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A new ophiacanthid brittle star (Echinodermata, Ophiuroidea) from sublittoral crinoid and seagrass communities of late Maastrichtian age in the southeast Netherlands

Ben Thuy [Corresp., 1], **Lea D Numberger-Thuy** [1], **John W M Jagt** [2]

[1] Department of Palaeontology, Natural History Museum Luxembourg, Luxembourg City, Luxembourg

[2] Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands

Corresponding Author: Ben Thuy
Email address: bthuy@mnhn.lu

A new species of brittle star, *Ophiomitrella floorae*, is recorded from the lower two meters of the Gronsveld Member (Maastricht Formation), of late Maastrichtian age (c. 66.7 Ma). These relatively fine-grained biocalcarenites reflect shallow-water deposition (20–40 meters) in a sheltered setting with a relatively firm sea floor and clear waters, under middle sublittoral and subtropical conditions. Associated echinoderm taxa comprise more robust, sturdy-plated ophiomusaid and ophiodermatid brittle stars and numerous bourgueticrinid sea lilies. The new brittle star described herein belongs to a family whose present-day members are predominantly restricted to bathyal depths. Its small size and the exceptional preservation of a single articulated specimen wrapped around the stalk of a bourgueticrinid suggest that *O. floorae* n. sp. was an epizoic associated with stalked crinoids.

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Ben Thuy[1], Lea D. Numberger-Thuy[1], John W.M. Jagt[2]

[1] Natural History Museum Luxembourg, Department of Palaeontology, 25, rue Münster, 2160 Luxembourg-city, Luxembourg
[2] Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7 6211 KJ Maastricht, The Netherlands.

Corresponding Author:
Ben Thuy [1]
Natural History Museum Luxembourg, Department of Palaeontology, 25, rue Münster, 2160 Luxembourg-city, Luxembourg
Email address: bthuy@mnhn.lu

Abstract

A new species of brittle star, *Ophiomitrella floorae*, is recorded from the lower two meters of the Gronsveld Member (Maastricht Formation), of late Maastrichtian age (c. 66.7 Ma). These relatively fine-grained biocalcarenites reflect shallow-water deposition (20–40 meters) in a sheltered setting with a relatively firm sea floor and clear waters, under middle sublittoral and subtropical conditions. Associated echinoderm taxa comprise more robust, sturdy-plated ophiomusaid and ophiodermatid brittle stars and numerous bourgueticrinid sea lilies. The new brittle star described herein belongs to a family whose present-day members are predominantly restricted to bathyal depths. Its small size and the exceptional preservation of a single articulated specimen wrapped around the stalk of a bourgueticrinid suggest that *O. floorae* n. sp. was an epizoic associated with stalked crinoids.

Introduction

During recent decades, a renewed interest in macrofossil assemblages from Upper Cretaceous (Campanian–Maastrichtian) strata in the type area of the Maastrichtian Stage (southeast Netherlands, northeast Belgium; Felder 1975a, b) has become apparent. This has resulted in the recovery of numerous previously unrecorded taxa, in particular amongst echinoderms. The former ENCI-HeidelbergCement Group quarry at Sint-Pietersberg, south of the city of

Maastricht (Figs. 1, 2), is the key locality in the area. Here the lower/middle portion of the Maastricht Formation (Valkenburg, Gronsveld, Schiepersberg and Emael members) has yielded a range of brittlestar taxa over recent years, amongst which sturdy-plated ophiomusaids and ophiodermatids predominate (Jagt 1999c, d, 2000a). Smaller-sized species are much rarer and often occur as dissociated ossicles of disc and arms only. An articulated specimen of an ophiacanthid wrapped around the stalk of a bourgueticrinid crinoid from the lower Gronsveld Member (Jagt 2000a), in which obrution-related echinoderm Lagerstätten have been recorded between the St Pieter and ENCI horizons (Fig. 3) (see Jagt et al. 1998; Jagt 1999b), provided the impetus for the present note.

Stratigraphical setting

The lower portion of the Maastricht Formation at the former ENCI-HeidelbergCement Group quarry comprises comparatively fine-grained, poorly indurated, pale yellow biocalcarenites with a diverse macrofossil content, in particular in the Valkenburg and Gronsveld members (Fig. 3). On the basis of recent cyclostratigraphical and chronostratigraphical age models for the type Maastrichtian (Keutgen 2018), the base of the Valkenburg Member (i.e., the contact between the Gulpen and Maastricht formations or Lichtenberg Horizon) can be dated at 66.8 Ma, and the base of the overlying Gronsveld Member (St Pieter Horizon) at 66.7 Ma. The latter horizon is thought to represent the early stages of a transgression from a relative lowstand during a tectonic inversion phase, while the overlying Gronsveld Member represents a relative highstand during tectonic relaxation, with the maximum flooding surface situated around the middle of this unit (Schiøler et al. 1997).

In more general terms, referring to the area west of the River Maas (Meuse), the lowest unit of the Maastricht Formation, the Valkenburg Member, comprises poorly indurated, white-yellowish to yellowish-grey, fine- to coarse-grained biocalcarenites, with greyish brown flint nodules of varying sizes. The overlying Gronsveld Member consists of poorly indurated, white-yellowish to yellowish-grey, fine- to coarse-grained biocalcarenites, with small, light to dark greyish-brown flint nodules of varying sizes and shapes occurring in the lower part. In the higher portion they are arranged in more or less regular beds of light-grey to greyish blue nodules (Fig. 3).

