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**Skeletal elements controlled soft-tissue preservation in echinoderms from  
the Early Ordovician Fezouata Biota**

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## Abstract

Exceptional fossils preserve non-biomineralized tissues in the geological record and provide crucial information on the evolution of life on Earth. Exceptionally preserved fossils are rarely discovered complete, challenging their morphological description and their palaeontological interpretation. Although decay experiments reconstructing degradation sequences in modern animals are necessary to better understand taphonomic processes involved in exceptional preservation, their applicability to some enigmatic and/or extinct fossil taxa is limited. Here, based on a representative sample of 423 specimens collected from a single stratigraphic level from the Early Ordovician Fezouata Biota, we reconstruct the degradation sequence of both skeletal remains and soft tissues of stylophorans, an extinct clade of echinoderms. The rare preservation of the water vascular system can be explained by the rapid post-mortem opening of cover plates resulting from the fast decay of associated muscles and the action of ligaments. In contrast, the proximal aulacophore and associated stylocone formed a particularly decay-resistant closed module, thus favouring the preferential preservation of included soft parts (fore-gut). The non-random location and frequency of pyritized intra-skeletal structures strongly suggest that skeletal elements dictated the preservation of underlying soft parts. As such, taphonomic investigations should not only focus on the environment surrounding a decaying animal, but also on the different environments created within a particular carcass.

*Keywords:* Echinodermata, Fezouata Shale, Morocco, Ordovician, Stylophora, taphonomy

## 1. Introduction

Since their first appearance in the fossil record in Cambrian Series 2, echinoderms are characterized by the possession of a multi-element calcite endoskeleton consisting of numerous, highly distinctive (e.g. three-dimensional stereom microstructure) skeletal elements (plates) more or less tightly bound together in life by mesodermal connective soft tissues (Ubaghs, 1968; Kouchinsky et al., 2012; Brusca et al., 2016). A corollary of this constructional pattern is that, within the weeks following the death of an echinoderm, once connective tissues (muscles, then ligaments) have decayed, its skeleton disarticulates into hundreds to thousands of individual elements (Donovan, 1991; Nebelsick, 1995, 2004; Ausich, 2001, 2021). Consequently, the preservation of intact, fully articulated echinoderm skeletons requires very specific taphonomic conditions, generally associated with obrution deposits (e.g. tempestites, turbidites; Brett et al., 1997; Ausich, 2021). The term 'echinoderm Lagerstätten' was coined by Smith (1988) to designate localities yielding such exceptionally preserved, fully articulated skeletal remains of fossil echinoderms (Brett et al., 1997; Nebelsick, 2004; Lefebvre, 2007; Thuy et al., 2011; Rousseau and Nakrem, 2012; Zamora et al., 2013; Cole et al., 2018). Although echinoderm Lagerstätten are known throughout the whole Phanerozoic, they are particularly abundant in the Palaeozoic, bringing invaluable information on the morphology, ontogeny, and/or palaeoecology of the first echinoderms, including those belonging to extinct clades (Durham and Caster, 1963; Sprinkle, 1973; Zhao et al., 2007; Parsley, 2009, 2012). Localities yielding fully articulated echinoderms are often also either Konzentrat-Lagerstätten (i.e. deposits characterized by very dense, packed accumulations of skeletal remains) or Konservat-Lagerstätten (i.e. sites where non-mineralized, soft or lightly sclerotized tissues can be exceptionally preserved) (Seilacher et al., 1985; Brett et al., 1997).

In recent years, the fossil record of exceptionally preserved soft parts in echinoderms (e.g. ambulacral system, gonads, gut) has increased markedly with the development of CT-scan imagery (Sutton et al., 2005; Rahman et al., 2015, 2019; Briggs et al., 2017) and new techniques for fossil preparation (Glass and Blake, 2004). However, in sharp contrast with some other metazoan phyla (e.g. arthropods), fossil evidence of soft tissues remains extremely scarce in echinoderms and restricted to a handful of Palaeozoic Konservat-Lagerstätten: primarily the Fezouata Shale (Lower Ordovician, Morocco; Lefebvre et al., 2019; Saleh et al., 2020a, 2021a), the upper part of the Wenlock Series (Silurian, UK; Sutton et al. 2005; Briggs et al., 2017; Rahman et al., 2019) and the Hunsrück Slate (Lower Devonian, Germany; Glass and Blake, 2004). Whereas plated ambulacral tube feet are relatively common in both bothriocidaroid echinoids (Männil, 1962; Thompson et al., 2022) and ophiocistioids (Rahman et al., 2019), soft parts belonging to the water-vascular system (podia, ambulacral rays, ring canal) are seldom preserved. They have only been reported in a dozen of specimens belonging to six distinct classes: asteroids (Gale, 1987; Sutton et al., 2005), edrioasteroids (Briggs et al., 2017), ophiocistioids (Rahman et al., 2019), ophiuroids (Glass and Blake, 2004; Glass, 2006), stylophorans (Lefebvre et al. 2019), and possibly solutans (Daley, 1996). The occurrence of putative tube feet was also repeatedly mentioned in some crinoids (Schmidt, 1934; Südkamp, 1997; Ausich et al., 2013) and holothurians (Lehman, 1958) from the Hunsrück Slate, but these reports were debated (Seilacher, 1961; Glass and Blake, 2004; Südkamp, 2011; Smith and Reich, 2013). With the exception of the Burlington and Harrodsburg formations (Mississippian, USA), which yielded abundant remains of camerate crinoids with three-dimensionally silicified guts in their calyx (Haugh, 1975), the digestive system was only reported in a handful of specimens belonging to four classes of Palaeozoic echinoderms: blastoids (Rahman et al., 2015), crinoids (Kammer and Ausich, 2007), solutans (Lefebvre et al., 2013; Saleh et al., 2021a), and stylophorans (Lefebvre et al., 2019). Finally, gonads (and

eggs) were so far described in a single female specimen of the blastoid *Pentremites rusticus* (Pennsylvanian, USA; Katz and Sprinkle, 1976; Sevastopulo, 2005). Exceptionally preserved soft parts are crucial for reconstructing the anatomy of extinct organisms and elucidating their phylogenetic affinities (Briggs, 1992; Vinther et al., 2008, 2017; Moysiuk et al., 2017). The nature of the stylophoran appendage (crinoid-like stem, chordate-like tail, hemichordate-like stalk or echinoderm feeding appendage) is a good example of a long-standing, hotly debated palaeontological conundrum (see e.g. Bather 1930; Ubaghs 1961; Jefferies, 1968; Smith, 2005), which could be clarified with the description of exceptionally preserved soft parts (ambulacral tube feet) in a specimen from the Fezouata Shale Lagerstätte (Lefebvre et al., 2019).

So as to better understand the taphonomic processes involved in exceptional preservation in fossil echinoderms, it is thus essential to investigate the successive stages occurring between the death of the organism and the decay of mesodermal connective soft parts, generally leading to the collapse and disarticulation of the skeleton. Field and laboratory decay experiments aiming at reconstructing degradation sequences of extant echinoderms demonstrated that soft parts are entirely decayed within two to three weeks (Meyer, 1971; Kidwell and Baumiller, 1990; Kerr and Twitchett, 2004). The timing of this process can be modulated by temperature, oxygenation, and/or turbulence (Meyer, 1971; Kidwell and Baumiller, 1990; Donovan, 1991; Nebelsick, 1995; Brett et al., 1997; Kerr and Twitchett, 2004). However, studies constraining decay sequences in extinct echinoderms are extremely rare, because they require a large-sized sample corresponding to an 'ecological snapshot' *sensu* Taylor and Brett (1996) (see also Ausich, 2021). Even if a given taxon is exceptionally preserved in several sites, it would be inaccurate to reconstruct its degradation sequence by the combination of data from different localities (and stratigraphic levels), very likely characterized by originally distinct environmental conditions (e.g. turbulence, oxygenation,

pH, temperature). In this study, we aim at reconstructing the degradation sequence of extinct echinoderms (cornute stylophorans), based on a large number of specimens illustrating different stages of decay, and all recovered from a single fossiliferous horizon within the Lower Ordovician Fezouata Shale Lagerstätte (Morocco).

## 2. Geological context

In the Zagora area (Central Anti-Atlas, Morocco), the Fezouata Shale (Tremadocian–Floian) consists of a ~900 m thick succession of blue-green to yellow-green sandy mudstones and siltstones that coarsen upwards (Fig. 1; Destombes et al., 1985; Martin et al., 2016). Sediments in this formation were deposited on a shallow, storm-dominated environment slightly deepening towards the northwest (in present-day orientation) and originally situated at high southern latitudes on the Gondwanan margin (Vaucher et al., 2016, 2017; Saleh et al., 2018, 2020b, 2021a). Two distinct, narrow intervals of the Fezouata Shale yielded abundant remains of organisms with both skeletal and soft tissue preservation (Van Roy et al., 2010; Martin et al. 2016; Vaucher et al., 2016, 2017; Lefebvre et al., 2018; Saleh et al., 2020b, 2021a).

The study material was collected at Bou Izargane (Fig. 1), along the slopes of a small hill located about 18 km north of Zagora (Lefebvre et al., 2019; Saleh et al., 2020a). All fossils were collected from a single, lenticular level (~2.25 m<sup>2</sup> wide and 3 cm thick) of fine, dark blue mudstones occurring ~270 m above the base of the Ordovician succession, within the lower interval with exceptional preservation (*Sagenograptus murrayi* Zone, late Tremadocian; Lefebvre et al., 2016, 2019; Martin, 2016). The Z-F4(15) fossiliferous lens yielded more than 500 specimens belonging to a low diversity assemblage, largely dominated by cornute stylophorans (*Bohemiaecystis* sp., *Chauvelicystis* sp. and *Hanusia* sp.), associated with relatively common trilobites (*Anacheirurus* sp., Asaphidae indet. and *Bavarilla* sp.) and rare

other taxa (brachiopods, graptolites, marrellomorphs, worms) (Fig. 2). Field observations suggest that the Z-F4(15) lens corresponds to three successive, superimposed assemblages (Lefebvre et al., 2019). The stratigraphically lower and less extensive one yielded several specimens of marrellomorphs associated with few trilobites and echinoderms. The intermediate assemblage is dominated by the two trilobites *Anacheirurus* and *Bavarilla*, whereas the upper and most extensive one comprises abundant cornute remains (*Bohemiaecystis*, *Hanusia* and *Chauvelicystis*).

Detailed sedimentological analysis of the Bou Izargane section suggests that the Z-F4(15) lens preserves autochthonous assemblages associated with quiet environmental conditions, right below Storm Wave Base (SWB). These assemblages were occasionally smothered by thin blankets of distal storm deposits, resulting from big storms in proximal settings, that could sometimes transport a little amount of sediment below the SWB (Vaucher et al., 2016; Saleh et al., 2020b). It is very likely that living members of the vagile benthos could escape from burial and are thus not preserved at Bou Izargane (Saleh et al., 2020b, 2021b). This interpretation is supported by the absence (or extreme rarity) of external soft parts and soft-bodied organisms and the occurrence of numerous escape traces across the storm deposits (Saleh et al., 2020b, 2021b). Consequently, it is very likely that fossils from the Bou Izargane Z-F4(15) lens correspond almost exclusively to decaying carcasses, sealed, and protected by a thin layer of sediments providing favourable conditions for exceptional preservation (Saleh et al., 2020b, 2021a). Thus, this locality offers a unique snapshot documenting almost all possible taphonomic grades for both cornute stylophorans and trilobites, ranging from disarticulated individuals to fully articulated ones with exceptionally preserved soft parts (Martin, 2016; Lefebvre et al., 2019; Saleh et al., 2020b).

