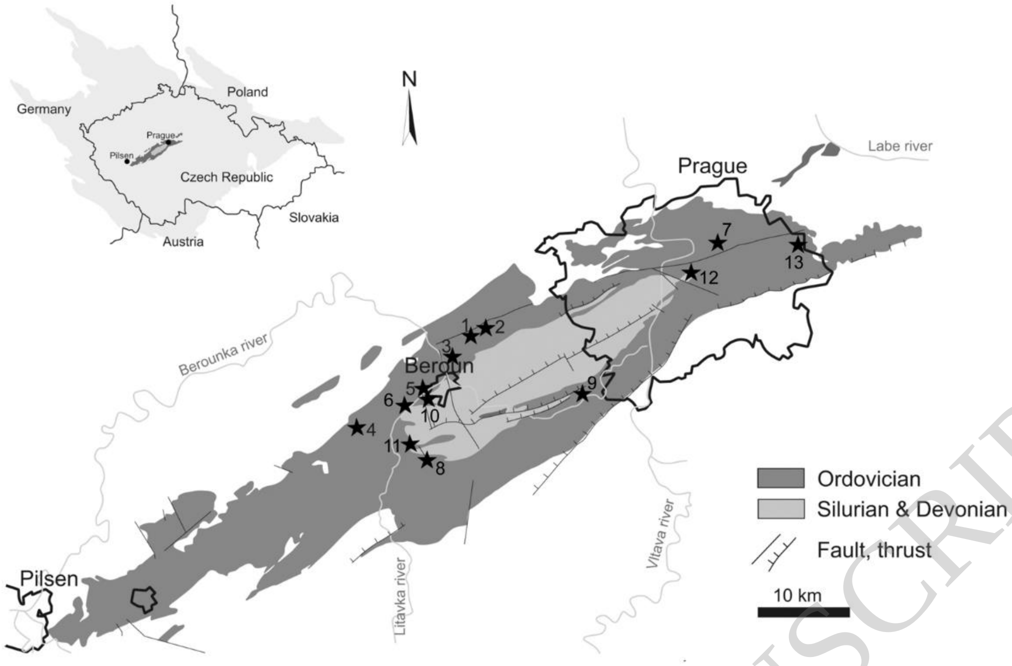
Germany
Poland
Prague
Pilsen
Czech Republic
Slovakia
Austria
N
Prague
Labe river
Berounka river
Beroun
Pilsen
Litavka river
Vltava river
1
2
3
4
5
6
7
8
9
10
11
12
13
Ordovician
Silurian & Devonian
Fault, thrust
10 km