The lower portion of the Maastricht Formation has been considered to represent a gravelly intrabiomicrosparite, with regional currents constant enough for horizontal displacement of sediment particles over the entire platform, at depths between 20 and 40 metres and sheltered from oceanic influence (Villain 1977; Jagt 1999a; Jagt & Jagt-Yazykova 2012). Frequent sediment reworking resulted in homogenisation over depths of a few decimetres, leading to a relatively firm sea floor and clear waters. This setting has been interpreted as middle sublittoral, under subtropical conditions and with sea grass communities (Liebau 1978; Jagt et al. 2019).

On evidence of index forms amongst coleoid cephalopods (Christensen et al. 2005; Jagt & Jagt-Yazykova 2019) and inoceramid bivalves (Jagt & Jagt-Yazykova 2018), the lower portion of the Maastricht Formation has been shown to be of late, though not latest, Maastrichtian age, thus

corroborating age assignments on the basis of dinoflagellates and calcareous nannoplankton (see Schiøler et al. 1997; Keutgen 2018). All these biota allow correlation of these shallow-water biocalcarenites along the fringes of Palaeozoic massifs (Fig. 4) with coeval levels in deeper-water settings (white chalk, Schreibkreide) elsewhere in Europe (northern Germany, Denmark and Poland).

Previous work on ophiuroids

Earlier records of late Maastrichtian echinoderms in the type area of the Maastrichtian Stage have demonstrated several Lagerstätten, comprising mostly bourgueticrinid crinoids (and other comatulids associated; see Jagt et al. 1998; Jagt 1999b) as well as lesser numbers of echinoids (Jagt 2000b), asteroids (Jagt 2000c; Blake & Jagt 2005; A.S. Gale & J.W.M. Jagt, work under way) and ophiuroids.

Brittle stars from the lower Gronsveld Member (Jagt 1999c, d, 2000a) include mostly semi-articulated individuals of the sturdy-plated *Ophiomusium granulosum* (Roemer, 1840) (= *Ophiura* (*Aspidura*) *subcylindrica* von Hagenow, 1840), *Ophiotitanos serrata* (Roemer, 1840) (= *Ophiura parvisentis* Spencer, 1908; *Ophioglypha gracilis* Valette, 1915) and *Ophiopeza*? *hagenowi* (Wienberg Rasmussen, 1950) (see Wienberg Rasmussen 1950; Jagt 2000a; Ishida et al. 2018). Other taxa, such as *Trichaster*? *ornatus* (Wienberg Rasmussen, 1950) and *Ophiothrix*? *bongaertsi* Kutscher & Jagt, in Jagt, 2000, are much rarer and occur only as dissociated vertebrae and lateral arm plates, respectively (Jagt 2000a). Part of Jagt's (2000a) records of the ophiacanthid *Ophiacantha*? *danica* Wienberg Rasmussen, 1952, as based on a single, articulated individual in life position around a crinoid stalk (NHMM K 3387), as well as a number of isolated ossicles from the lower Gronsveld Member, is revised herein. A re-examination of the remaining material will be deferred to another occasion.

Materials & Methods

The material described herein was illustrated and/or mentioned in previous studies (Jagt 2000a; Thuy 2013). For the purpose of the present reassessment, dissociated lateral arm plates and the disc of the articulated specimen, detached from the matrix, were mounted on a stub and gold-coated for scanning electron microscopy. Morphological terminologies follow Stöhr et al. (2012) for general skeletal features, Thuy & Stöhr (2011) for lateral arm plates and Hendler (2018) for the mouth skeleton. We adopt the classification proposed by O'Hara et al. (2017, 2018). To denote the repositories of the material described and illustrated here, the following abbreviations are used: NHMM, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; USNM, Smithsonian National Museum of Natural History, Washington DC, USA.

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Results

Systematic palaeontology

Class Ophiuroidea Gray, 1840
Subclass Myophiuroidea Matsumoto, 1915
Infraclass Metophiurida Matsumoto, 1913 (crown-group of Ophiuroidea)
Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Suborder Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Family Ophiacanthidae Ljungman, 1867
Genus Ophiomitrella Verrill, 1899

Ophiomitrella floorae n. sp.
Fig. 5A-C

Etymology: Named after Floor Jansen, lead singer of the Finnish band Nightwish in recognition of her long-standing career in metal, her general interest in all things (palaeo)biological and her and the band's use of fossils for artwork (Metal Mike, 2020).

Holotype: NHMM JJ 5104
Type locality and stratum: lower Gronsveld Member (Maastricht Formation; St Pieter and ENCI horizons) at the former ENCI-HeidelbergCement Group quarry, Maastricht, the Netherlands.
Paratypes: NHMM K 3387
Diagnosis: Small species of *Ophiomitrella* with high lateral arm plates showing up to eight large spine articulations and a very weak and fine vertical striation; large, wide adoral shields; two to three large, conical oral papillae sensu lato and a single large, conical ventralmost tooth.