### **3. Palaeobiology of cornute stylophorans**



The class Stylophora is an extinct clade of echinoderms (Miaolingian–Pennsylvanian), which was particularly abundant, morphologically diverse, and palaeobiogeographically widespread during the late Cambrian (Furongian) – Early Ordovician (Tremadocian and Floian) time interval (Lefebvre et al., 2006, 2013, 2022; Lefebvre, 2007). This class is traditionally subdivided into the two orders Cornuta and Mitrata, with mitrates deriving from paraphyletic cornutes (Jefferies and Prokop, 1972; Derstler, 1979; Cripps, 1991; Parsley, 1997; Lefebvre et al., 2022). The systematics of cornutes (~30 genera ranging from the early Wuliuan to the late Katian) was recently reevaluated by Lefebvre et al. (2022), who identified seven main clades (families). The main palaeobiological features of cornutes are summarized below, with a special emphasis on the three clades (Chauvelicystidae, Hanusiidae and Scotiaecystidae) occurring in the Z-F4(15) stylophoran-dominated lens.

### *3.1. Skeletal morphology*

Descriptive terms used below follow Ubaghs (1963, 1968, 1970) and Lefebvre et al. (2022). Cornutes are characterized by a fundamentally bipartite organization, consisting of a single, delicate, articulated appendage ('aulacophore') inserted into a massive, flattened, and asymmetrical body ('theca') (Fig. 3). The aulacophore (housing the mouth) is considered as anterior, and the theca (bearing the periproct), is posterior (Fig. 3). By convention, the contact between the appendage and the theca is considered as a landmark for orientation: structures close to it are designated 'proximal', and those away from it, 'distal'.

The cornute appendage consists of two distinct, bilaterally symmetrical parts. The first one ('proximal aulacophore') forms a relatively wide, moderately elongate cylindrical structure, posteriorly in contact with the theca (Figs 3, 4). It is made of several imbricate rings ('proximal rings'), each formed by four tightly sutured plates: one upper pair of 'tectals', and one lower pair of more extensive 'inferolaterals'. The proximal aulacophore formed during life

a particularly flexible, telescopic structure, which could be flexed in almost any direction, laterally and vertically (Ubaghs, 1968; Lefebvre, 2003; Clark et al., 2020). The proximal rings were enclosing a wide lumen ('proximal cavity'), which was communicating posteriorly with the main body cavity ('intrathecal cavity') (Fig. 4(B)).

In marked contrast, the second region of the appendage ('distal aulacophore') is particularly long, narrow, and formed a stiff structure. The distal appendage comprises a single lower series of relatively stout, semi-cylindrical 'ossicles' and, articulated to them, two (left and right) upper sets of delicate, fan-shaped 'cover plates' (Fig. 4(A)). The morphology of the proximal-most ossicle ('stylocone') is funnel-shaped, so as to accommodate the transition between proximal rings (posteriorly) and narrower, more distal ossicles (anteriorly). The large posterior region of the stylocone was partly overlapped by distal-most proximal rings and housed the anterior-most extremity of the proximal cavity (Fig. 4(B)). Ossicles are abutting against each other along almost flat interossicular surfaces, thus supporting the view that the distal aulacophore formed a relatively rigid structure (Ubaghs, 1968, 1970; Lefebvre, 2003; Clark et al., 2020; Lefebvre et al., 2022). The lower surface of ossicles is typically smooth and rounded (e.g. *Bohemiaecystis*, *Chauvelicystis*, *Hanusia*; Ubaghs, 1968, 1970; Cripps, 1989; Lefebvre et al., 2022), but a spike can be present in some taxa (e.g. *Nanocarpus*, *Reticulocarpus*; Jefferies and Prokop, 1972; Ubaghs, 1991).

A well-defined, deep 'median longitudinal groove' occurs on the upper (internal) surface of all ossicles. This groove extends from the distal tip of the appendage (anteriorly) to the 'proximal notch' on the stylocone (posteriorly), where it plunges into the proximal cavity (Ubaghs, 1968, 1970; Lefebvre et al., 2019, 2022). On both sides of the longitudinal median groove, the upper surface of each ossicle bears two opposite (left and right) shallow lateral depressions. In most taxa, each lateral depression is connected to the longitudinal median groove by a deep, narrow 'transverse channel'. Left and right cover plates were articulated to

the lateral edges of the upper surface of underlying ossicles (Fig. 4(A)). In cornutes, cover plates are thin, fan-shaped elements, frequently ornamented with delicate radiating ridges. Their movements (opening, closure) were controlled by muscles (internally) and ligament (externally) (Ubaghs, 1970; Lefebvre et al., 2022). However, all cover plates belonging to the same lateral set were partly overlapping each other distally, so that individual movement was not possible.

The theca is strongly flattened and comprises two opposite sides: a flat to slightly concave lower surface, originally in contact with the substrate and a gently convex upper surface, facing the water column. In most cornutes (e.g. *Bohemiaecystis*, *Chauvelicystis*, *Hanusia*), the theca is well-delimited by a series of relatively massive plates ('marginals') forming a delicate but rigid 'marginal frame' (Fig. 4(A)). The two most anterior marginals are always associated to two (e.g. *Bohemiaecystis*, *Hanusia*) or three (e.g. *Chauvelicystis*) additional overlying skeletal elements (the 'adorals'): all together these four (or five) plates are framing the aulacophore insertion. The communication between the proximal lumen and the intrathecal cavity was partly occluded by two vertical walls (the left and right 'apophyses') emitted by the two anterior-most marginals (Fig. 4(B)). In cornutes, the right adoral plate generally bears a distinct orifice ('right adoral orifice'), which is connected to a cavity ('infundibulum') borne by the underlying marginal (Ubaghs, 1968, 1970; Lefebvre et al., 2022). Two grooves radiating from the infundibulum suggest that this cavity was originally communicating with both the proximal lumen (through the 'anterior oblique groove') and the intrathecal cavity (through the 'anterior transverse groove').

Anterior marginals are typically high, thick, and massive. Their lower surface commonly bears protuberances and/or spikes directed downwards and laterally (e.g. *Bohemiaecystis*, *Hanusia*), which probably helped anchoring the organism into the substrate (Ubaghs, 1968, 1970; Parsley, 1988; Lefebvre, 2003). Some other cornutes (e.g. *Chauvelicystis*) are lacking

protuberances but are displaying a fringe of articulated spines along the lateral and/or posterior edges of their marginal frame (Chauvel, 1966; Ubaghs, 1970, 1983; Lefebvre et al., 2022). Posteriorly, the marginal frame regularly decreases in height, with its distal-most elements frequently modified into thin, elongate blade-like processes ('digital', 'glossal' and 'spinal'; Fig. 4(A)), which probably helped maintain the organism on the surface of soft substrates ('snowshoe strategy'; Jefferies and Prokop, 1972; Woods and Jefferies, 1992; Lefebvre, 2003; Lefebvre et al., 2006; Noailles, 2016).

Most of the lower and upper thecal surfaces are paved by numerous, unorganized, adjoining platelets forming two thin, delicate, and flexible integumentary membranes: the 'infracentral' and 'supracentral' areas, respectively (Ubaghs, 1963, 1968; Lefebvre and Vizcaïno, 1999). In cornutes, the lower side of the theca is generally divided into two unequal fields (the 'left and right infracentral areas') by an oblique strut (the 'zygal bar') emitted by two opposite plates of the marginal frame (Fig. 3). On its upper (internal) side, the zygal bar bears a well-defined ridge (the 'zygal crest'), which extends from the posterior wall of the left apophysis (anteriorly) and regularly decreases in height posteriorly, towards the anal opening (Ubaghs, 1968, 1970; Lefebvre et al., 1998, 2022). In hanusiids (e.g. *Hanusia*), a second strut is also present on the upper thecal surface, which is then subdivided into two unequal 'anterior and posterior supracentral areas' (Ubaghs, 1970; Jefferies and Prokop, 1972; Cripps, 1989; Lefebvre et al., 2022). In cornutes, the anal pyramid corresponds to a well-defined, cone-shaped structure occurring either at the posterior extremity of the supracentral area on the upper thecal surface (e.g. *Bohemiaecystis*; Fig. 4(A)) or in a more terminal position at the distal end of the left infracentral and supracentral areas (e.g. *Chauvelicystis*) (Ubaghs, 1968, 1970; Parsley, 1988; Lefebvre et al., 2022).

Respiratory structures also occur within the supracentral area of many cornutes (Ubaghs, 1968, 1970; Lefebvre and Vizcaïno, 1999; Lefebvre et al. 2022). They can consist of

numerous orifices shared by two large adjoining plates and morphologically similar to the 'sutural pores' (or 'epispores') of other echinoderms (e.g. cinctans, edrioasteroids, eocrinoids). Such sutural pores can be distributed everywhere within the supracentral area (e.g. *Nevadaecystis*; Ubaghs, 1963), but they are generally restricted to the right anterior corner of the upper thecal surface (e.g. *Ceratocystis*, *Protocystites*; Ubaghs, 1968; Jefferies, 1969; Jefferies et al., 1987). In several taxa, sutural pores correspond to small-sized, cone-shaped chimneys elaborated at the junction between several adjoining supracentrals. Such pores can be more or less randomly distributed in the right anterior corner of the upper thecal surface (e.g. *Phyllocystis crassimarginata*) or grouped within small clusters ('cothurnopores') protected by two opposite U-shaped elements (e.g. *Chauvelicystis*) (Ubaghs, 1968, 1970; Lefebvre and Vizcaïno, 1999). In some other taxa (e.g. *Bohemiaecystis*; Fig. 4(A)), small chimney-like sutural pores are totally lacking, and respiratory structures correspond to thin, slit-like openings ('lamellipores') between numerous, tightly packed U-shaped plates forming together an elongate, oblique structure ('lamellate organ') in the right anterior corner of the supracentral area (Ubaghs, 1968, 1970; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). Finally, respiratory structures are totally absent in several cornute taxa (e.g. *Hanusia*).