Figure 2

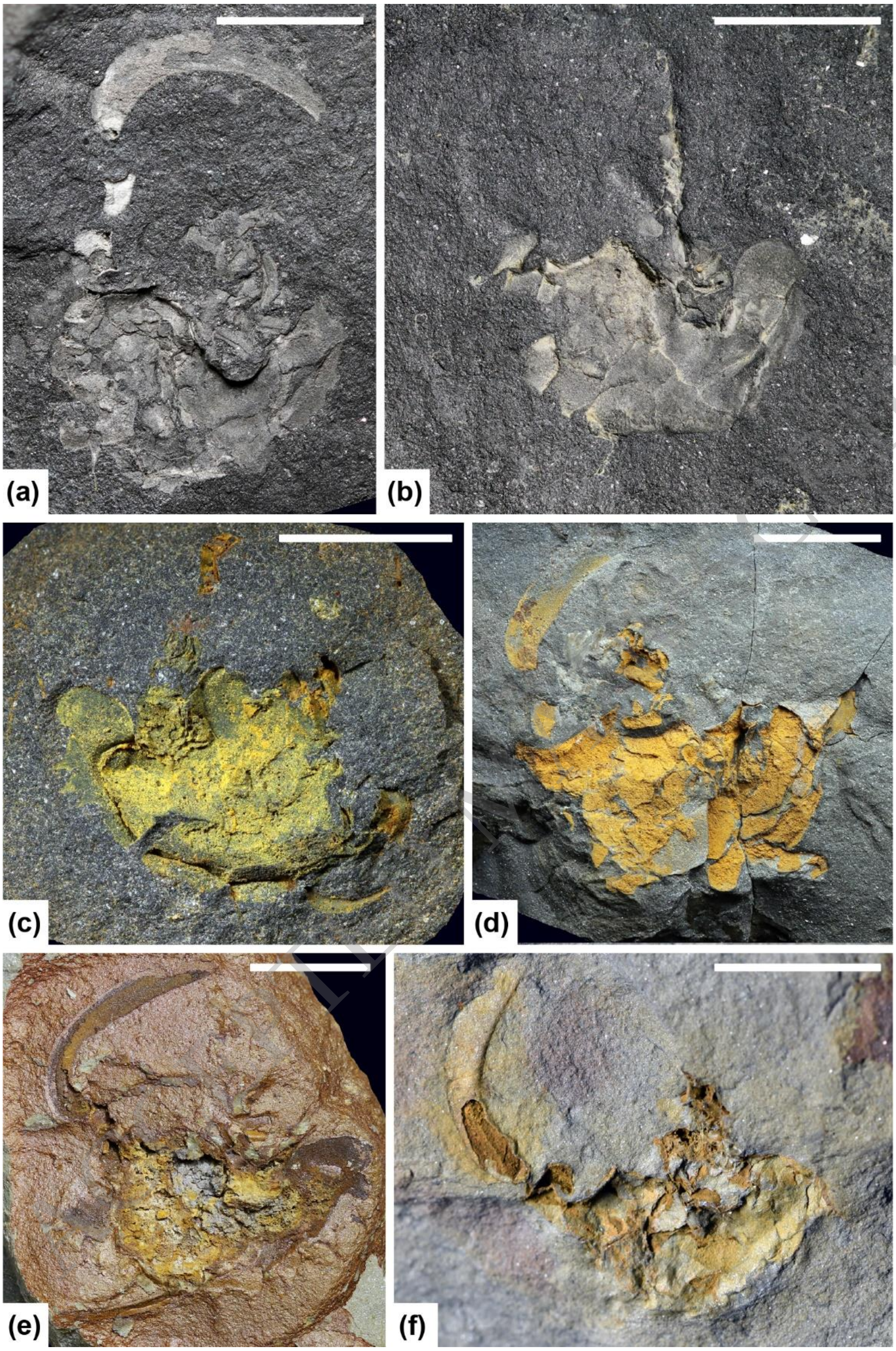

Figure 3

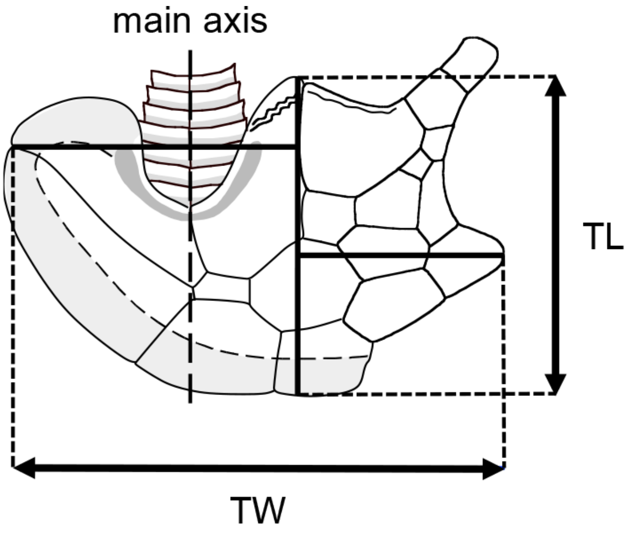

Figure 4

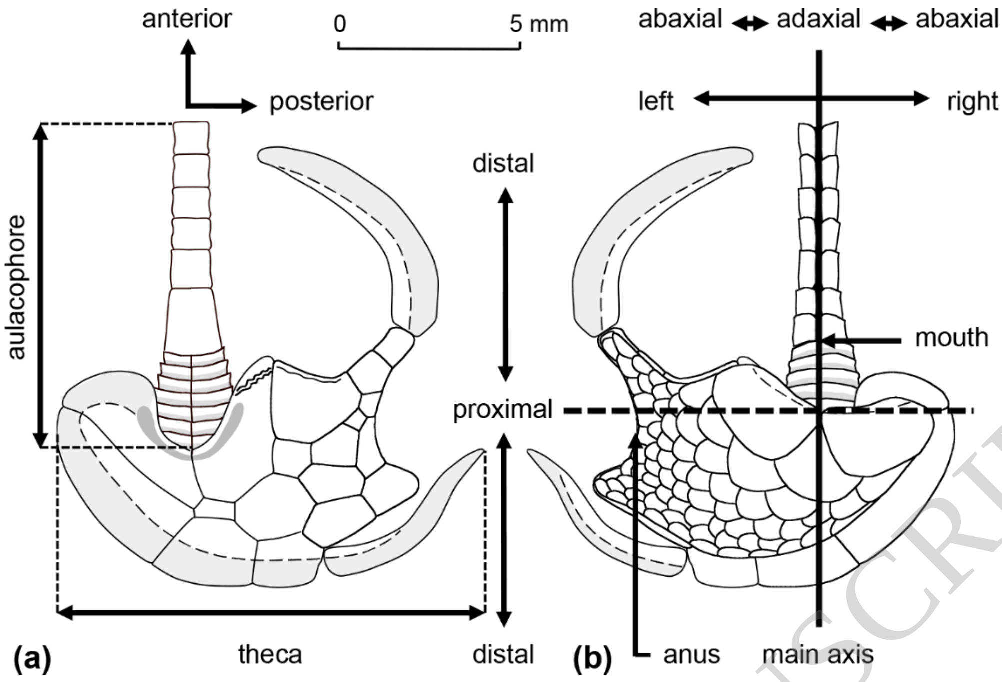
anterior
posterior
0
5 mm
aulacophore
distal
proximal
distal
theca
(a)
abaxial
adaxial
abaxial
left
right
mouth
(b)
anus
main axis