Description of holotype: NHMM JJ 5104 (Fig. 5A-B) is a dissociated proximal lateral arm plate, almost two times taller than long; dorsal edge concave due to a strong constriction; distal edge strongly and regularly convex; proximal edge weakly concave and devoid of spurs; ventral portion of lateral arm plate not protruding. Outer surface with finely meshed stereom and a very weak, fine vertical striation close to ridge of spine articulations. Eight large, ear-shaped spine articulations on a strongly elevated distal portion of lateral arm plate; row of spine articulations

proximally bordered by thick, conspicuous, straight ridge; spine articulations each consisting of large muscle opening enclosed by dorsal and ventral lobes forming round, continuous ring, and separated from smaller nerve opening by well-developed sigmoidal fold; weak dorsalward increase in size of spine articulations and distance between them. Ventral edge of lateral arm plate oblique; tentacle notch invisible in external view; row of spine articulations protruding ventralwards. Inner side of lateral arm plate with large, well-defined vertebral articulation shaped like slightly rotated digit one; tentacle notch small but well defined, distally bordering thickened ventral edge of lateral arm plate; poorly defined vertical furrow running parallel to row of spine articulations but presence of perforations ambiguous due to insufficient preservation.

The paratype (NHMM K 3387, Fig. 5C) is an articulated skeleton with an arm wrapped around a bourgueticrinid stalk; the proximal arm portions show lateral arm plates similar to the holotype; the disc is poorly preserved due to coarse recrystallisation, blurring all details on the dorsal side; ventral side of the disc preserving a few details of the skeleton; four arm bases preserved intact, showing strongly recrystallised lateral and ventral arm plates and ventral arm spines; lateral arm plates similar to holotype; ventral arm plates with a strongly convex distal edge, deeply incised lateral edges and a pointed proximal tip; arm spines at least as long as one arm segment; adoral shields large and wide; two to three large, conical oral papillae sensu lato and a large, conical ventralmost tooth.

Discussion

The material described herein unambiguously belongs to the family Ophiacanthidae as defined by O'Hara et al. (2018) on account of the large, ear-shaped spine articulations proximally bordered by a sharply defined ridge, the non-protruding ventral portion of the lateral arm plates, and the shape of the ridge on the inner side of the lateral arm plates. Within this family, several clades were resolved using molecular evidence (O'Hara et al. 2017), but only very few agree with previously defined genera (e.g., *Ophioplinthaca*). Most traditional ophiacanthid genera are poly- or paraphyletic, challenging the diagnostic value of the characters used to define these taxa (O'Hara et al. 2017). In contrast, patterns in lateral arm plate morphology seem to agree with molecular evidence in many aspects (O'Hara et al. 2014; Thuy & Stöhr 2016), corroborating that lateral arm plates can be used to constrain the position of a species within the family Ophiacanthidae (Thuy 2013).

In the light of this conclusion, and due to the poor preservation of the single articulated individual, we have chosen the dissociated proximal lateral arm plate as the holotype of the new species. The outer surface ornamentation, the shape of the ridge proximally bordering the row of spine articulations, and the shape of the vertebral articulation on the inner side of the lateral arm plate suggest close ties with extant members of the genus *Ophiomitrella*, in particular *O. conferta* (Koehler, 1922) and *O. clavigera* (Ljungman, 1865) (Thuy & Stöhr 2011), as already suggested by Thuy (2013). The mouth skeleton of the paratype specimen corroborates this position. It must

be stressed, however, that the genus *Ophiomitrella*, as currently understood, is paraphyletic (O'Hara et al. 2017), and that the type species of the genus, *O. laevipellis*, has been neither genetically sequenced nor morphologically dissected as yet. As long as the systematic position of the type species is unresolved, assignment to *Ophiomitrella* is tentative and should merely underline the close relationship with *O. conferta* and *O. clavigera*.

The material described herein differs from previously described fossils assigned to *Ophiomitrella* in the higher number of spine articulations and the finer, less pronounced vertical striation on the outer surface of the lateral arm plates (Thuy 2013). Assignment to a Recent species is precluded by the stratigraphical age of the fossils, implying an implausibly long range; we therefore assign the material described herein to a new species.

Conclusions

Recent members of *Ophiomitrella*, and of the family Ophiacanthidae in general, predominantly live at deep sublittoral to bathyal depths, i.e., between 150 and 2,000 m, (O'Hara & Stöhr 2006; O'Hara et al. 2017). Thus, the discovery of *Ophiomitrella floorae* n, sp. aligns with the co-occurring ophiomusaid brittle stars and bourgueticrinid sea lilies in belonging to groups once common and widespread at shallow depths but nowadays restricted to deeper waters (e.g., Thuy et al. 2012). Their occurrence at middle sublittoral paleo-depths (20–40 m) during the late Maastrichtian is a relict of their mid-Mesozoic expansion into shallow waters (Thuy et al. 2012; Thuy & Meyer 2013; Thuy 2013).

Ophiomitrella floorae is one of the first fossil ophiuroids shown to be associated with stalked crinoids. The exceptional discovery of an articulated individual wrapped around the stalk of a bourgueticrinid (Jagt 2000a) is a rare case of an ophiuroid-crinoid association preserved in the fossil record. The small size and general morphology of *Ophiomitrella floorae* n. sp. conforms to an epizoic lifestyle as commonly observed in living congeners (e.g., O'Hara & Stöhr 2006). The only other unambiguous example of an ophiuroid-crinoid association in the fossil record is the Paleozoic stem ophiuroid *Onychaster* that lived epizoic on stalked crinoids (Hotchkiss & Glass 2012).

The case of *Ophiomitrella floorae* n. sp. demonstrates that a significant portion of ophiuroid palaeo-biodiversity is easily overlooked. Due to the small size and delicate skeleton of the species, it was much less likely to be noticed than the larger, sturdy-plated and therefore more conspicuous co-occurring ophiomusaid and ophiodermatid brittle stars. The single articulated individual was previously too poorly preserved to allow for unambiguous species-level identification (Jagt 2000a). It was only thanks to co-occurring dissociated lateral arm plates that the species could be described, thus underscoring the importance of microfossils in assessing the paleo-biodiversity of taxa with multi-element skeletons such as brittle stars.