### 3.2. Soft anatomy

Several specimens of the cornutes *Bohemiaecystis* and *Hanusia* extracted from the Z-F4(15) lens at Bou Izargane provided the first evidence of exceptionally preserved soft parts in the stylophoran appendage and theca (Lefebvre et al., 2019). All specimens are preserved in a siliciclastic matrix (argillaceous silts). Structures found within the skeleton are preserved as iron oxides (Figs 5, 6; Lefebvre et al., 2019). Iron oxides are in the shape of small euhedral crystals, and rarely framboids, indicating that intra-skeletal structures were pyritized (Gabbott et al., 2004). Thus, these structures represent real anatomical features that were replaced by

authigenic minerals early on during the fossilization process (Gabbott et al., 2004), and they are not preservational artefacts (Saleh et al., 2020a). Authigenic mineralization through pyritization was shown to play a major role in the preservation of soft tissues in the Fezouata Shale (Saleh et al., 2020b, 2020c, 2021a). Pyrite replicates in this formation replaced the original organic matter of certain tissues that could have been otherwise lost during decay (Saleh et al., 2019, 2020c, 2021a). Pyrite was then weathered by water circulations at outcrop, and S was lost, resulting in the transformation of pyrite crystals in iron oxides (Saleh et al., 2020b, 2021a). An accessory product of this reaction is sulfuric acid (i.e.,  $2\text{FeS}_2 + 19\text{H}_2\text{O} \rightarrow \text{Fe}_2\text{O}_3 + 15\text{H}_2 + 4\text{H}_2\text{SO}_4$ ) (Saleh et al., 2020c, 2021a). The formation of  $\text{H}_2\text{SO}_4$  leads to the dissolution of nearby carbonate in the skeletal parts of calcified taxa, which can explain why skeletal elements of stylophorans are preserved as imprints having the same chemical signal as the matrix (Saleh et al., 2021a).

In Bou Izargane cornutes, exceptionally preserved, pyritized intra-skeletal structures were evidenced in three distinct parts of their body (Lefebvre et al., 2019). In the distal aulacophore, the most obvious 'soft' parts correspond to a well-defined longitudinal canal running within the longitudinal median groove, on the upper surface of the stylocone and all more distal ossicles (Lefebvre et al., 2019). Laterally, this canal gives rise to regularly spaced, narrow, delicate, and elongate tube-like extensions, protruding beyond the cover plates (Figs 4, 5(A)). Proximally, this canal stops at the deep 'proximal notch' of the stylocone. The soft anatomical structures preserved in the Bou Izargane cornutes confirmed previous interpretations of the stylophoran distal aulacophore as a feeding appendage carrying a single ambulacral canal of the water-vascular system (longitudinal canal) and its associated tube feet (lateral extensions) (Ubaghs, 1963, 1968, 1970; Nichols, 1972; Parsley, 1988; David et al., 2000; Lefebvre, 2003). In this context, the proximal notch on the upper surface of the

stylocone very likely corresponds to the mouth (Fig. 4(B)) and the right adoral orifice, to the hydropore (Ubaghs, 1968; Nichols, 1972; David et al., 2000; Lefebvre et al., 2022).

A second, fainter and less regular longitudinal structure was also evidenced, running inside the stylocone and other ossicles, below the ambulacral canal (Fig. 4(B); Lefebvre et al., 2019). No intra-ossicular canal was previously detected in cornutes (no evidence on inter-ossicular facets), but its presence is well-known in mitrates (Jefferies, 1968). This structure was tentatively interpreted as a possible coelomic canal by Lefebvre et al. (2019). However, this seems unlikely because of its irregular aspect and the absence of a clear connection with the proximal cavity. Comparison with other Palaeozoic echinoderms rather suggests that this structure is more likely equivalent to the 'median canal' occurring inside the flooring plates of brachioles in many blastozoans (see Sprinkle, 1973; Clausen et al., 2009; Sheffield and Sumrall, 2019). This median canal probably housed nerves.

A large, elongate, spindle-shaped, intra-skeletal pyritized structure was also documented for the first time within the proximal cavity of Bou Izargane cornutes (Figs 4–6; Lefebvre et al., 2019). Anteriorly, this internal structure extends into the enlarged posterior region of the stylocone, where it tapers upwards into the proximal notch. Posteriorly, this structure is similarly narrowing upwards, along the anterior wall of the apophyses. This internal structure, which is connected to the intrathecal cavity (posteriorly), the mouth, and the water-vascular system (anteriorly), was interpreted as the fore-gut (oesophagus) by Lefebvre et al. (2019). Additional skeletal evidence (labyrinthic stereom meshwork within the posterior region of the stylocone and on the anterior wall of the apophyses) suggests that proximal rings were also housing powerful muscles, which could be flexed to move the whole appendage laterally (Ubaghs, 1968; Clausen and Smith, 2005; Lefebvre et al., 2019; Clark et al., 2020).

Finally, an elongate, relatively complex internal pyritized structure was also evidenced within the intrathecal cavity (Figs 4, 5). Its connection with both the spindle-shaped structure

housed within proximal rings (anteriorly) and the anal pyramid (posteriorly) supports its interpretation as the posterior part of the gut (Lefebvre et al., 2019). This identification is in good accordance with previous hypotheses suggesting that the digestive system of stylophorans was closely associated to the zygial crest (Chauvel, 1941; Caster, 1954; Lefebvre, 1999).

### 3.3. Mode of life

The wide, flattened, lightly built theca of asymmetrical cornutes (e.g. *Bohemiaecystis*, *Chauvelicystis*, *Hanusia*), along with the frequent occurrence of elongate posterior spine-shaped plates represent adaptations for an epibenthic mode of life on soft substrates (Jefferies and Prokop, 1972; Woods and Jefferies, 1992; Lefebvre, 2003; Lefebvre et al., 2006, 2022; Noailles, 2016). With the exception of some heavily plated Cambrian taxa (e.g. *Ceratocystis*), most cornutes were generally living in quiet, low-energy settings (below storm-wave base), where they could locally form particularly dense, gregarious communities (Lefebvre, 2007; Botting et al., 2013; Lefebvre et al., 2016). However, recent reports of abundant cornute remains in Ordovician storm deposits indicate that they could also occur massively in more proximal settings (Lefebvre et al., 2022). By analogy with extant echinoderms (Warner, 1971; Fujita, 1992; Aronson and Blake, 1997), it is possible that such a gregarious mode of life provided several advantages, e.g. for feeding, reproduction, stability and/or protection against slow-moving predators (Lefebvre, 2007). Cornutes were free-living (unattached) mobile organisms, which were very likely capable of active reorientation and limited movements by wagging their aulacophore from side to side. However, the frequent presence of strong protuberances on the lower surface of anterior marginals probably largely hindered any efficient forward movement in most taxa (e.g. *Bohemiaecystis*; Ubaghs, 1968; Parsley, 1988; Lefebvre, 2003; Clark et al., 2020). This interpretation is also supported by the lack (or



extreme reduction) of sediment-gripping devices (e.g. spikes) on the lower surface of ossicles, and the absence of any differentiated interossicular articulations (Lefebvre, 2003).

A low-level suspension-feeding or a detritus-feeding mode of life is generally inferred for cornutes (Ubaghs, 1968; Parsley, 1988; Guensburg and Sprinkle, 2000; Lefebvre, 2007).

Minute food particles were probably collected from the sea water and/or from the surrounding sediment by the tube feet. Cornutes were very likely feeding with their appendage lying over the substrate and facing the current (Parsley, 1988; Lefebvre, 2003, 2007). The frequent preservation of distal aulacophores with widely open cover plates was often interpreted as the original feeding posture of cornutes (Ubaghs, 1968; Parsley, 1988; Lefebvre, 2003; Martin et al., 2015). However, this interpretation was recently questioned by the observation of numerous fully articulated specimens preserved in life position with ajar cover plates (Lefebvre et al., 2022). This rather suggests that, in life, cover plates were probably maintained in a nearly closed position by (internal) muscles, with tube feet protruding in between them (Fig. 4). This implies that the opening of the two lateral sets of cover plates was probably post-mortem and resulted both from the decay of muscles and the antagonistic action of (external) ligaments (Ubaghs, 1970; Lefebvre et al., 2022). The resulting mechanical opening of cover plates in cornutes would then be relatively similar to the post-mortem, ligamentary-induced 'butterfly position' observed in bivalves (Polechová, 2016). Although specialized respiratory structures (sutural pores, cothurnopores, lamellipores) are present in some cornutes, it is very likely that, similarly to the situation in extant echinoderms, ambulacral tube feet were also involved in respiration (Ubaghs, 1968).

#### **4. Material and methods**

The study material comprises 423 specimens of cornutes (Fig. 2(B)) from the lower part of the Fezouata Formation (late Tremadocian). They were all extracted during the same field

campaign (January–February 2014) from the Z-F4(15) lenticular level at Bou Izargane (Zagora Province, Morocco; Fig. 1). Sampling during field work tried to be as exhaustive as possible, but it cannot be excluded that small isolated skeletal elements were possibly under-sampled compared to more eye-catching, complete, articulated individuals. All specimens belong to the palaeontological collections of Cadi-Ayyad University, Marrakesh (Morocco). Thecal width (TW) was estimated perpendicularly to the main body axis (Fig. 3), following the same procedure as in Lefebvre et al. (2022).

All specimens were observed with a Zeiss SteREO Discovery.V8 stereoscopic binocular. For each individual specimen, the quality of preservation of its skeletal remains was estimated based on the taphonomic classification proposed by Martin et al. (2015) for cornute stylophorans. This classification was slightly amended to better describe the diversity of observed taphonomic grades (Fig. 7). For example, taphonomic group 1 was subdivided into the two subgroups (1a) for individuals with closed or ajar cover plates, and (1b) for those with widely open sets of cover plates on both sides of the aulacophore. Similarly, taphonomic group 3 was split into two subsets, corresponding to more or less articulated thecae associated with (3a) proximal rings and the stylocone, or (3b) only the proximal appendage. Moreover, each incomplete individual was coded so as to specify if the missing parts were originally absent or if they could not be observed because of sampling (e.g. specimen broken during extraction in the field) or observational limitations (e.g. only parts of the specimen exposed on the rock surface). Finally, when pyritized intra-skeletal structures were observed, they were coded into three categories related to the region where they were occurring: (A) in the distal appendage (ambulacral canal, ambulacral tube feet, median canal); (B) in proximal rings (fore-gut); and (C) within the theca (mid- and hind-gut).

Specimens were photographed in the palaeontological collections of Lyon 1 University, Villeurbanne (France) with a Canon 5DSR camera, equipped with a MP-E 65 mm macro lens.

## 5. Results

### 5.1. Taphonomy

On large slabs displaying several co-occurring cornutes, individuals are randomly distributed (no obvious orientation) and generally preserved on the same (lower or upper) side (Fig. 8(A)). Rarely, some thecae are twisted, and a few specimens are exposed in lateral position (Fig. 5). Stylophoran skeletal elements are generally relatively poorly preserved, as faint, flattened imprints in the rock, whereas pyritized intra-skeletal remains correspond to colourful (white, yellow, red or purple), three-dimensionally preserved structures (Figs 5, 6). The most abundant cornute, *Bohemiaecystis* sp., displays a wide range of thecal sizes, from relatively small (TW = 7 mm) to very large individuals (TW = 21 mm).

### 5.2. Skeletal elements

Cornute stylophorans from Z-F4(15) can be assigned to two main taphonomic grades. About 30 percent of individuals are characterized by a fully preserved appendage inserted into a more or less complete and articulated theca (Figs 6(C), 9). Most of them display widely open cover plates on both sides of the stylocone and more distal ossicles (taphonomic grade 1b). However, due to the poor preservation of skeletal elements, the imprint left by cover plates is sometimes very faint and hardly visible. For the same reason, it is likely that cover plates are closed or ajar in the rare individuals preserved in lateral position (see below, Fig. 5; taphonomic grade 1a). The theca is sometimes fully articulated, but very often, the two particularly elongate posterior spine-shaped marginals (glossal and spinal) are displaced or missing. Rare individuals display a twisted, fully articulated theca, i.e. with its right, spinal-bearing side superimposed over its left, glossal-bearing margin. With the exception of the single specimen of *Chauvelicystis*, which displays a fully articulated supracentral area (Fig.

