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Source: Paleontological Research, 27(2) : 147-159

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/PR210014

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Paleontological Research, vol. 27, no. 2, pp. 147–159, April 1, 2023
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doi:10.2517/PR210014

A new genus and species of brittle star (Ophiuroidea: Ophioleucida) from the Upper Triassic (Carnian) of northern Vietnam

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Received May 26, 2021; Revised manuscript accepted October 3, 2021; Published online November 1, 2022

Abstract. The fossil record of brittle stars, one of the five extant classes of echinoderms, is still rather poorly known. In particular for the Triassic Period, occurrences published to date are strongly biased toward Europe, with only two exhaustively described taxa recorded from the East Asian part of the Tethys Ocean. Here, we record new ophiuroids from the Carnian (Upper Triassic) of the Me area in Ninh Binh Province, Vietnam. The fossils comprise articulated disks and arm fragments preserved as external molds, all original calcite dissolved. We introduce a new genus and species, *Triadoleucella meensis*, for these specimens that represent the oldest known member of the order Ophioleucida. The ophiuroids were found in mudstones deposited in outer shelf environments below storm wave base. The intact articulation, combined with random orientation and intense fragmentation of individuals suggest effective burial by downslope mudflow prior to or soon after death.

ZooBank registration: urn:lsid:zoobank.org:pub:82C22900-E4F8-43C3-8F34-468C38AF6C73

Keywords: Me area, new taxa, Ninh Binh Province, paleoenvironment, Suoi Bang Formation, taphonomy

Introduction

The Triassic is a pivotal time interval in the evolution of modern marine communities (e.g. Brayard *et al*., 2017). Many extant invertebrate clades originated in or radiated during the Triassic, following biotic recovery after the end-Permian mass extinction (e.g. Kroh and Smith, 2010). The most recent molecular (O'Hara *et al*., 2014, 2017) and morphological evidence (Thuy and Stöhr, 2016, 2018) has shown that the brittle stars, one of the five extant classes of echinoderms, underwent major cladogenesis in the Triassic. Given the importance of extinct stem members with transitional morphologies for accurate reconstructions of deep branches (e.g. Thuy and Stöhr, 2018), detailed knowledge of fossils is a key factor in understanding the evolutionary history of a clade.

At first sight, the Triassic fossil record of ophiuroids is comparatively rich (e.g. Hess, 1965; Twitchett and Oji, 2005). Fossils have been reported from virtually all stages of the Triassic and from all major parts of the world. A more detailed examination of the currently known Triassic ophiuroid fossil record, however, reveals a more differentiated picture in that many records are based on unidentified occurrences (Kummel and Teichert, 1970; Hess, 1972; Zonneveld, 2001; Twitchett and Oji, 2005; Ishida *et al*., 2011). Among Triassic ophiuroids identified to species level, the vast majority have been recorded from Europe (Hess, 1965, 1970; Bachmayer and Kollmann, 1968; Broglio and Berti, 1972; Donofrio and Mostler, 1977; Kutscher, 1987, 2000; Calzada and Gutiérrez, 1988; Radwański, 2002; Salamon, 2004; Thuy *et al*., 2012; Thuy, 2013; Moosleitner, 2021) and the Middle East (Kristan-Tollmann *et al*., 1979), suggesting a significant geographic bias toward the western part of the Triassic Tethys Ocean. A number of latest Permian to earliest Triassic brittle stars have been described from China