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References

Blake, D.B. & Jagt, J.W.M., 2005. New latest Cretaceous and earliest Paleogene asteroids (Echinodermata) from The Netherlands and Denmark and their palaeobiological significance. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 75, 183–200.

Christensen, W., Schmid, F. & Schulz, M.-G., 2005. *Belemnitella* from the Upper Maastrichtian of Hemmoor, northwest Germany. Geologisches Jahrbuch, A157 (for 2004), 23–67.

Felder, W.M., 1975a. Lithostratigraphische Gliederung der Oberen Kreide in Süd-Limburg (Niederlande) und den Nachbargebieten. 1. Teil: Der Raum westlich der Maas, Typusgebiet des' Maastricht'. Publicaties van het Natuurhistorisch Genootschap in Limburg, 24, 1–43.

Felder, W.M., 1975b. Lithostratigrafie van het Boven-Krijt en het Dano-Montien in Zuid-Limburg en het aangrenzende gebied, 63–72. In: Zagwijn, W.H. & Van Staalduinen, C.J. (eds.). Toelichting bij geologische overzichtskaarten van Nederland. Rijks Geologische Dienst, Haarlem.

Felder, W.M. & Bosch, P.W., 1998. Geologie van de St. Pietersberg bij Maastricht. Grondboor & Hamer, 52(3) [Limburgnummer 9A: Geologie van de St. Pietersberg], 53–63.

Gray, J.E., 1840. Room II: Synopsis of the contents of the British Museum. British Museum, London, 57–65.

Hagenow, F. von, 1840. Monographie der Rügen'schen Kreideversteinerungen. Abtheilung 2. Radiarien und Annulaten nebst Nachträge zur 1. Abtheilung. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1840, 631–672.

Hendler, G., 2018. Armed to the teeth: a new paradigm for the buccal skeleton of brittle stars (Echinodermata: Ophiuroidea). Contributions in Science, 526, 189–311.

Hotchkiss, F.H.C. & Glass, A., 2012. Observations on *Onychaster* Meek & Worthen, 1868 (Ophiuroidea: Onychasteridae) (Famennian – Visean age) In: Kroh, A. & Reich, M. (Eds.) Echinoderm Research 2010: Proceedings of the Seventh European Conference on Echinoderms, Göttingen, Germany, 2–9 October 2010. Zoosymposia, 7, 121-138.

Ishida, Y., Thuy, B., Fujita, T., Kadokawa, M., Ikegami, N. & Numberger-Thuy, L.D., 2018. A new species of *Stegophiura* (Ophiuroidea, Ophiopyrgidae) from the mid-Cretaceous of southern Japan. Swiss Journal of Palaeontology, 137, 319–325.

Jagt, J.W.M., 1999a. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 1: Introduction and stratigraphy. Scripta Geologica, 116, 1–57.

Jagt, J.W.M., 1999b. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 2: Crinoids. Scripta Geologica, 116, 59–255.

Jagt, J.W.M., 1999c. An overview of Late Cretaceous and Early Palaeogene echinoderm faunas from Liège-Limburg (Belgium, The Netherlands). In: Dhondt, A.V. & Alekseev, A.S. (eds). D.P. Naidin Festschrift (INTAS 94-1414). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 69 (Suppl. A), 103–118.

Jagt, J.W.M., 1999d. Ophiuroid diversity in the type area of the Maastrichtian Stage. In: Vergoossen, J.M.J. & Lambers, P.H. (eds). Actual paleontology - paleontology in action: a tribute to Bert Boekschoten. Geologie en Mijnbouw, 78(2), 197–206.

Jagt, J.W.M., 2000a. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 3: Ophiuroids. With a chapter on: Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by Manfred Kutscher & John W.M. Jagt. Scripta Geologica, 121, 1–179.

Jagt, J.W.M., 2000b. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 4: Echinoids. Scripta Geologica, 121, 181–375.

Jagt, J.W.M., 2000c. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 5: Asteroids. Scripta Geologica, 121, 377–503.

Jagt, J.W.M., Deckers, M., Donovan, S.K., Fraaije, R., Goolaerts, S., Van der Ham, R., Hart, M.B., Jagt-Yazykova, E.A., Van Konijnenburg-van Cittert, J. & Renkens, S., 2019. Latest Cretaceous storm-generated sea grass accumulations in the Maastrichtian type area, the Netherlands – preliminary observations. Proceedings of the Geologists' Association, 130, 590–598.

Jagt, J.W.M., Donovan, S.K., Deckers, M.J.M., Dortangs, R.W., Kuypers, M.M.M. & Veltkamp, C.J., 1998. The Late Maastrichtian bourgueticrinid crinoid *Dunnicrinus aequalis* (d'Orbigny, 1841) from The Netherlands and Belgium. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 68, 129–154.

Jagt, J.W.M., Deckers, M.J.M., De Leebeeck, M., Donovan, S.K. & Nieuwenhuis, E., 2020. Episkeletozoans and bioerosional ichnotaxa on isolated bones of Late Cretaceous mosasaurs and cheloniid turtles from the Maastricht area, the Netherlands. Geologos (in press).