Figure 5

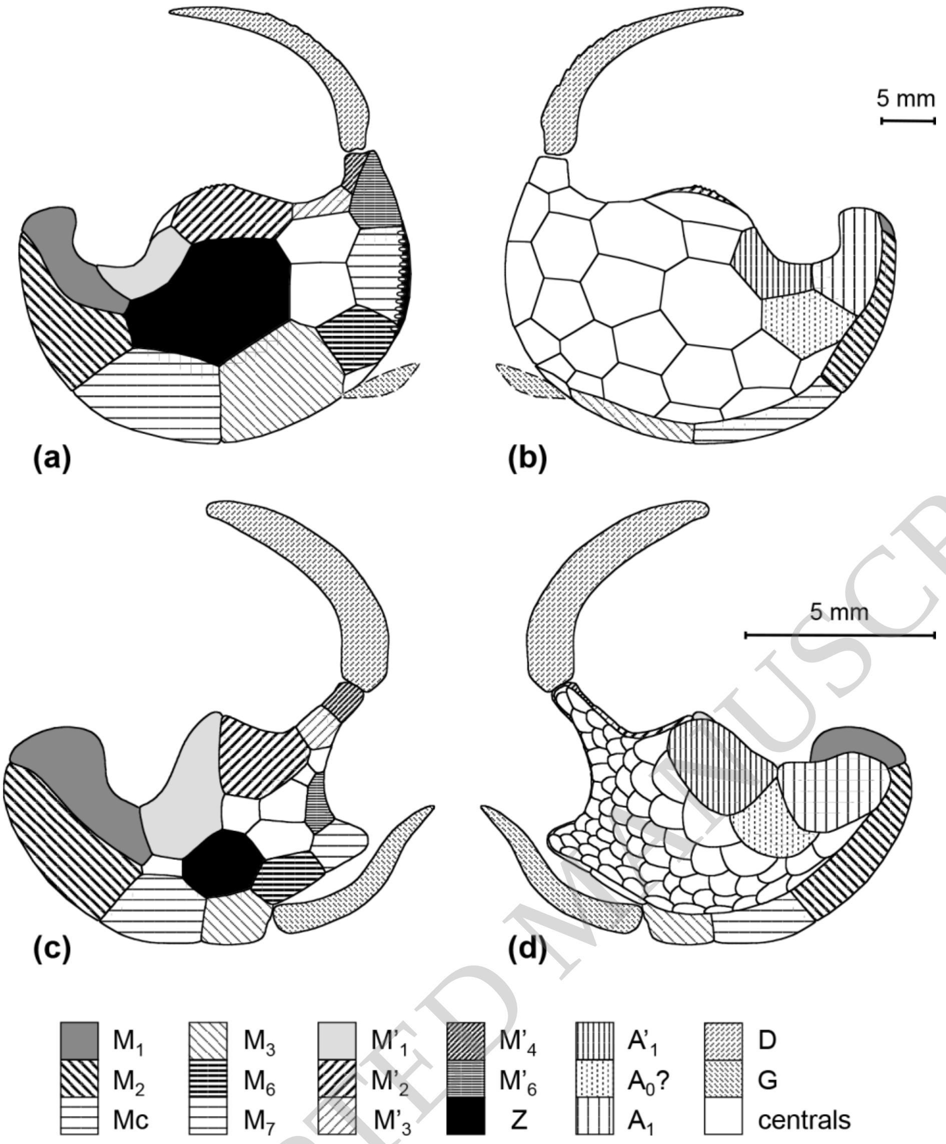

Figure 6

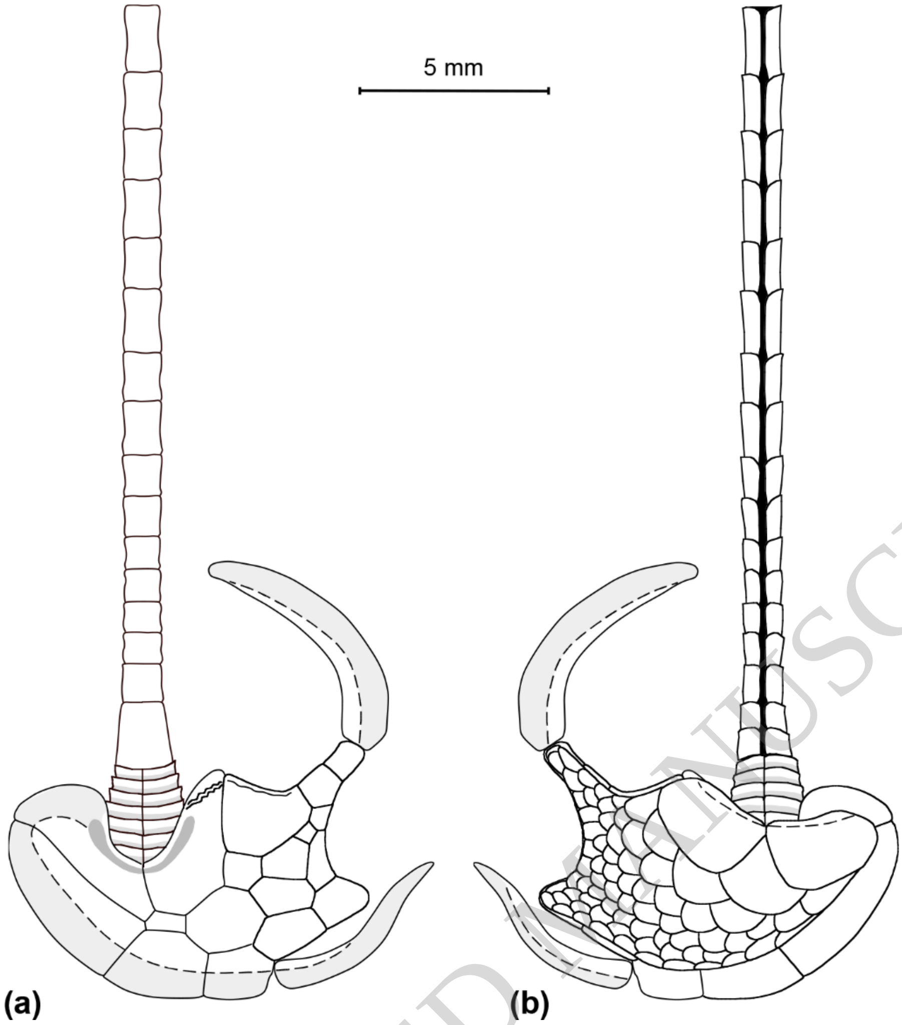

Figure 7

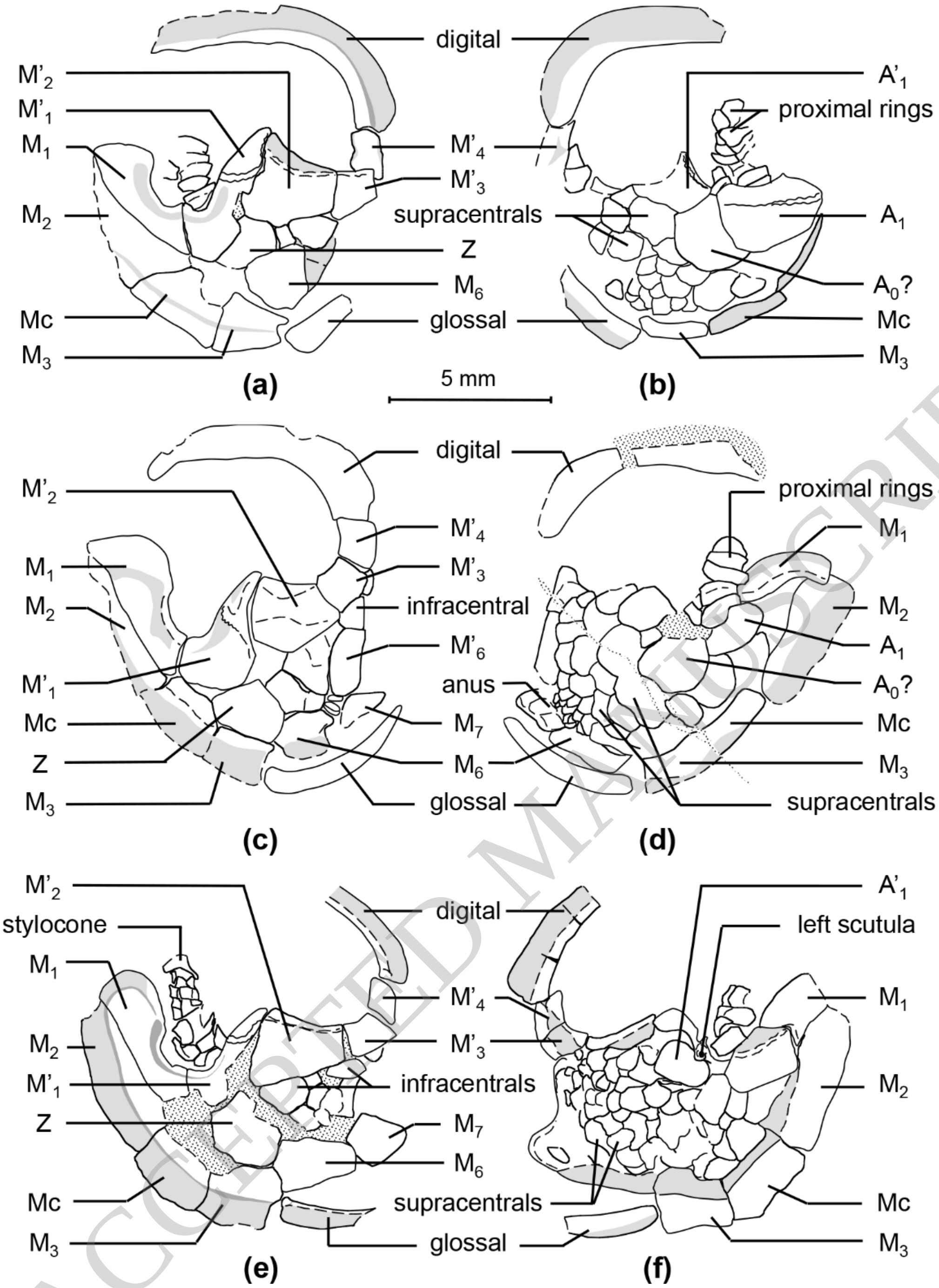
digital
M’$_2$
A’$_1$
M’$_1$
proximal rings
M$_1$
M’$_4$
M’$_3$
M$_2$
supracentrals
A$_1$
Z
M$_6$
A$_0$?
Mc
glossal
Mc
M$_3$
M$_3$
(a)
5 mm
(b)
digital
proximal rings
M’$_2$
M’$_4$
M$_1$
M$_1$
M’$_3$
M$_2$
infracentral
M$_2$
M’$_6$
A$_1$
M’$_1$
anus
A$_0$?
Mc
M$_7$
Mc
Z
M$_6$
M$_3$
M$_3$
glossal
supracentrals
(c)
(d)
M’$_2$
A’$_1$
stylocone
digital
left scutula
M$_1$
M’$_4$
M$_1$
M$_2$
M’$_3$
M’$_1$
infracentrals
M$_2$
Z
M$_7$
M$_6$
Mc
supracentrals
Mc
M$_3$
glossal
M$_3$
(e)
(f)