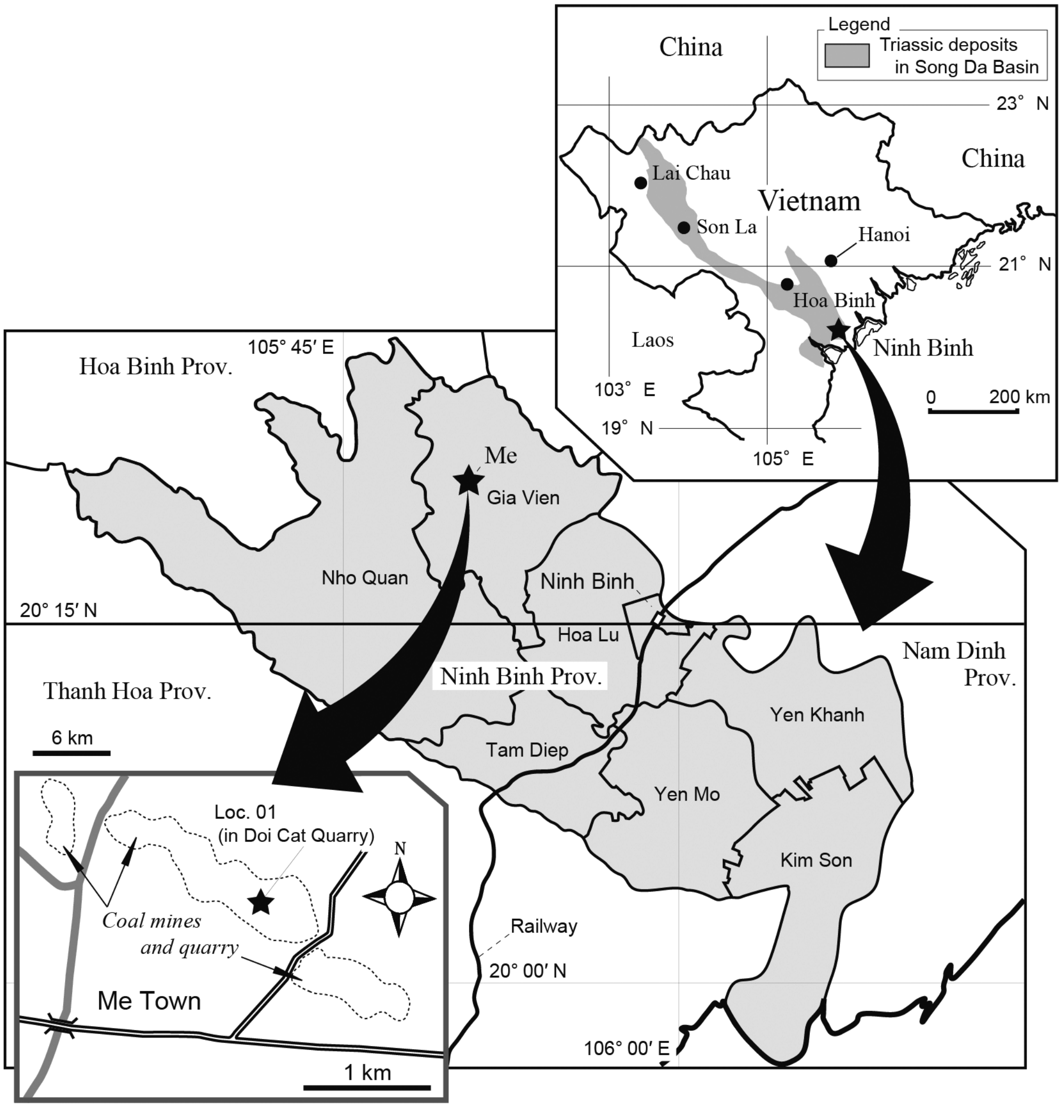

Figure 1. Map showing the position of the type locality of *Triadoleucella meensis* gen. et sp. nov. (marked by star) from the Upper Triassic Suoi Bang Formation.

(Yang, 1960; Feng, 1985; Chen *et al*., 2004; Chen and McNamara, 2006), but these are based on insufficiently preserved material and/or superficial descriptions, thus precluding a meaningful comparison with other ophiuroid taxa (Thuy *et al*., 2019). The sole well-known Triassic ophiuroids from the East Asian part of the Tethys are *Leadagmara gracilispina* Thuy, Ishida, Doi and Kroh, 2013 from the Carnian of Japan, and *Eolaxoporus hagdorni* Thuy, 2013 from the Carnian of China.

Here, we describe a new ophiuroid from the Carnian of Vietnam. The articulated skeletons and arm fragments display sufficient detail for an exhaustive morphological analysis, allowing identification at the species level. We assign the Vietnamese fossils to a new genus and species *Triadoleucella meensis*, thus adding another record to the sparse Triassic ophiuroid record from the eastern Tethys.

Geological setting

The ophiuroid fossils described herein originate from the Suoi Bang Formation of northern Vietnam, at a locality in the Me area, Ninh Binh Province (Figure 1). The Suoi Bang Formation is widely distributed in northwest Vietnam and includes three parts: a lower part consisting of siltstones, shales, calcareous shales and limestones yielding ammonoids and marine bivalves, a middle part