Jagt, J.W.M. & Jagt-Yazykova, E.A., 2012. Stratigraphy of the type Maastrichtian – a synthesis. In: Jagt, J.W.M., Donovan, S.K. & Jagt-Yazykova, E.A. (eds). Fossils of the type Maastrichtian (Part 1). Scripta Geologica Special Issue, 8, 5–32.

Jagt, J.W.M. & Jagt-Yazykova, E.A., 2018. Stratigraphical ranges of tegulated inoceramid bivalves in the type area of the Maastrichtian Stage (Belgium, the Netherlands). In: Jagt-Yazykova, E.A., Jagt, J.W.M. & Mortimore, R.N. (eds). Advances in Cretaceous palaeontology and stratigraphy – Christopher John Wood Memorial Volume. Cretaceous Research, 87, 385–394.

Jagt, J.W.M. & Jagt-Yazykova, E.A., 2019. Late Cretaceous and Cenozoic cephalopods from the southern North Sea Basin: stocktaking and future directions. Vita Malacologica, 18, 1–33.

Keutgen, N., 2018. A bioclast-based astronomical timescale for the Maastrichtian in the type area (southeast Netherlands, northeast Belgium) and stratigraphic implications: the legacy of P.J. Felder. Netherlands Journal of Geosciences, 97, 229–260.

Koehler, R., 1922. Echinodermata: Ophiuroidea. Australasian Antarctic Expedition 1911-1914. Scientific Report Series C., 8(2), 5-98, pls 76-90.

Liebau, A., 1978. Paläobathymetrische und paläoklimatische Veränderungen im Mikrofaunenbild der Maastrichter Tuffkreide. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 157, 233–237.

Ljungman, A.V., 1865. Tillägg till kännedom af Skandinaviens Ophiurider. Öfversigt af Kgl. Vetenskaps-Akademiens Förhandlingar 1863, 21(7), 359-367, pl. XV.

Ljungman, A., 1867. Ophiuroidea viventia huc usque cognita enumerat. Öfversigt af Kongeliga Vetenskaps-Akademiens Förhandlingar 1866, 23(9), 303–336.

Matsumoto, H., 1913. Evolutionary history of the class Ophiuroidea and a note on the new classification of the class. Zoological Magazine, 25, 521–527.

Matsumoto, H., 1915. A new classification of the Ophiuroidea: with descriptions of new genera and species. Proceedings of the Academy of Natural Sciences of Philadelphia, 67, 43–92.

Metal Mike, 2020. Floor Jansen. Via bergen en dalen naar de top. Aardschok (Internationaal Metal Magazine), 41(3), 12–21 (www.aardschok.com).

O'Hara, T.D., Hugall, A.F., Thuy, B. & Moussalli, A., 2014. Phylogenomic resolution of the class Ophiuroidea unlocks a global microfossil record. Current Biology, 24, 1874–1879. https://doi.org/10.1016/j.cub.2014.06.060

O'Hara, T.D., Hugall, A.F., Thuy, B., Stöhr, S. & Martynov, A.V., 2017. Restructuring higher taxonomy using broad-scale phylogenomics: the living ophiuroidea. Molecular Biology and Evolution, 107, 415–430 DOI 10.1016/j.ympev.2016.12.006.

O'Hara, T.D. & Stöhr, S., 2006. Deep water Ophiuroidea (Echinodermata) of New Caledonia: Ophiacanthidae and Hemieuryalidae, in Richer de Forges, B & Justine, J.-L. (eds), Tropical Deep-Sea Benthos, volume 24. Mémoires du Muséum national d'Histoire naturelle, 193, 33-141.

O'Hara, T.D., Stöhr, S., Hugall, A.F., Thuy, B. & Martynov, A., 2018. Morphological diagnoses of higher taxa in ophiuroidea (Echinodermata) in support of a new classification. European Journal of Taxonomy, 416, 1–35.

Roemer, F.A., 1840–1841. Die Versteinerungen des norddeutschen Kreidegebirges, iv + 1–48, 49–145. Hahn'sche Hofbuchhandlung, Hannover.

Schiøler, P., Brinkhuis, H., Roncaglia, L. & Wilson, G.J., 1997. Dinoflagellate biostratigraphy and sequence stratigraphy of the type Maastrichtian (Upper Cretaceous), ENCI Quarry, The Netherlands. Marine Micropaleontology, 31, 65–95.

Spencer, W.K., 1905–1908. A monograph on the British fossil Echinodermata from the Cretaceous formations, 2. The Asteroidea and Ophiuroidea. Monograph of the Palaeontographical Society London, 67–90 (1905), 91–132 (1907), 133–138 (1908).

Stöhr, S., O'Hara, T.D. & Thuy, B., 2012. Global diversity of brittle stars (echinodermata: ophiuroidea). PLOS ONE, 7(3), e31940 DOI 10.1371/journal.pone.0031940.

Thuy, B., 2013. Temporary expansion to shelf depths rather than an onshore-offshore trend: the shallow-water rise and demise of the modern deep-sea brittle star family Ophiacanthidae (echinodermata: ophiuroidea). European Journal of Taxonomy, 48(48), 1–242.

Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D., Reich, M. & Stöhr, S., 2012. Ancient Origin of the Modern Deep-Sea Fauna. PLoS ONE, 7(10), e46913. doi:10.1371/journal.pone.0046913

Thuy, B. & Meyer, C.A., 2013. The pitfalls of extrapolating modern depth ranges to fossil assemblages: new insights from Middle Jurassic brittle stars (Echinodermata: Ophiuroidea) from Switzerland. Swiss Journal of Palaeontology, 132(1), 5-21.