Figure 8

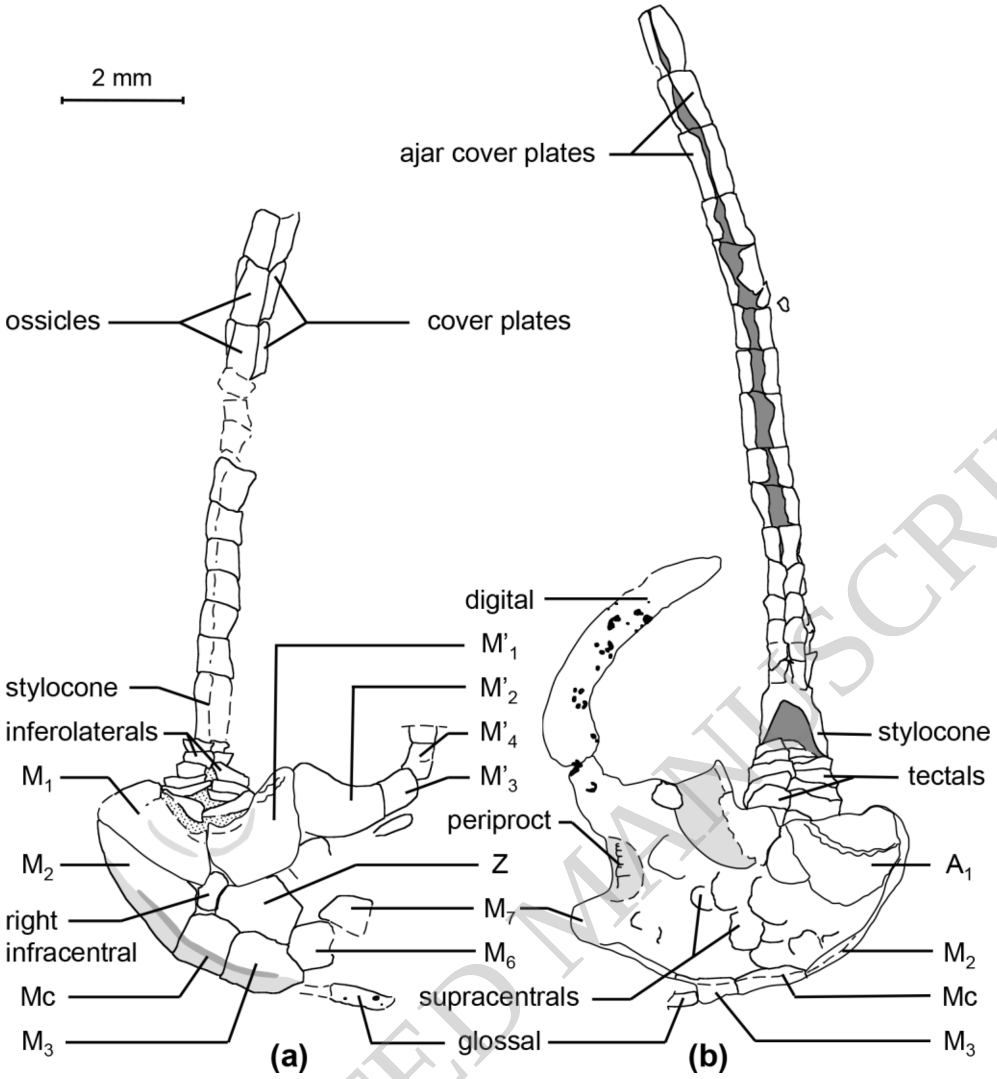
2 mm
ajar cover plates
ossicles
cover plates
digital
M'$_1$
M'$_2$
stylocone
inferolaterals
M'$_4$
M$_1$
M'$_3$
periproct
M$_2$
Z
right infracentral
M$_7$
M$_6$
Mc
supracentrals
M$_3$
(a)
glossal
(b)
stylocone
tectals
A$_1$
M$_2$
Mc
M$_3$

Figure 9

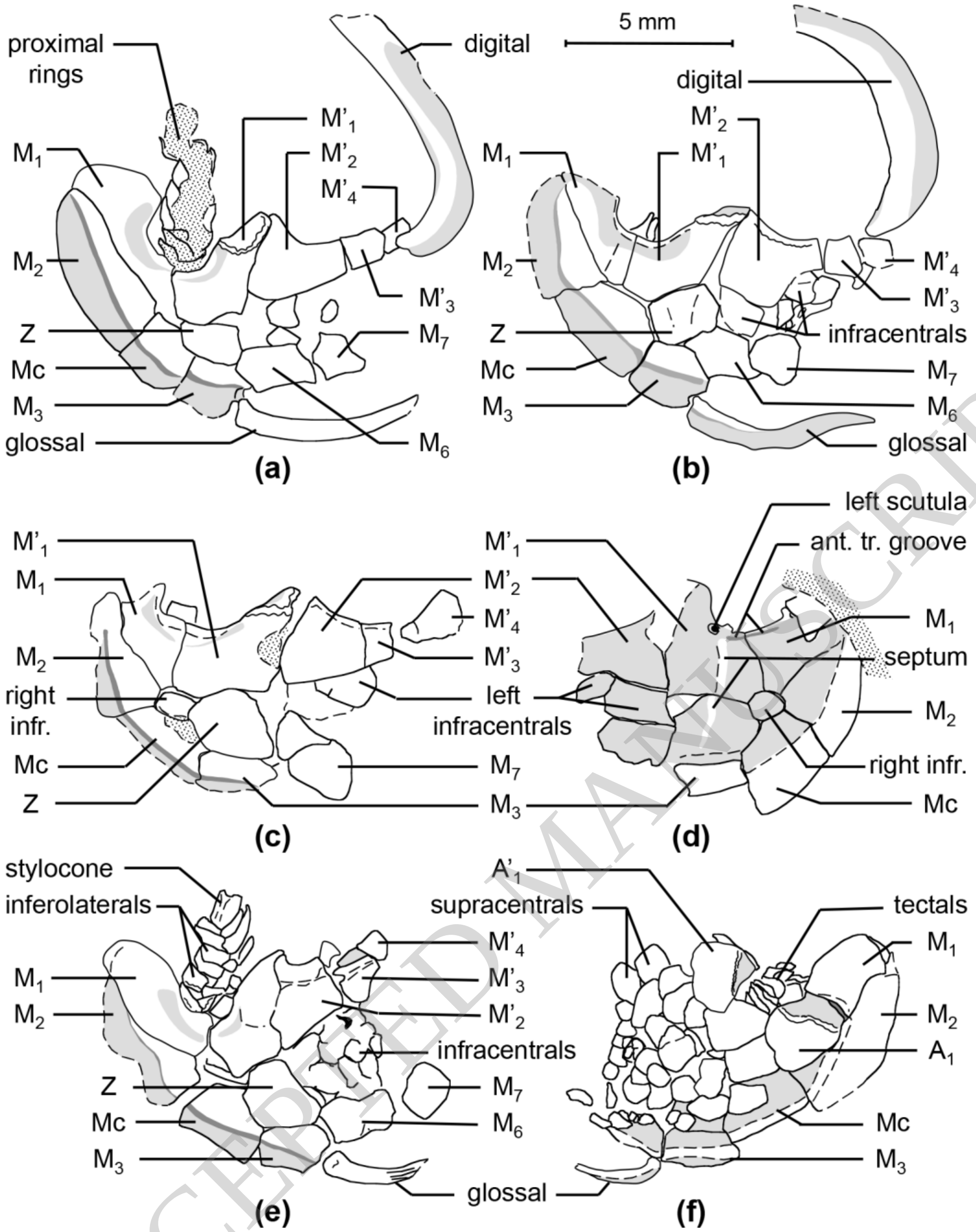
proximal rings
digital
M'_1
M'_2
M'_4
M_1
M_2
M'_3
Z
M_7
Mc
M_3
glossal
M_6
(a)
5 mm
digital
M'_2
M'_1
M_1
M_2
M'_4
M'_3
Z
infracentrals
Mc
M_7
M_3
M_6
glossal
(b)
M'_1
M_1
M'_2
M'_4
M_2
M'_3
right infr.
left infracentrals
Mc
M_7
Z
M_3
(c)
left scutula
ant. tr. groove
M'_1
M_1
septum
M_2
right infr.
Mc
(d)
stylocone
inferolaterals
M'_4
M'_3
M_1
M_2
M'_2
infracentrals
Z
M_7
Mc
M_6
M_3
glossal
(e)
A'_1
supracentrals
tectals
M_1
M_2
A_1
Mc
M_3
(f)