10), very little information on the preservation of these thin, delicate membranes is available for individuals belonging to the two other genera. In some individuals, their presence is suggested by numerous faint, tiny, polygonal imprints probably corresponding to poorly preserved integumentary platelets. In specimens of *Bohemiaecystis*, lamellipores are generally clearly visible and fully articulated in the right anterior corner of the upper thecal surface (Fig. 9(B)). In Z-F4(15), the proportion of cornutes belonging to taphonomic grade 1b is probably slightly underestimated, because several fully articulated thecae are located on slab edges, making it impossible to document if the distal appendage was originally present or not.

Around 66 percent of cornute specimens correspond to more or less articulated thecae closely associated to intact proximal rings and stylocone (taphonomic grade 3a; Figs 6(A, B), 8(B–D, G)). Cover plates and more distal ossicles are absent. Posterior spines (glossal, spinal) are seldom present. The marginal frame is sometimes intact, but generally more or less disarticulated, with marginals no longer tightly sutured to each other and frequently slightly displaced. No clear evidence of supracentral or infracentral areas could be observed in these specimens.

Finally, the remaining 4 percent of cornutes correspond mainly to more or less disarticulated thecae, with no associated aulacophore (taphonomic grade 4; Fig. 8(E)) and rare, isolated skeletal elements (taphonomic grade 5). However, the latter are generally well-preserved, intact posterior spine-shaped marginals (glossal, spinal), probably dissociated from nearby individuals belonging to taphonomic grades 1b or 3a (Fig. 8(F)).

### 5.3. *Soft parts*

Clear evidence of pyritized structures corresponding to originally 'soft' parts could be unambiguously observed in five specimens (i.e. about 1.2 percent of the total sample). A single individual (AA.BIZ15.OI.259; Fig. 5(A)) exhibits widespread exceptional preservation

(A+B+C), with pyritized intra-skeletal structures occurring within the distal aulacophore (ambulacral canal and associated tube feet, median canal), proximal rings (oesophagus), and the theca (mid- and hind-gut). This cornute is a fully articulated specimen of *Bohemiaecystis* sp. exposed in lateral position, with its distal aulacophore and posterior thecal spine (spinal) almost parallel to each other and unusually bent upwards. In this specimen, the observation of regularly arranged imbricate cover plates articulated to underlying ossicles strongly suggests that cover plates were either closed or ajar. In lateral view, widely open cover plates would be hardly visible, because they would be almost perpendicular to ossicles.

In specimen AA.BIZ15.OI.110 (Fig. 5(B)), exceptional preservation is restricted to proximal rings (oesophagus) and the intrathecal cavity (mid- and hind-gut) (B+C). In this individual, the spindle-shaped morphology of the elongate fore-gut is remarkably preserved in three dimensions. This specimen of *Hanusia* sp. is exposed in lateral view, with its aulacophore in a straight to gently curved forward position. Similarly to AA.BIZ15.OI.259, the observed arrangement of cover plates in AA.BIZ15.OI.110 indicates that they were not horizontal and widely open on both sides of the distal appendage but vertical and either closed or ajar.

In the last three specimens, exceptional preservation is restricted to proximal rings (B). The spindle-shaped morphology of the fore-gut is particularly obvious in AA.BIZ15.OI.80 (Fig. 6(A)). In this incomplete specimen of *Hanusia* sp. exposed in life position (taphonomic grade 3a), the oesophagus corresponds to a well-defined intra-skeletal reddish structure extending longitudinally across proximal rings, and tapering both anteriorly (into the proximal notch of the stylocone) and posteriorly (towards the apophyses and the intrathecal cavity). A similar spindle-shaped pyritized intra-skeletal structure occurs in two other individuals: AA.BIZ15.OI.58 (Fig. 6(C)) is a specimen of *Bohemiaecystis* sp. consisting of a well-preserved appendage (including widely open cover plates) and a partly disarticulated theca

(taphonomic grade 1b), whereas AA.BIZ.OI.132 (Fig. 6(B)) is a more incomplete cornute (distal appendage restricted to the stylocone), which can be also assigned to *B. sp.* based on the presence of poorly preserved lamellipores (taphonomic grade 3a).

Finally, very faint evidence of putative pyritized intra-skeletal structures restricted to the proximal aulacophore (B) can be documented, though less convincingly, in five additional cornutes belonging to taphonomic grades 1b (AA.BIZ15.OI.30, 41 and 67; Fig. 9(D, E)) and 3a (AA.BIZ15.OI.116, 156).

## 6. Discussion

The occurrence of more than 400 cornutes collected from a same horizon (the Z-F4(15) lens, at Bou Izargane) provides a rare opportunity to document their biostratinomy, and to compare it to the few other studies devoted to stylophoran taphonomy (e.g. Lefebvre, 2007; Martin et al., 2015; Reid et al., 2015; Lefebvre et al., 2016, 2022). In Z-F4(15), the random orientation of cornutes, their preservation in life position (very few individuals upside-down or in lateral aspect), as well as the occurrence of a significant proportion (~30 percent) of fully articulated specimens with even their very delicate sets of cover plates preserved in open position on both sides of the distal aulacophore (taphonomic grade 1b), are all indications suggesting relatively distal, quiet environmental conditions. More incomplete specimens (taphonomic grades 3 to 5) result from the *in situ* collapse of carcasses on the sea floor, and the action of very limited bottom currents (or infaunal organisms?) slightly displacing some skeletal elements. These biostratinomic characteristics are comparable to those reported by Martin et al. (2015) in their third cornute taphofacies, at Jbel Tizagzaouine. They are also in good agreement with sedimentological data suggesting distal, low turbulence (below storm wave base) environmental conditions at Bou Izargane (Vaucher et al., 2016; Saleh et al., 2020b).

Moreover, with the possible exception of the two specimens preserved in lateral position with their cover plates very likely closed or ajar (taphonomic grade 1a; see below), all other cornutes collected in Z-F4(15) correspond to various stages of decaying carcasses (taphonomic grades 1b–5). This result confirms previous biostratinomic interpretations of Bou Izargane assemblages as resulting from the burial of already dead, more or less decayed organisms by a thin blanket of distal storm deposits (Vaucher et al., 2016, 2017; Saleh et al., 2020a, 2020d). The observation of escape traces in Bou Izargane suggests that obrution deposits were not enough to kill most benthic animals in this locality (Saleh et al., 2021c), corroborating why preservation is often solely associated with exposed carcasses decaying on the seafloor. This is the case for most sites preserving soft tissues from this Lagerstätte, except the recently discovered one in Taichoute, in which carcasses were transported by sedimentary flows to a setting well below storm wave, where they got dominantly preserved in concretions (Saleh et al., 2022). The very unusual lateral position of the two specimens AA.BIZ15.OI.110 (Fig. 5(B)) and 259 (Fig. 5(A)) possibly results from their desperate and unsuccessful efforts to escape from obrution deposits: the preservation of their cover plates in closed or ajar position implies that these two cornutes were either alive or recently dead when burial occurred (Lefebvre et al., 2022). If this interpretation is correct, the distal aulacophore of AA.BIZ15.OI.110 then appears surprisingly much shorter (stylocone and seven ossicles, with their associated cover plates) and apparently distally truncated, compared to that of AA.BIZ15.OI.259 (stylocone and over 25 ossicles, and associated cover plates). It is possible that the absence of a significant part of the distal aulacophore of AA.BIZ15.OI.110 results from its autotomy, which is widespread in extant echinoderms submitted to stressful conditions (Ausich, 2021).

The relatively wide range of skeletal disarticulation exhibited by the Z-F4(15) cornutes makes it possible to document that this process did not occur randomly but always following

the same order, with some parts of their skeleton forming more resistant modules than others. The resulting taphonomic sequence of skeletal disarticulation documented in Bou Izargane (Fig. 7) largely confirms the preliminary results of Martin et al. (2015) and their identification of successive taphonomic grades in cornutes (see also Lefebvre et al., 2022). Experimental studies on extant echinoderms indicate that muscles decay faster than ligaments (Ausich, 2021). This probably explains the ligament-induced opening of the cover plates (taphonomic grade 1b; Fig. 7(B)), as a consequence of the decay of the muscles maintaining them in ajar position in life (Fig. 7(A); Lefebvre et al., 2022). In cornutes, the next biostratinomic stage (Fig. 7(C)) corresponds to the loss of the cover plates, the disarticulation of the long posterior thecal spines (glossal and digital), and the collapse of integumentary areas (taphonomic grade 2). This stage is followed by the loss of the distal appendage ossicles and the progressive disarticulation and collapse of most marginals (taphonomic grade 3a). At this stage, the stylocone, the proximal rings and the anterior-most thecal plates framing the aulacophore insertion are still tightly articulated to each other and constitute a relatively decay-resistant module (Fig. 7(D)). The subsequent loss of the stylocone and increased disarticulation of thecal plates are generally associated to the collapse (taphonomic grade 3b; Fig. 7(E)), disarticulation, and loss of proximal rings (taphonomic grade 4; Fig. 7(F)). The last biostratinomic stage (Fig. 7(G)) corresponds to totally dissociated, scattered skeletal elements (taphonomic grade 5).

Soft tissue preservation in stylophorans from the Z-F4(15) lens was limited to a very low number of specimens. The same phenomenon occurs also in the Hunsrück Slate (Emsian, Germany). Although this Lagerstätte yielded hundreds of fully articulated ophiuroids pyritized soft parts (ambulacral tube feet) have only been reported in six specimens of protasterids (Glass and Blake, 2004). Similarly, although trilobites are abundant in the Z-F4(15) lens, lightly sclerotized appendages are exceptionally preserved only in a minority of



individuals (Martin, 2016). Moreover, although pyritization played a major role in soft tissue preservation in Bou Izargane cornutes, not all specimens were equally pyritized. The most complete specimen in terms of exceptional preservation is AA.BIZ15.OI.259 (Fig. 5(A)), in which both the water-vascular and digestive systems are entirely pyritized. Pyritization is less complete in AA.BIZ15.OI.110 (Fig. 5(B)), as only the digestive system is preserved. Finally, in AA.BIZ15.OI.58, 80 and 132 (and less convincingly in five additional specimens; see above), pyritization is restricted to the fore-gut (Figs 6, 9(D, E)). These observations indicate that in most cases, soft parts decayed and disappeared prior to the establishment of permissive conditions suitable for their pyritization.

As skeletal remains of Bou Izargane cornutes document a wide biostratinomic range from alive or recently dead organisms (taphonomic grade 1a) to totally disarticulated individuals (taphonomic grade 5), it can be postulated that the different degrees of pyritization are also the result of varying pre-burial decay of soft parts (Fig. 7). This implies that, when burial occurred, a freshly killed organism had a greater chance of retaining soft parts, that could be eventually pyritized than another individual decaying on the sea floor for several days or weeks (Parry et al., 2018; Saleh et al., 2020a, 2021a). This pre-burial decay of soft parts is not random in Z-F4(15) cornutes, as the oesophagus is the most frequently preserved organ, whereas the water vascular system occurs only in one specimen. This preservational heterogeneity of soft-tissues can be correlated to skeletal element disposition and disarticulation in stylophorans (Fig. 7; Martin et al., 2015).