Thuy, B. & Stöhr, S., 2011. Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. Zootaxa, 3013(1), 1–47 DOI 10.11646/zootaxa.3013.1.1.

Thuy, B. & Stöhr, S., 2016. A new morphological phylogeny of the Ophiuroidea (Echinodermata) accords with molecular evidence and renders microfossils accessible for cladistics. PLoS One, 11 (5), e0156140.https://doi.org/10.1371/journal.pone.0156140

Valette, A., 1915. Les ophiures de la craie des environs de Sens. Bulletin de la Société des Sciences historiques et naturelles de l'Yonne, 68, 125–150.

Verrill, A.E., 1899. Report on the Ophiuroidea collected by the Bahama expedition in 1893. Bulletin from the Laboratories of Natural History of the State University of Iowa, 5, 1–86.

Villain, J.-M., 1977. Le Maastrichtien dans sa région type (Limbourg, Pays-Bas). Étude stratigraphique et micropaléontologique. Palaeontographica, A157, 1–87.

Wienberg Rasmussen, H., 1950. Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. Danmarks geologiske Undersøgelse, 77, 1–134.

Wienberg Rasmussen, H., 1952. Cretaceous Ophiuroidea from Germany, Sweden, Spain and New Jersey. Meddelelser fra Dansk Geologisk Forening, 12 (for 1951), 47–57.

Figure 1. Map of southern Limburg and contiguous areas in Belgium and Germany, representing the extended type area of the Maastrichtian Stage and showing the location of the former ENCI-HeidelbergCement Group quarry (modified from Jagt et al., 2020).

Figure 2. The northeast corner of the former ENCI-HeidelbergCement Group quarry (Maastricht), looking southwest (Spring 2019); the level with tyre tracks corresponds roughly to the lower Gronsveld Member (St Pieter and ENCI horizons; see Fig. 3; photograph by M.J.M. Deckers).

Figure 3. Litholog of the lower Maastricht Formation (modified from Felder & Bosch, 1998), with the St Pieter and ENCI horizons in the lower part of the Gronsveld Member. The arrow in the higher part of that unit refers to one of the more spectacular storm levels in the section (for details, see Jagt et al., 2019).

Figure 4. Reconstruction of oceans, epicontinental seas and land masses during the late Late Cretaceous (c. 75 Ma; modified from Ron Blakey, deeptimemaps.com).

Figure 5. *Ophiomitrella floorae* n. sp., from the lower Gronsveld Member (Maastricht Formation; St Pieter and ENCI horizons) at the former ENCI-HeidelbergCement Group quarry, Maastricht, the Netherlands. A-B: holotype (NHMM JJ 5104), dissociated proximal lateral arm plate in external (A) and internal (B) views; C: paratype (NHMM K 3387), articulated disc with basal arm segments in ventral view. *Ophiomitrella conferta*, Recent, as a close living relative of *O. floorae* n. sp. D-E: proximal lateral arm plate (USNM e44295) in external (D) and internal (E) views; F-G: complete individual (USNM e44198) lacking one arm, in dorsal view (F) and with detail of ventral disc skeleton (G). Abbreviations: AOS: adoral shield; AS: arm spine; do: dorsal; LAP: lateral arm plate; MO: muscle opening; NO: nerve opening; OS: oral shield; pr: proximal; R: ridge; T: tooth; VA: vertebral articulation; VAP: ventral arm plate. Scale bars equal 0,25 mm in A-B and D-E, and 1 mm in C and F-G.

Figure 1

Locality map

Map of southern Limburg and contiguous areas in Belgium and Germany, representing the extended type area of the Maastrichtian Stage and showing the location of the former ENCI-HeidelbergCement Group quarry (modified from Jagt et al., 2020).