Figure 10

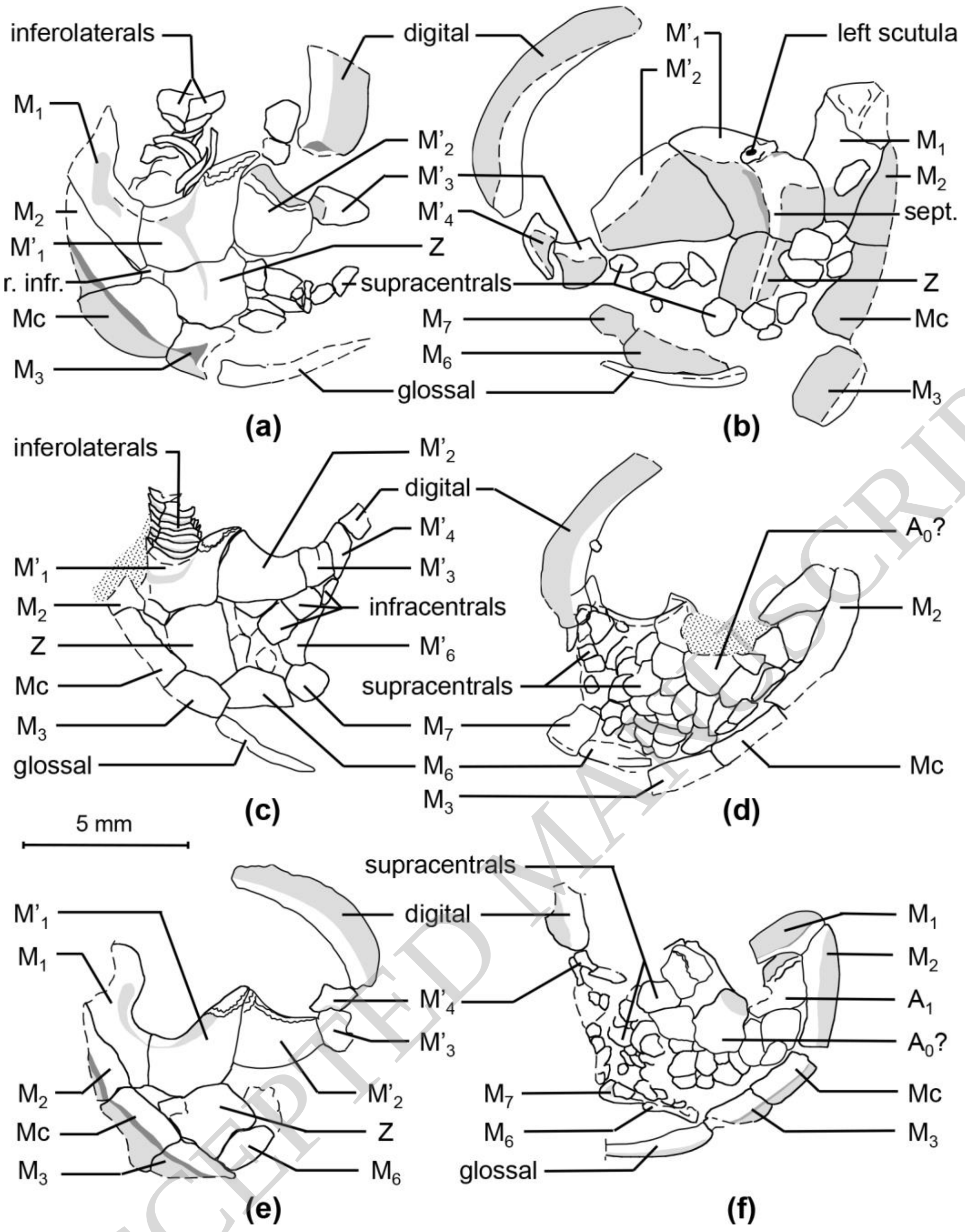
inferolaterals
digital
M_1
M'_2
M'_3
M_2
M'_4
M'_1
Z
r. infr.
supracentrals
Mc
M_7
M_6
M_3
glossal
(a)
M'_1
left scutula
M'_2
M_1
M_2
sept.
Z
Mc
M_3
(b)
inferolaterals
M'_2
digital
M'_4
M'_1
M'_3
M_2
infracentrals
Z
M'_6
Mc
supracentrals
M_3
M_7
glossal
M_6
M_3
(c)
A_0?
M_2
Mc
(d)
5 mm
supracentrals
M'_1
digital
M_1
M_1
M_2
M'_4
A_1
M'_3
A_0?
M_2
M'_2
M_7
Mc
Mc
Z
M_6
M_3
M_3
M_6
glossal
(e)
(f)