The progressive disarticulation of the cornute skeleton certainly played a key role during decay by creating different and separate microenvironments within the carcass, thus, controlling the access of scavengers, sea water, and decaying bacteria. In this context, cover plates are the most delicate skeletal elements and the first parts to disarticulate, thus directly exposing the water vascular system (taphonomic grade 1b; Fig. 7(B)). Concomitantly, the

collapse of integumentary areas and the progressive disarticulation of marginals certainly result in the disappearance of the intrathecal cavity (taphonomic grade 1b; Fig. 7(B)). Until their final disarticulation, the stylocone, the proximal aulacophore and associated anterior-most thecal plates together formed the most resistant skeletal module in cornutes (taphonomic grade 3a; Fig. 7(B–D)). In life, this module was housing powerful muscles and the oesophagus. This remarkable correlation between skeletal disarticulation, and the distribution and frequency of exceptionally preserved soft parts within the body are in good accordance with results from probabilistic modelling highlighting that the presence of solid mineralized skeletal parts favoured the preservation of underlying soft-tissues within the Fezouata Shale (Saleh et al., 2020d, 2021c). The role of proximal rings in preserving the oesophagus might not have been limited to slowing down pre-burial decay by isolating the tissue from its surrounding environmental conditions. It is most likely that the relatively closed environment within proximal rings also created more permissive conditions for pyrite precipitation than in the rest of the carcass. All these suggestions do not exclude that the favourable preservation/loss of some tissues might be controlled as well, at least partially, by their own chemical compositions, enzymes, and bacterial communities (Lerosey-Aubril et al., 2012; Hancy and Antcliffe, 2020).

## **7. Conclusions**

A single upper Tremadocian level of the Fezouata Shale (i.e. the Z-F4(15) lens at Bou Izargane, Zagora area, Morocco) yielded a low diversity assemblage dominated by cornutes (more than 400 specimens belonging to three distinct taxa), associated with arthropods (marrellomorphs, trilobites), brachiopods, graptolites, and worm-like organisms. The detailed biostratigraphic analysis of this stylophoran dense bed made it possible to reconstruct with unprecedented detail the sequence of skeletal disarticulation in cornutes originally proposed

by Martin et al. (2015). Moreover, structures preserved within the skeleton of several cornutes from Z-F4(15) represent replicates of original tissues in pyrite crystals (Lefebvre et al., 2019; Saleh et al., 2020a). Here, we suggest that the frequency and distribution of exceptionally preserved soft parts in cornutes is not random but directly controlled by their heterogenous exoskeleton. Their water vascular system is only partially protected by moveable cover plates. These plates are the first skeletal elements to disarticulate after death, thus exposing the water vascular system to water chemistry, external bacteria, and scavengers. In contrast, the oesophagus is the last organ to decay, because it is fully protected by resistant proximal rings. The correlation between skeletal element disarticulation and soft tissue degradation in stylophorans highlights that non-random decay pathways exist within echinoderms. However, generalization on different animal groups, and other fossiliferous localities should be made carefully, due to differences in biotic and abiotic conditions.

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**Figure captions**

**Fig. 1.** Geographical and geological context of the Bou Izargane locality. **A.** Location of B in Africa. **B.** Location of C and main areas of Ordovician outcrops in northwestern Africa; scale bar: 200 km. **C.** Location of Bou Izargane hill and main areas of Ordovician outcrops in the Zagora area, Central Anti-Atlas (Morocco); scale bar: 50 km. **D.** Sedimentary succession at Bou Izargane hill showing the location of the Z-F4(15) stylophoran dense bed, lower part of the Fezouata Formation (*S. murrayi* Zone; upper Tremadocian); adapted from Martin (2016), Lefebvre et al. (2019), and Saleh et al. (2020b).

**Fig. 2.** Taxonomic composition and relative abundance of taxa within the Z-F4(15) level at Bou Izargane (Zagora area, Morocco), lower part of the Fezouata Formation (*S. murrayi* Zone; upper Tremadocian); n: number of specimens. **A.** Global composition and relative abundance of main taxonomic groups occurring within the Z-F4(15) low diversity echinoderm dense bed; other taxa include brachiopods, graptolites, marrellomorphs, and worm-like organisms. **B.** Taxonomic composition and relative abundance of the echinoderm component of the Z-F4(15) assemblage. **C.** Taxonomic composition and relative abundance of trilobites within the stylophoran dense bed. Redrawn and modified from Martin (2016).

**Fig. 3.** Skeletal morphology, orientation and measurement of thecal width (TW) in the cornute stylophoran *Bohemiaecystis* sp. from the lower part of the Fezouata Formation (upper Tremadocian), Zagora area, Central Anti-Atlas (Morocco). Reconstruction of lower side, with cover plates in open, post-mortem position.

**Fig. 4.** Skeletal morphology and associated soft parts of the cornute stylophoran *Bohemiaecystis* sp. from the lower part of the Fezouata Formation (upper Tremadocian), Zagora area, Central Anti-Atlas (Morocco). **A.** Reconstruction of upper side, with ambulacral tube feet protruding in between ajar cover plates. Some skeletal elements are removed or sectioned, so as to illustrate the internal anatomy. **B.** Longitudinal cross section along A-A' in A.

**Fig. 5.** Cornutes with exceptionally preserved soft parts, level Z-F4(15), Bou Izargane, Zagora Province, Morocco, lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale bars: 5 mm. **A.** *Bohemiaecystis* sp. (AA.BIZ15.OI.259): complete, fully articulated specimen in lateral aspect (taphonomic grade 1a); pyritized, dark intra-skeletal structures are preserved in the distal aulacophore (longitudinal ambulacral canal and regularly spaced tube feet), in proximal rings (fore-gut) and within the theca (mid- and hind-gut). **B.** *Hanusia* sp. (AA.BIZ15.OI.100): fully articulated individual in lateral view; anterior truncature of distal aulacophore, possibly resulting from autotomy (taphonomic grade 1a); pyritized, dark intra-skeletal structures are preserved in proximal rings (spindle-shaped fore-gut) and also within the theca (mid- and hind-gut).

**Fig. 6.** Cornutes with exceptionally preserved soft parts, level Z-F4(15), Bou Izargane, Zagora Province, Morocco, lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale bars: 2 mm. **A.** *Hanusia* sp. (AA.BIZ15.OI.80): complete, slightly disarticulated theca (in upper aspect), with proximal aulacophore and stylocone (taphonomic grade 3a); the red, elongate intra-skeletal structure extending longitudinally within the proximal appendage corresponds to the oesophagus; the fore-gut is tapering both anteriorly (into the stylocone notch) and posteriorly (towards the thecal apophyses). **B.** *Bohemiaecystis*

1014 sp. (AA.BIZ15.OI.132): incomplete, disarticulated theca, with poorly preserved lamellipores,  
1015 and appendage restricted to proximal rings and stylocone (taphonomic grade 3a); the red,  
1016 elongate intra-skeletal structure extending longitudinally within the proximal appendage  
1017 probably corresponds to the oesophagus. **C.** *Bohemiaecystis* sp. (AA.BIZ15.OI.58): partly  
1018 disarticulated, incomplete theca (broken during sampling) and complete, fully articulated  
1019 aulacophore, with cover plates in open position (taphonomic grade 1b); the yellow, elongate  
1020 intra-skeletal structure extending longitudinally within the proximal appendage probably  
1021 corresponds to the oesophagus.

1022

1023 **Fig. 7.** Degradation sequence of the cornute stylophoran *Bohemiaecystis* sp., based on the  
1024 observation of 410 individuals from level Z-F4(15), Bou Izargane (Zagora area, Morocco),  
1025 lower part of the Fezouata Formation (*S. murrayi* Zone, upper Tremadocian). **A.** Taphonomic  
1026 grade 1a. **B.** Taphonomic grade 1b. **C.** Taphonomic grade 2. **D.** Taphonomic grade 3a. **E.**  
1027 Taphonomic grade 3b. **F.** Taphonomic grade 4. **G.** Taphonomic grade 5.

1028

1029 **Fig. 8.** Cornutes from level Z-F4(15), Bou Izargane, Zagora Province, Morocco, lower part of  
1030 the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale bars: 2 mm. **A.**  
1031 *Bohemiaecystis* sp. (AA.BIZ15.OI.69): three side by side, differently oriented, slightly  
1032 disarticulated individuals in upper aspect. **B.** *Bohemiaecystis* sp. (AA.BIZ15.OI.109): slightly  
1033 disarticulated theca (with well-preserved lamellipores) in upper aspect, proximal rings and  
1034 stylocone; more distal ossicles and cover plates missing (taphonomic grade 3a). **C.** *Hanusia*  
1035 sp. (AA.BIZ15.OI.30): slightly disarticulated theca in upper aspect, proximal rings and  
1036 stylocone (taphonomic grade 3a). **D.** *Bohemiaecystis* sp. (AA.BIZ15.OI.101): slightly  
1037 disarticulated theca in lower aspect, with long spinal blade, proximal aulacophore and  
1038 stylocone. **E.** *Bohemiaecystis* sp. (AA.BIZ15.OI.94): poorly preserved, partly disarticulated,



1039 with elongate spinal blade; aulacophore entirely missing (taphonomic grade 4). **F.**

1040 *Bohemiaecystis* sp. (AA.BIZ15.OI.136): on the left, isolated spinal blade (taphonomic grade

1041 5); on the right, stump of fully articulated distal aulacophore consisting of nine ossicles and

1042 associated cover plates in closed position (taphonomic grade 1a), and possibly corresponding

1043 to an autotomized portion of appendage. **G.** *Bohemiaecystis* sp. (AA.BIZ15.OI.202):

1044 incomplete, slightly disarticulated theca in upper view, with distinct lamellipores;

1045 aulacophore consisting of proximal rings and stylocone (taphonomic grade 3a).