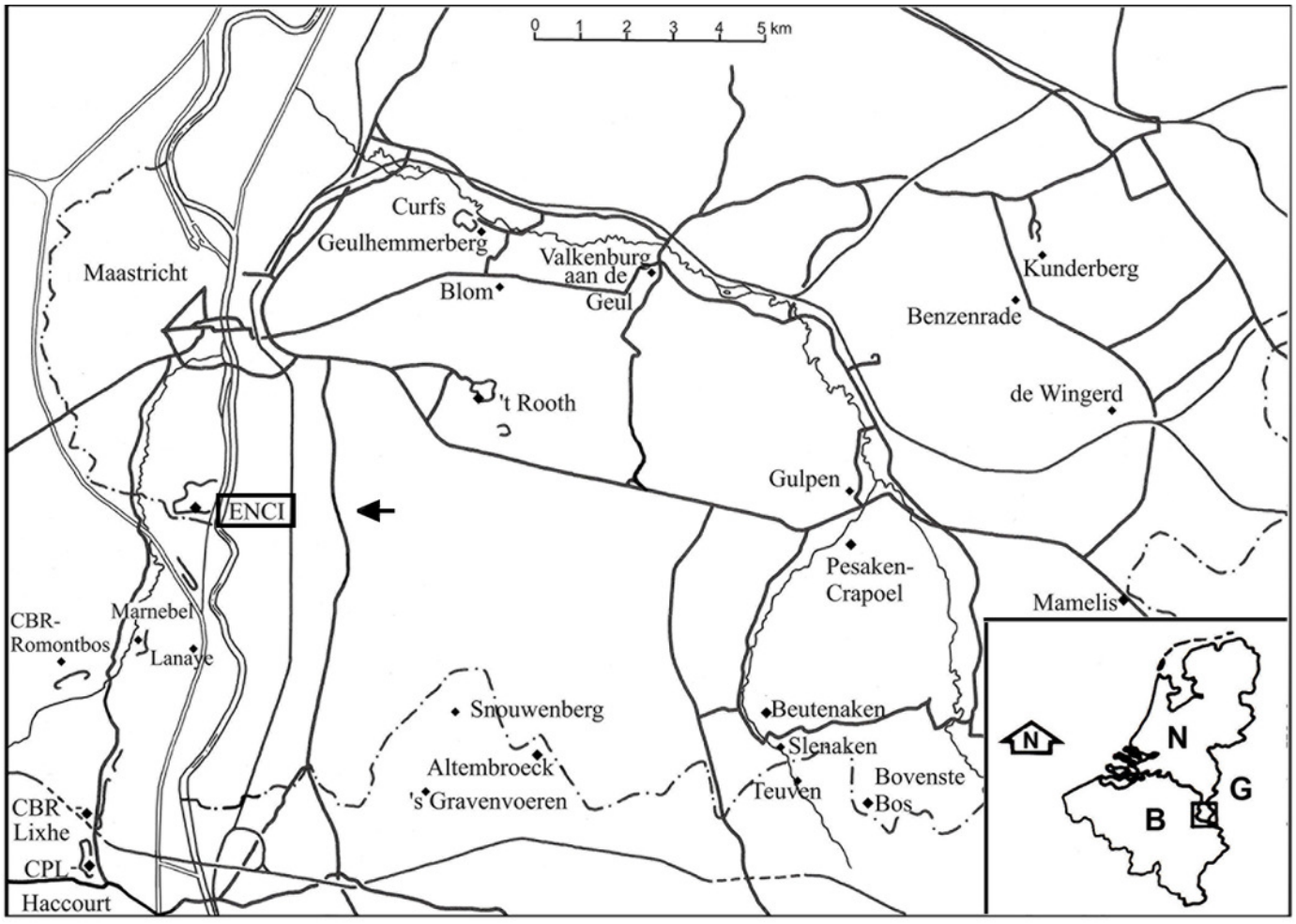

Figure 2

ENCI-HeidelbergCement Group quarry.

The northeast corner of the former ENCI-HeidelbergCement Group quarry (Maastricht), looking southwest (Spring 2019); the level with tyre tracks corresponds roughly to the lower Gronsveld Member (St Pieter and ENCI horizons; see Fig. 3; photograph by M.J.M. Deckers).

Figure 3

Litholog of the lower Maastricht Formatio.

Log (modified from Felder & Bosch, 1998), with the St Pieter and ENCI horizons in the lower part of the Gronsveld Member. The arrow in the higher part of that unit refers to one of the more spectacular storm levels in the section (for details, see Jagt et al., 2019).

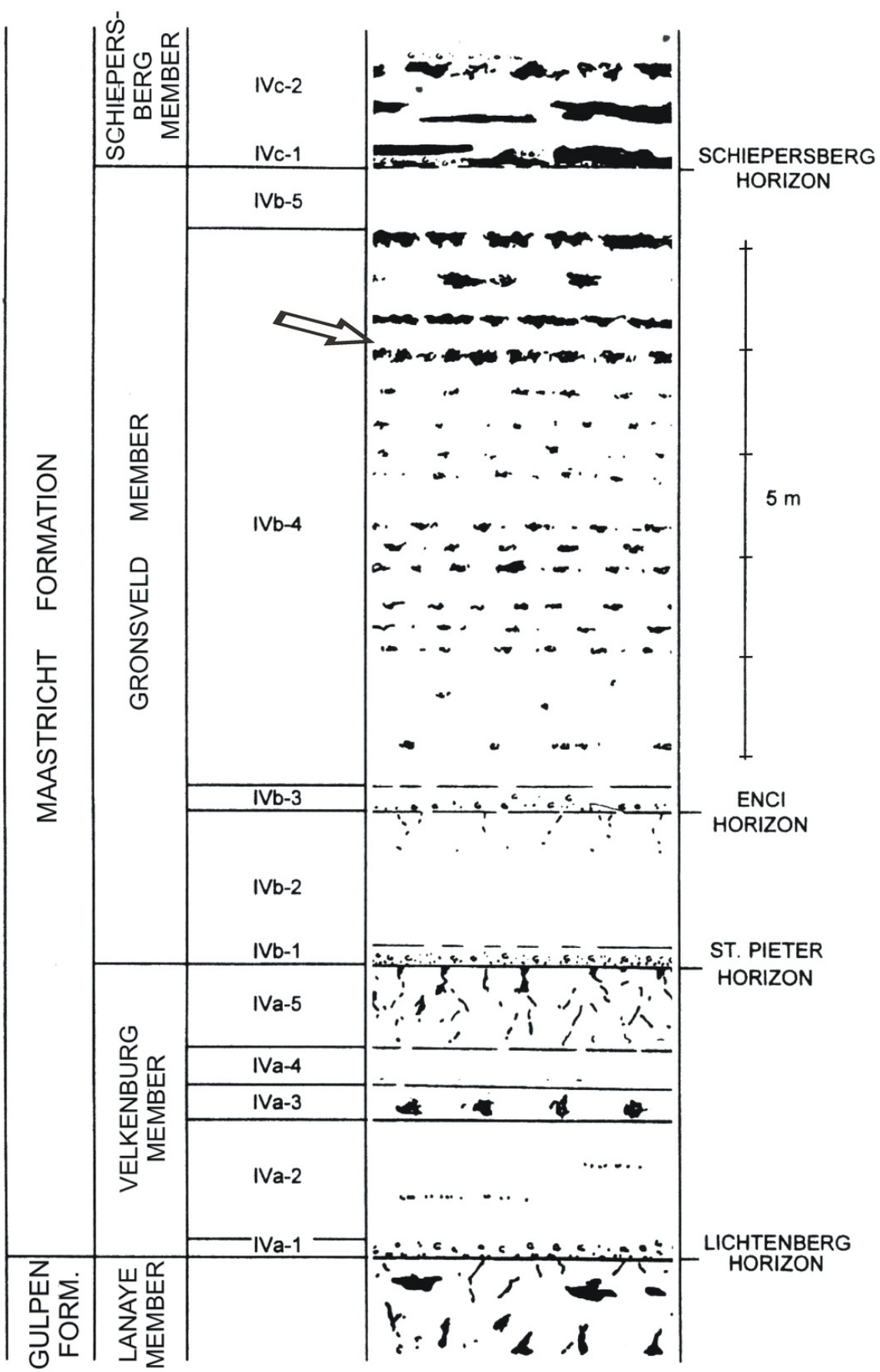
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Figure 4