Figure 11

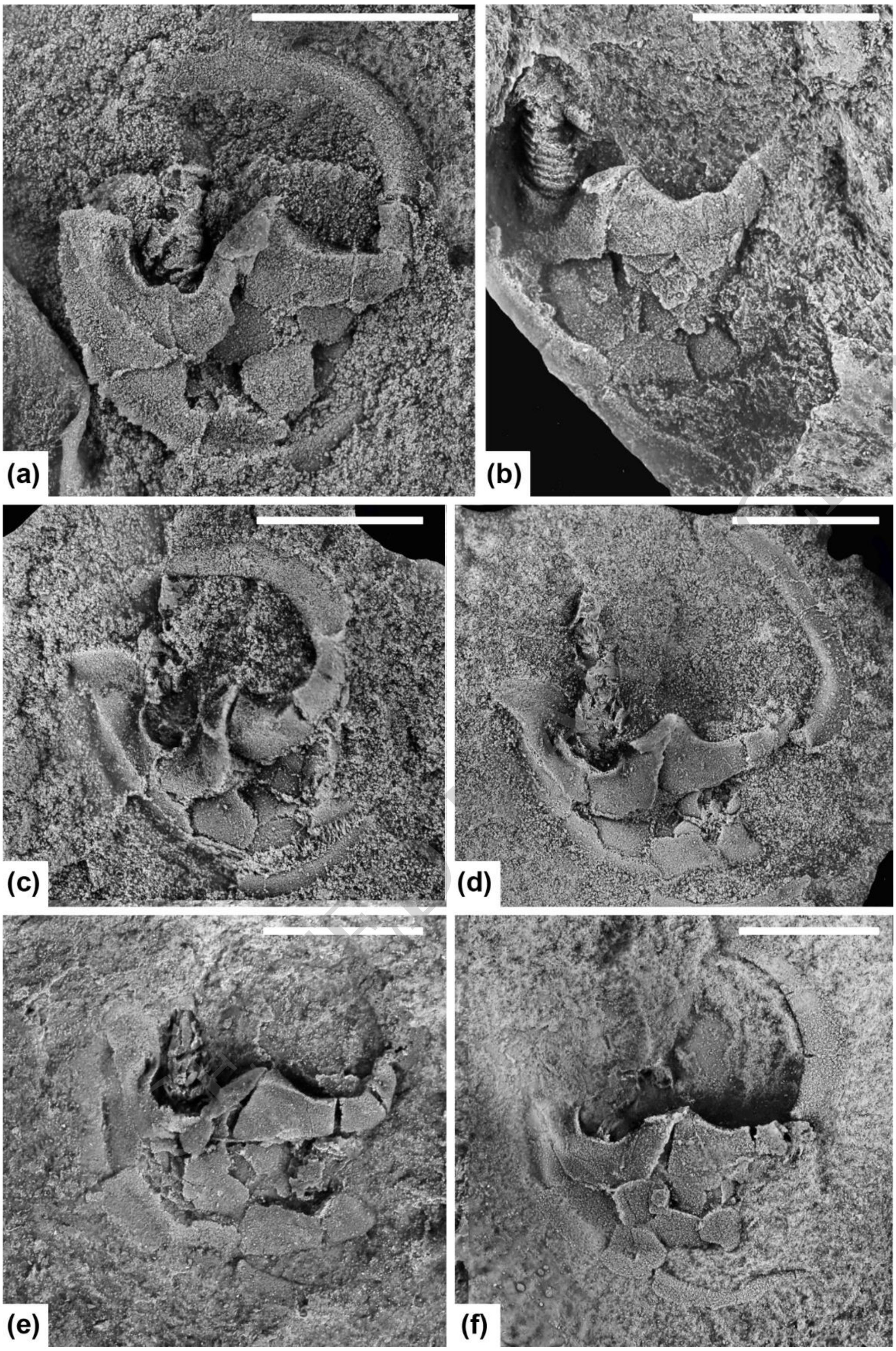

Figure 12