1046

1047 **Fig. 9.** Well-preserved cornutes, level Z-F4(15), Bou Izargane, Zagora Province, Morocco,

1048 lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale

1049 bars: 2 mm. **A.** *Bohemiaecystis* sp. (AA.BIZ15.OI.249): slightly disarticulated theca in lower

1050 aspect, with well-preserved left posterior spine (digital), and complete aulacophore, with

1051 widely open cover plates (taphonomic grade 1b). **B.** *Bohemiaecystis* sp. (AA.BIZ15.OI.289):

1052 slightly disarticulated theca in lower aspect, with elongate isolated glossal lying posteriorly to

1053 it; proximal rings well-preserved, but more putative more distal parts of aulacophore not

1054 visible (unexposed). **C.** *Bohemiaecystis* sp. (AA.BIZ15.OI.227): fully articulated, complete

1055 theca and aulacophore (in upper aspect), with widely open cover plates (taphonomic grade

1056 1b). **D.** *Hanusia* sp. (AA.BIZ15.OI.67): complete, slightly disarticulated theca in lower

1057 aspect; well-preserved aulacophore with widely open cover plates (taphonomic grade 1b); the

1058 white, elongate intra-skeletal structure extending longitudinally within proximal rings

1059 possibly represents a poorly preserved oesophagus. **E.** *Bohemiaecystis* sp. (AA.BIZ15.OI.41):

1060 slightly disarticulated theca, posteriorly broken during sampling; well-preserved aulacophore,

1061 with widely open cover plates; the white, elongate intra-skeletal structure extending

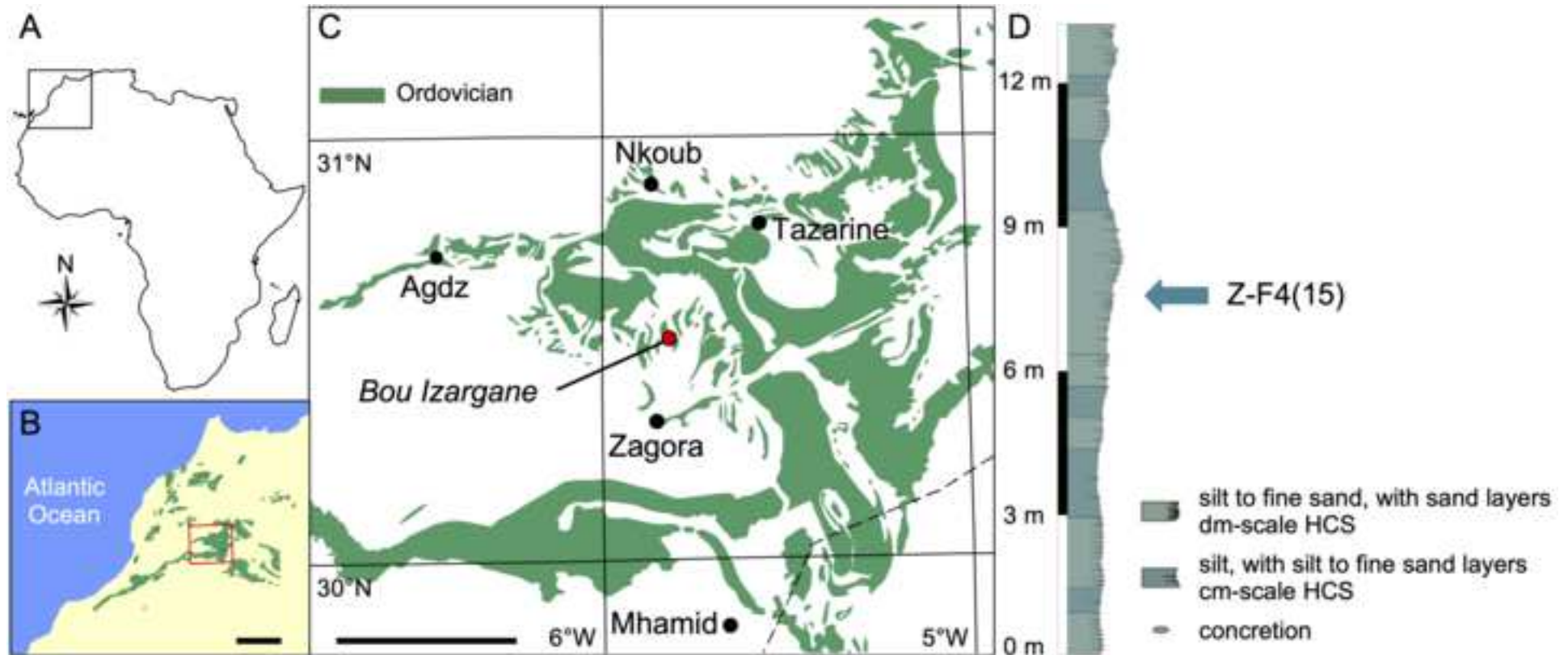
1062 longitudinally within the proximal aulacophore probably corresponds to the fore-gut. **F.**

1063 *Bohemiaecystis* sp. (AA.BIZ15.OI.235): well-preserved, fully articulated distal aulacophore,  
1064 with wide open cover plates, still attached to underlying ossicles.

1065

1066 **Fig. 10.** *Chauvelicystis* sp. (AA.BIZ15.OI.121), Bou Izargane, Zagora Province, Morocco,  
1067 lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian); scale bar: 2  
1068 mm. Fully articulated theca (including very well-preserved supracentral area) and proximal  
1069 rings in upper aspect; right thecal side unexposed; distal aulacophore broken during sampling.

1070



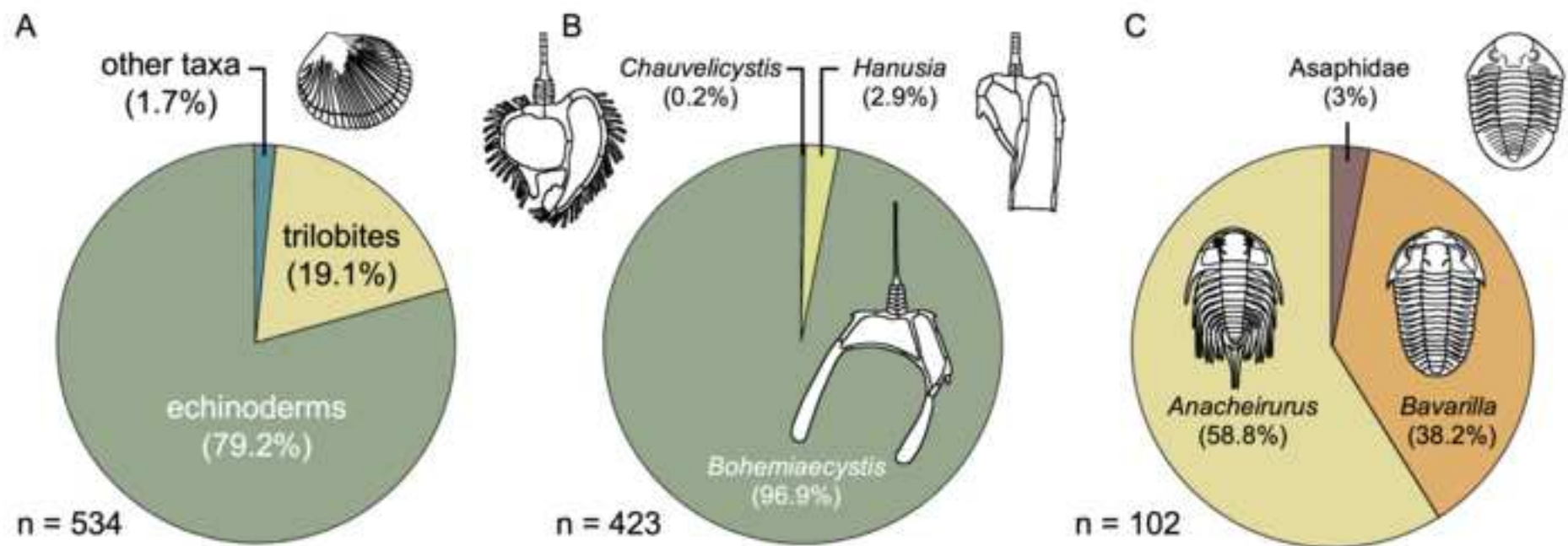


Figure 3

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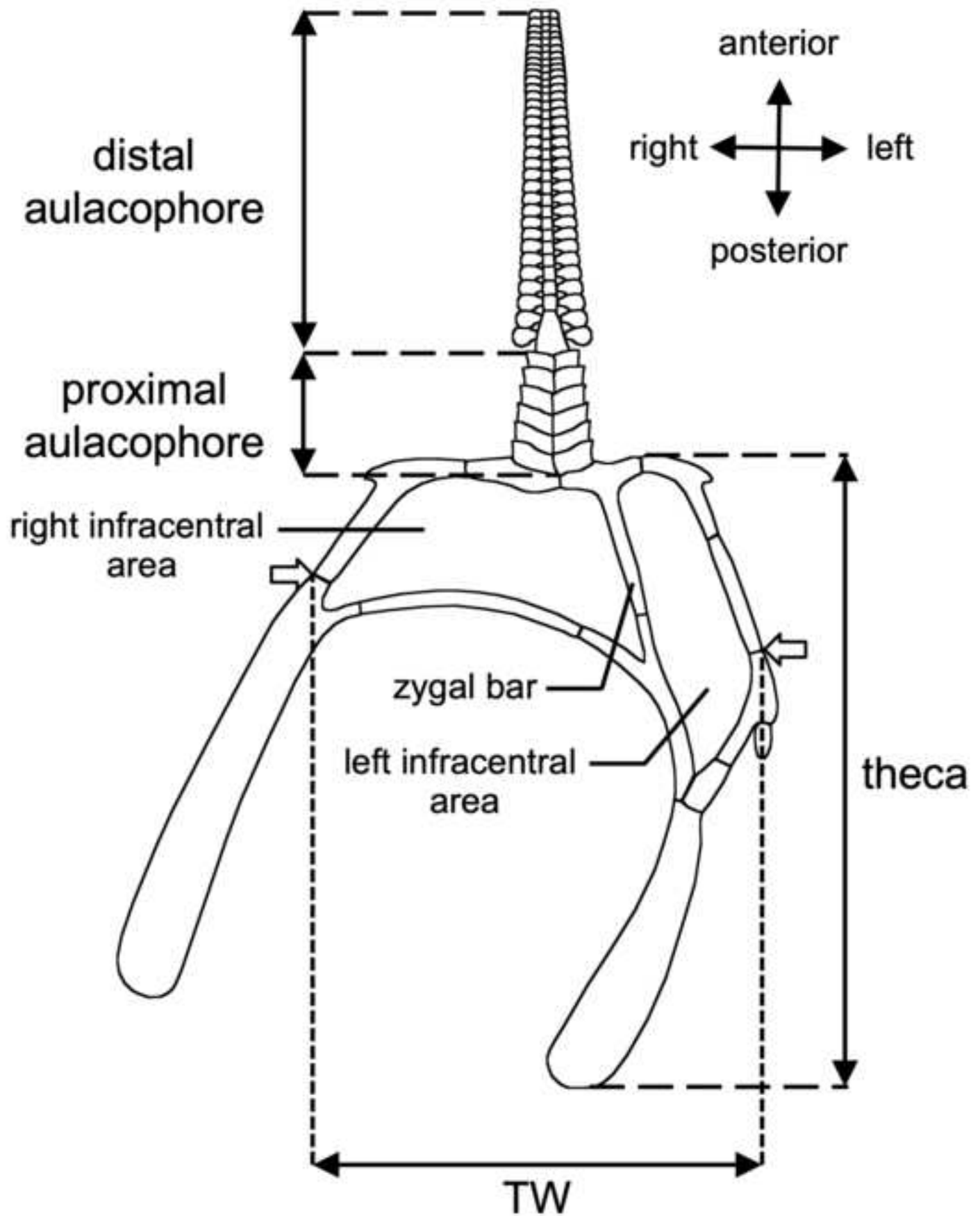