Plaeogeographical map.

Reconstruction of oceans, epicontinental seas and land masses during the late Late Cretaceous (c. 75 Ma; modified from Ron Blakey, deeptimemaps.com.

Figure 5

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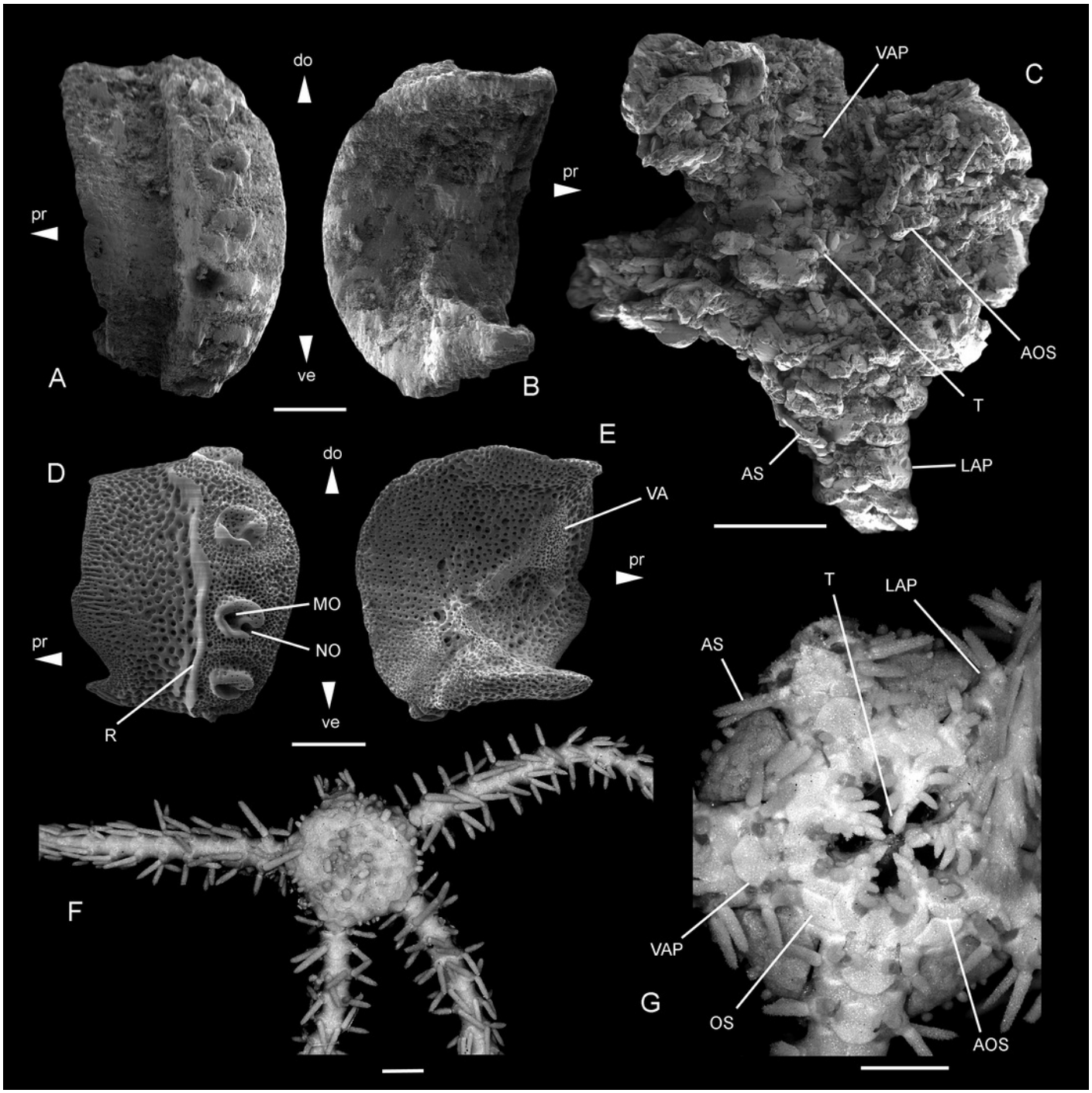
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