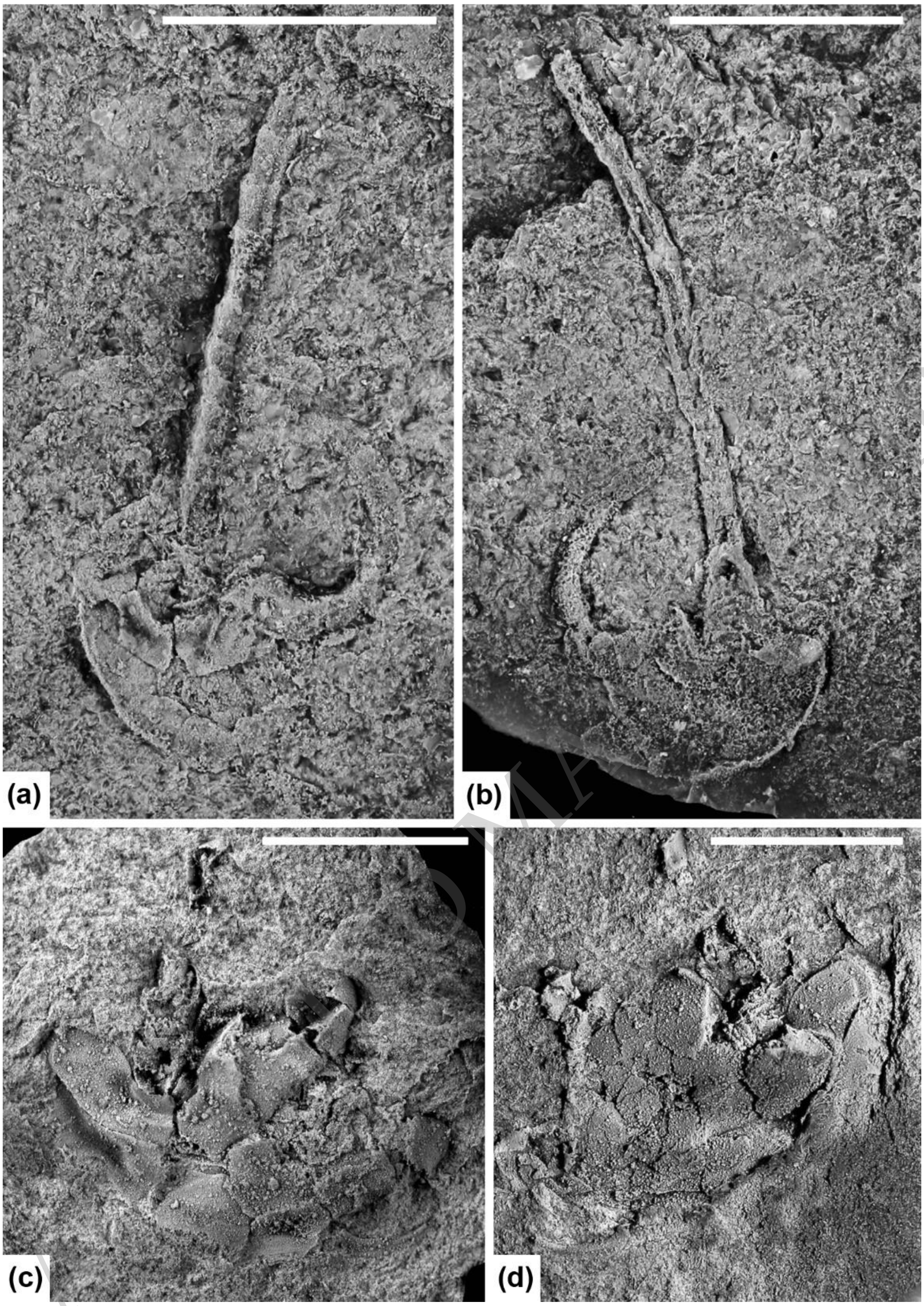

Figure 13

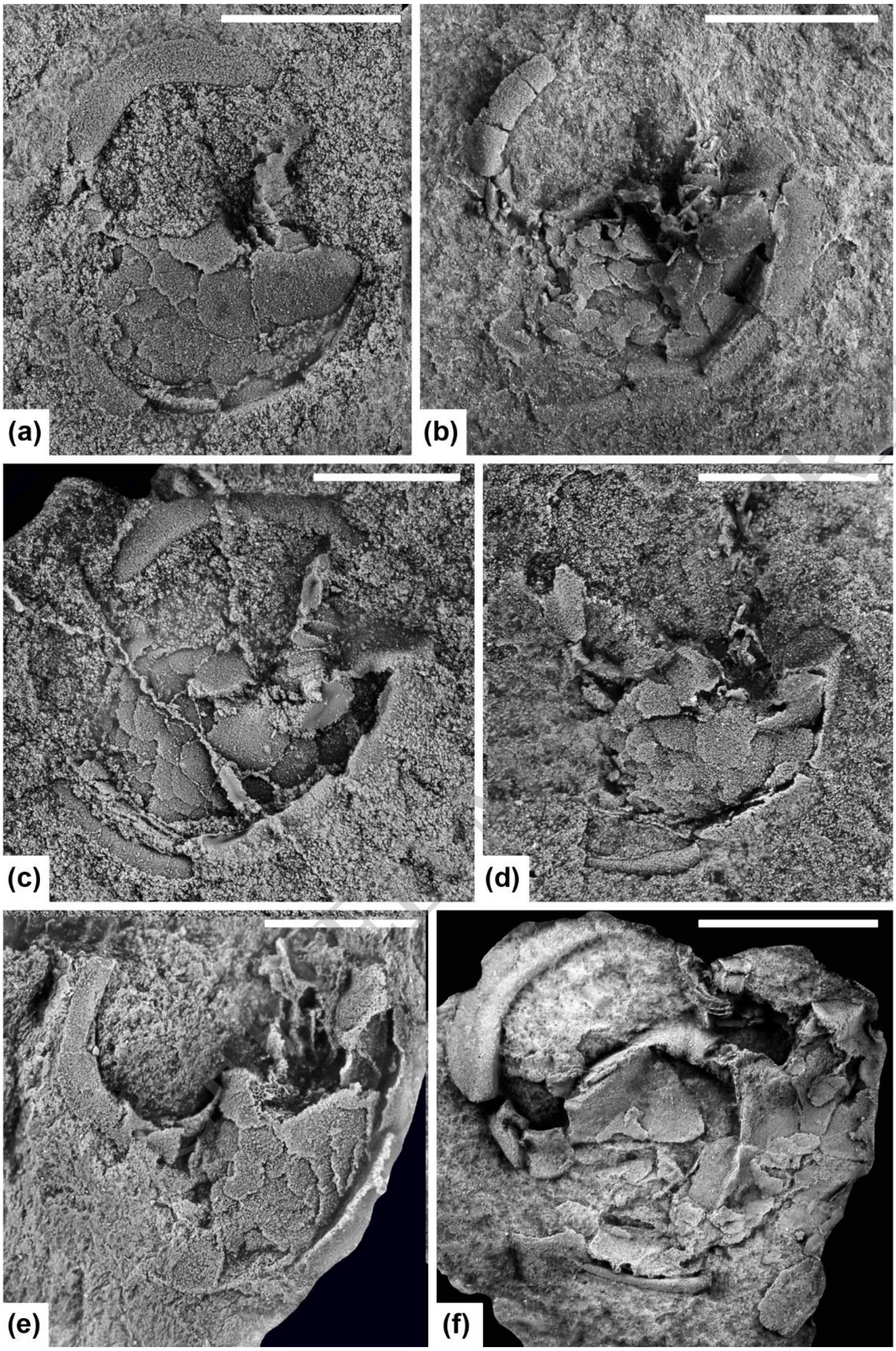

Figure 14