Figure 4

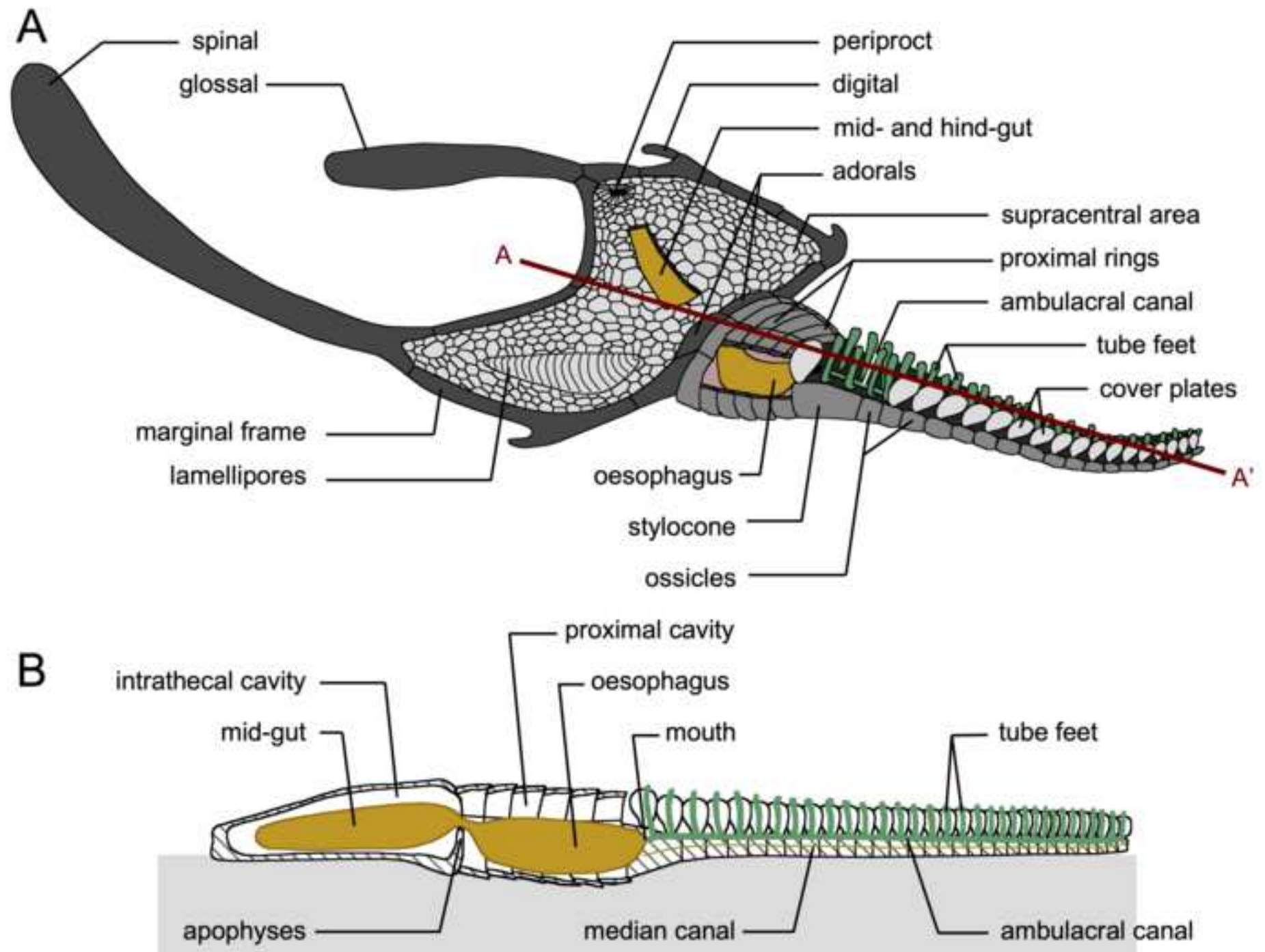




Figure 5

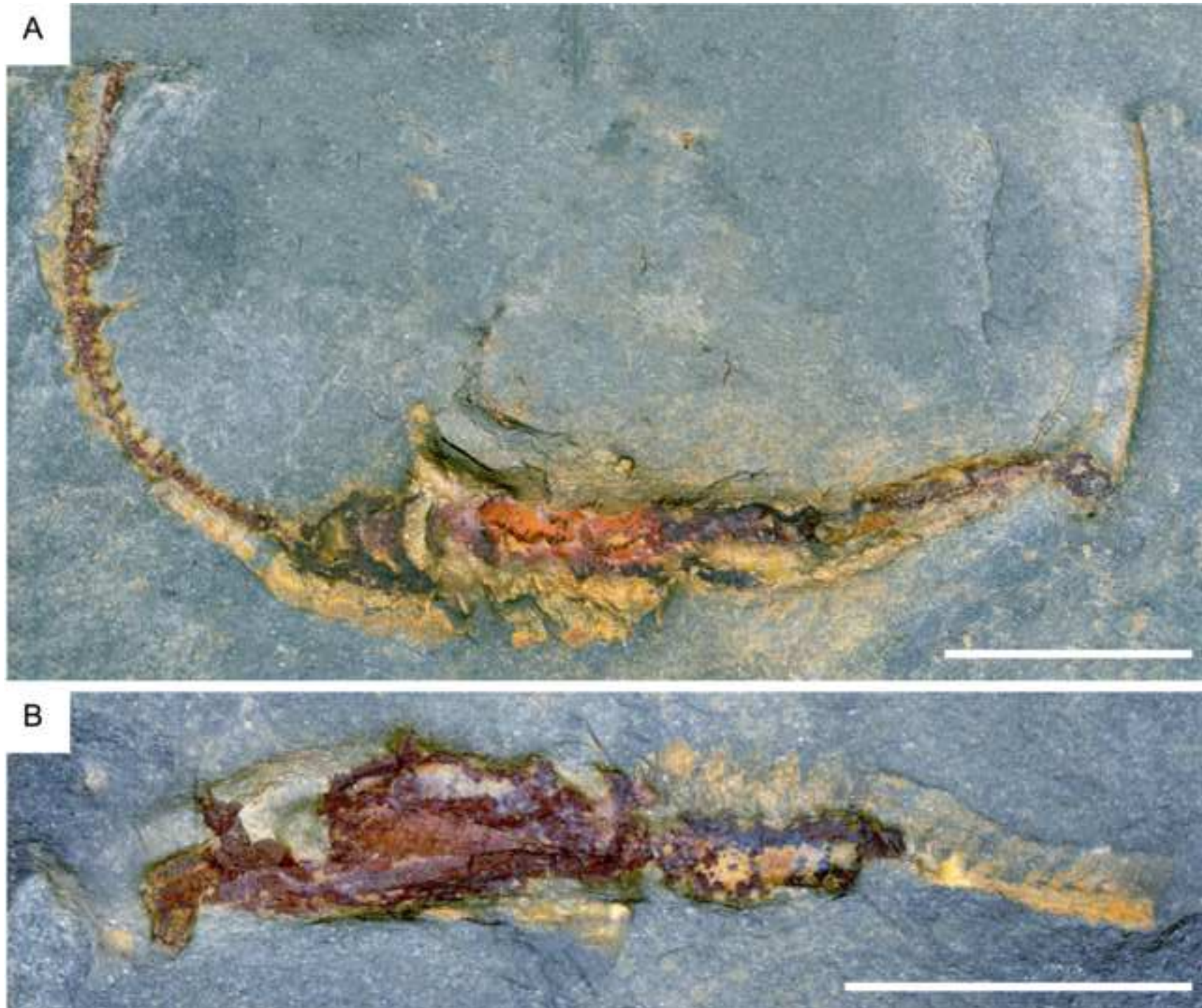
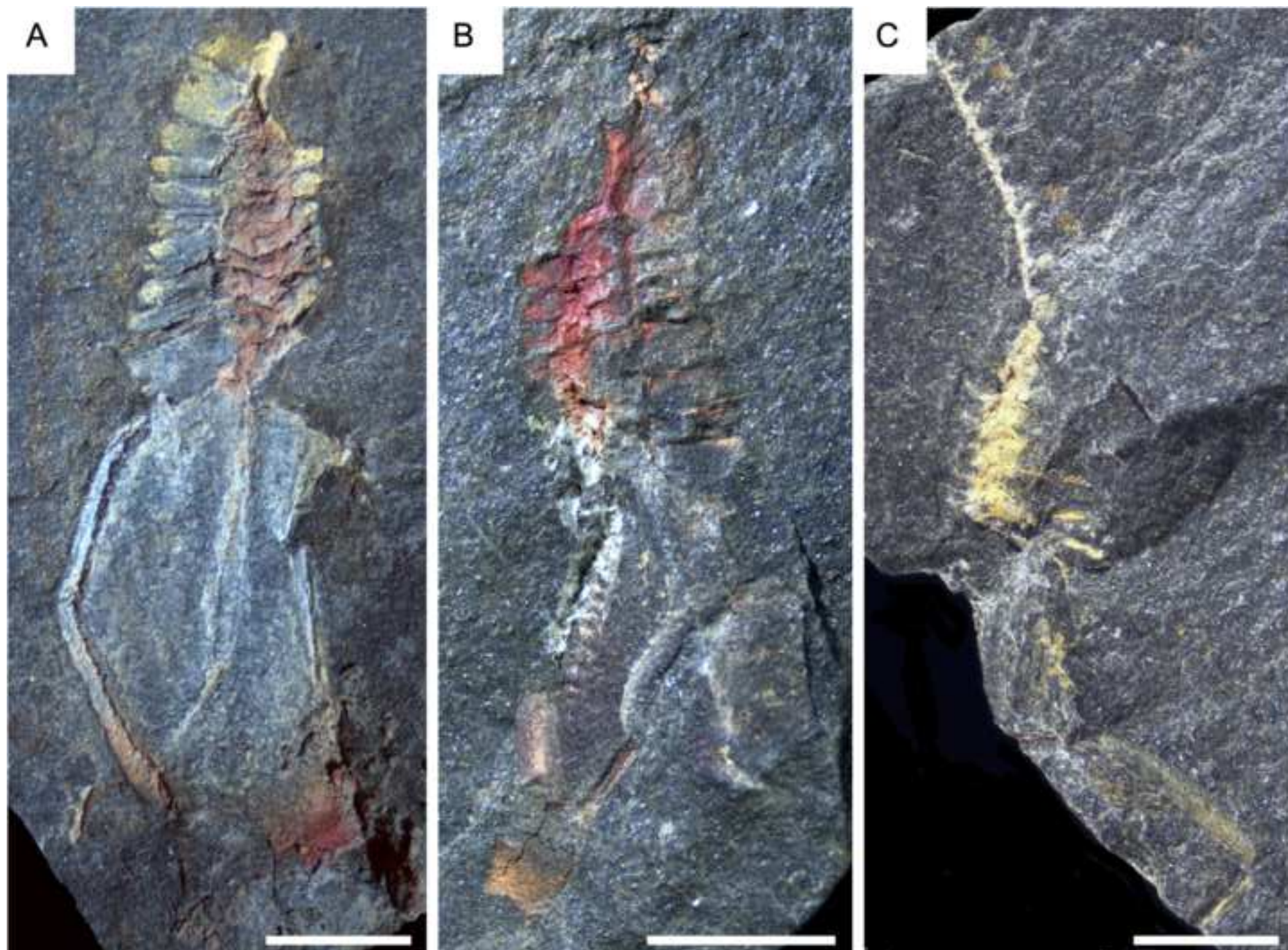




Figure 6





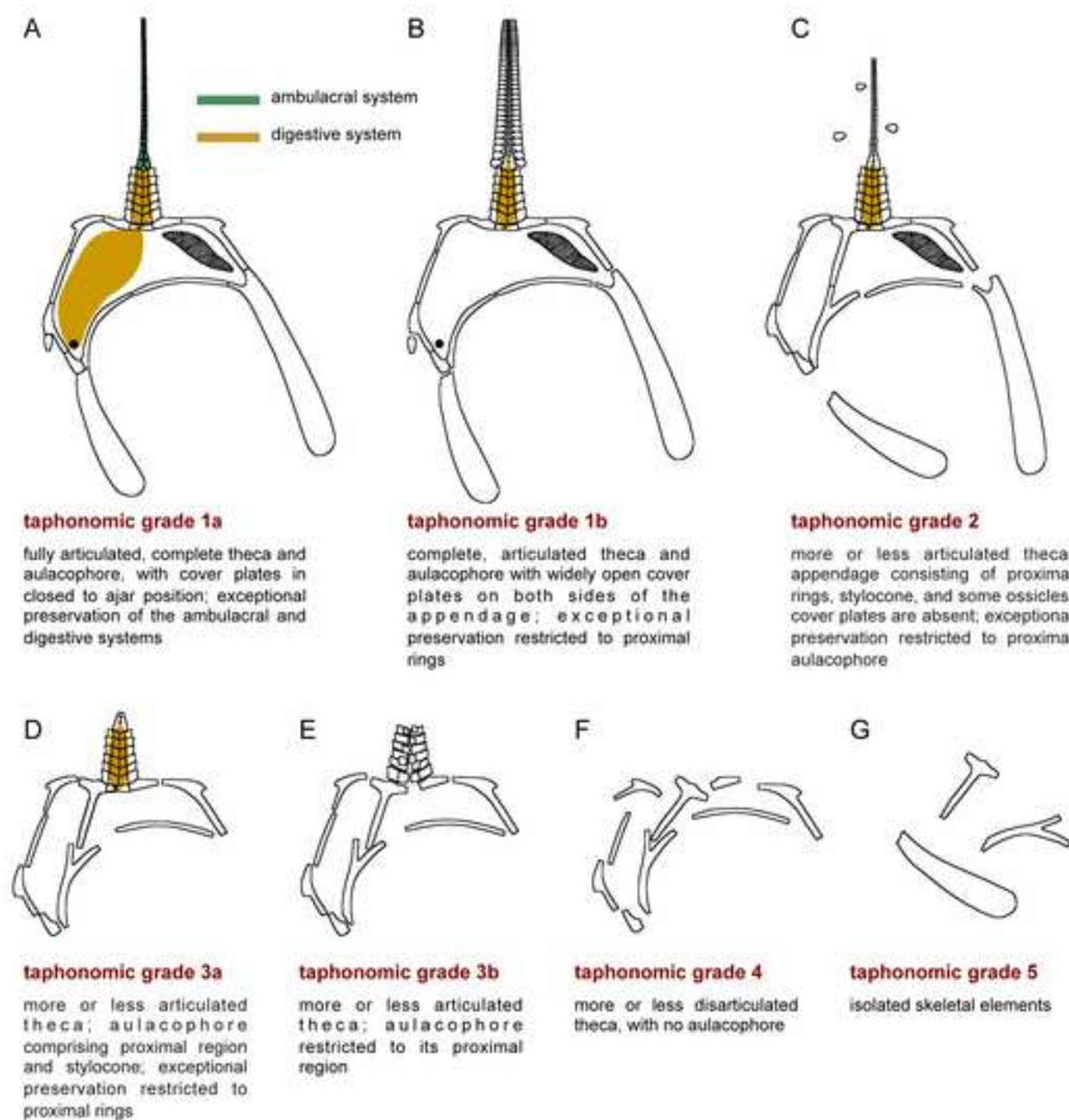


Figure 8

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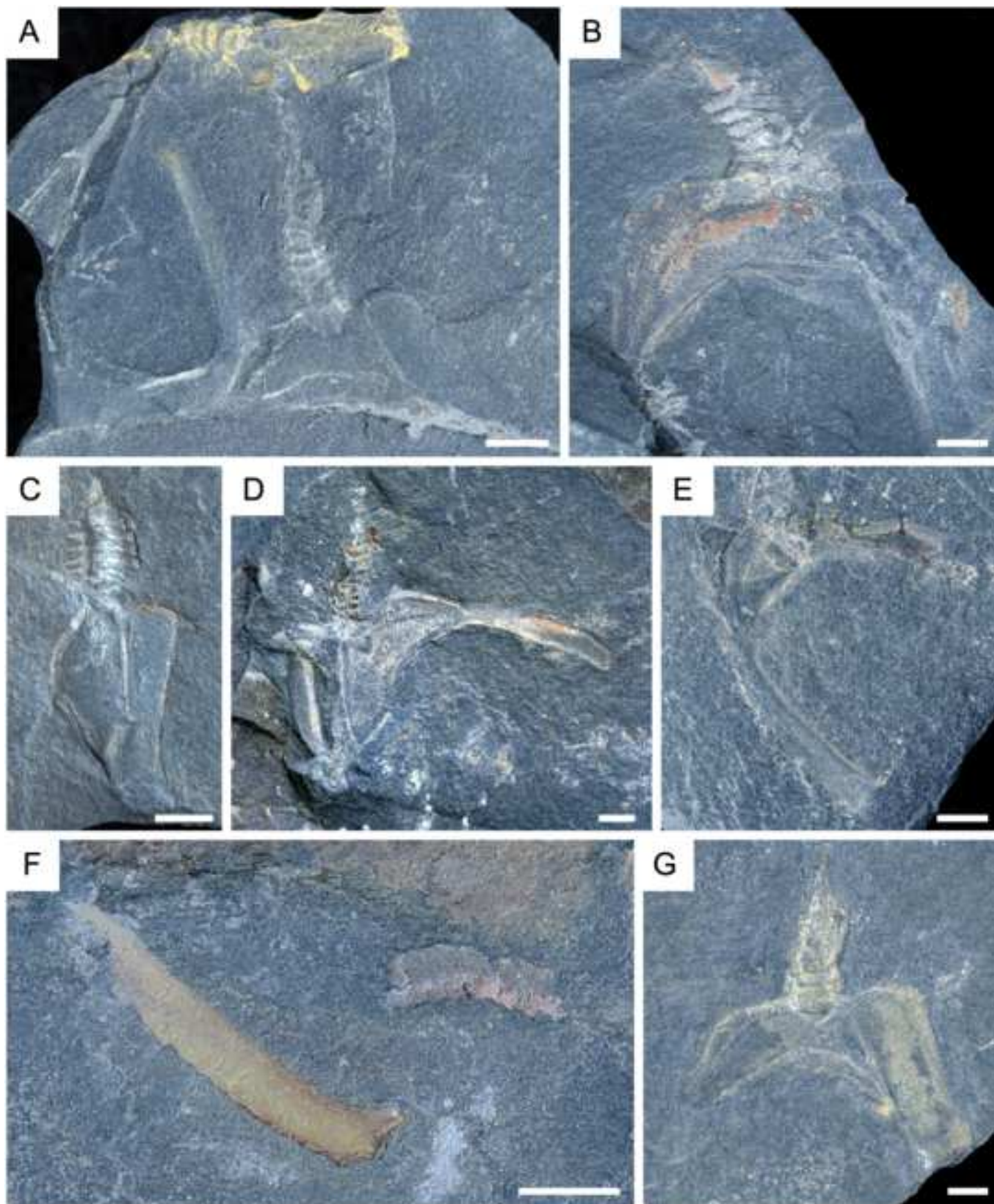




Figure 9

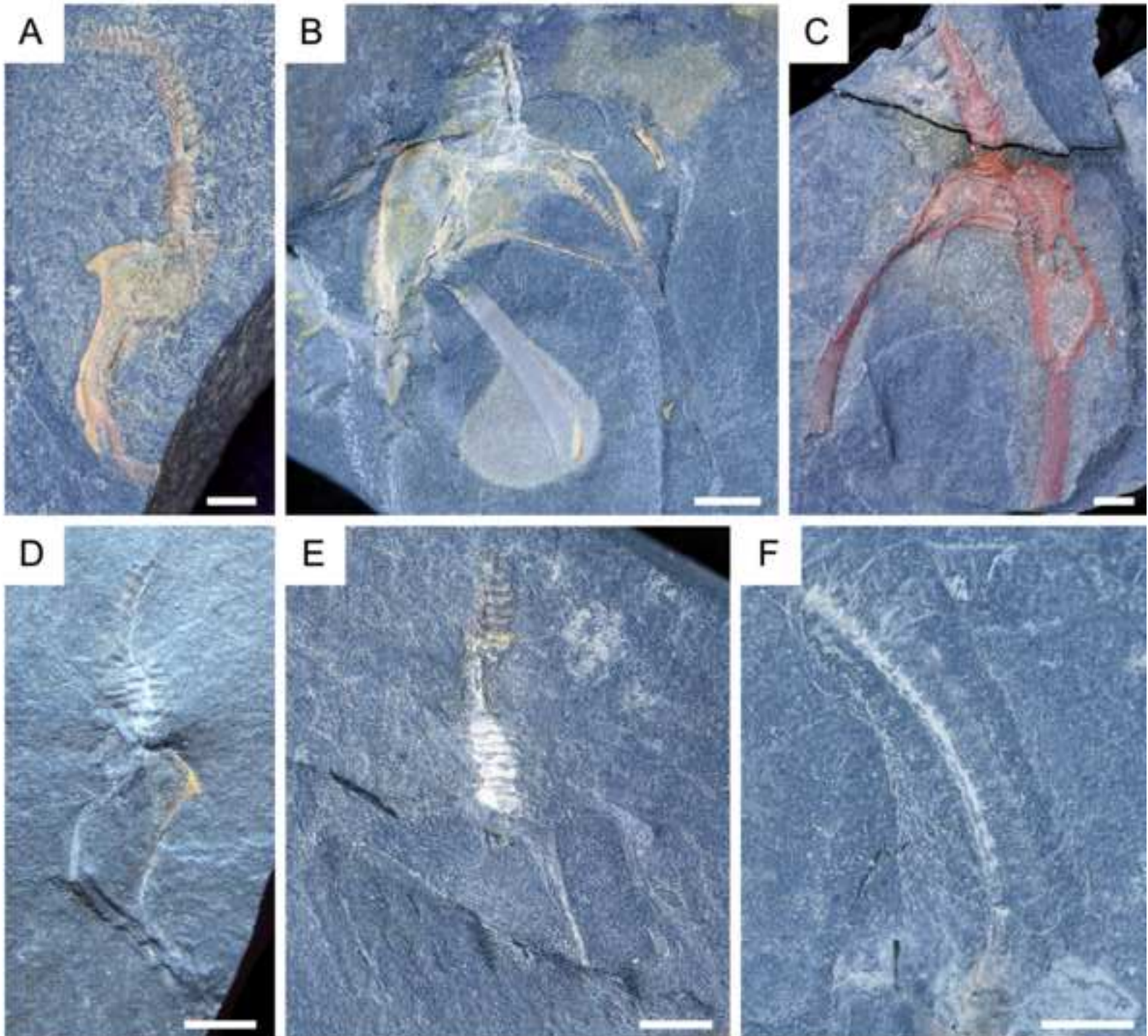




Figure 10

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