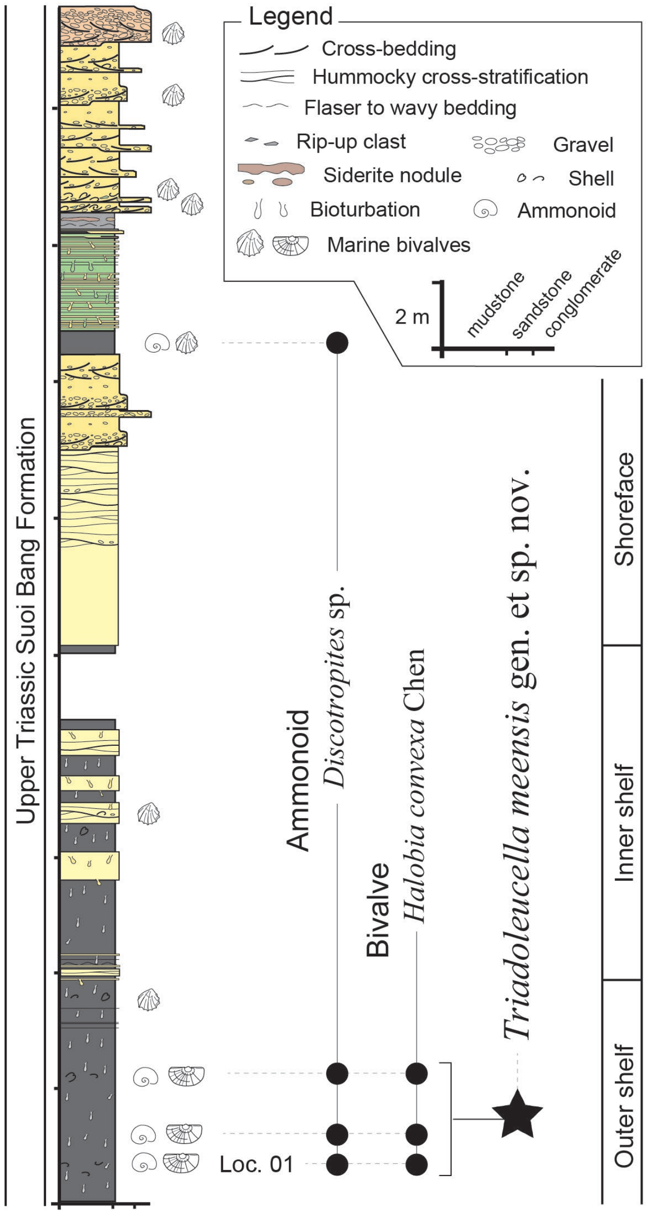

Figure 2. Columnar section showing the horizon that has yielded *Triadoleucella meensis* gen. et sp. nov. (marked by star) from the Upper Triassic Suoi Bang Formation (modified from Komatsu *et al*., 2017, fig. 2).

with medium- to coarse-grained quartz sandstones with intercalating layers of pebbles and gravels yielding marine biota similar to those of the lower part, and an upper part consisting of shales and siltstones with coal seams containing marine bivalves and the so-called Hon Gai fern assemblage (Vu Khuc and Nguyen, 1967; Vu Khuc, 2005).

The present ophiuroid remains were recovered from a mudstone block at Loc. 01 of Komatsu *et al*. (2017) in the Doi Cat Quarry, approximately 1 km from the town of Me Town. The ophiuroid-bearing mudstone belongs to the lower part of the Upper Triassic Suoi Bang Formation (Nguyen *et al*., 2016), which contains the ammonoid genus *Discotropites* Hyatt and Smith, 1905 and the bivalve *Halobia convexa* (Chen, 1964), which are indicative of a Carnian age (Komatsu *et al*., 2017).

The mudstones that yielded the ophiuroid fossils represent the deepest deposits exposed within a shallowing-upward succession (Figure 2; see Komatsu *et al*., 2017). Sedimentary structures, bivalve associations and the general geological context suggest deposition below storm wave base in a deep shelf setting (Komatsu *et al*., 2017).

Material and methods

We have analyzed three articulated individuals and 25 articulated arm fragments, almost all preserved as external molds after calcite dissolution. To enable a detailed morphological observation of these specimens, synthetic resin casts were produced: the fossil molds were thinly coated with acrylic resin dissolved in acetone, filled with the flexible type of silicone resin in a pressure machine, and then the resins were carefully peeled off from the fossils by hand after hardening. Selected resin casts were painted black, whitened with ammonium chloride, and photographed.

Line drawings and mode of occurrence of the brittle stars were produced with the help of a camera-lucida device. For morphological comparison of microstructural features, we took scanning electron microscope (SEM) images of macerated lateral arm plates of extant *Ophiernus adspersus adspersus* Lyman, 1883 and *Ophioleuce seminudum* Koehler, 1904 housed in the collections of the National Museum of Nature and Science, Tsukuba (registration numbers NSMT E-11836 and 3101, respectively).

We have adopted the classification by O'Hara *et al*. (2017, 2018) and our terminology follows Stöhr *et al*. (2012), Thuy and Stöhr (2011, 2016) and Hendler (2018).

Three sets of resin casts of the original specimens were made. All specimens as well as one set of casts are housed in the collections of the Vietnam National Museum (registration numbers VNMN-P-0278–0284); the two additional sets of casts are kept at the National Museum of Nature and Science, Tsukuba, Japan (registration numbers NMNS PA 20004–20009) and the Natural History Museum Luxembourg (registration number MnhnL OPH 176), respectively. The figures in the present paper were created from the original specimens (VNMN-P-0278, 0284) and resin casts (NMNS PA 20004–20009).

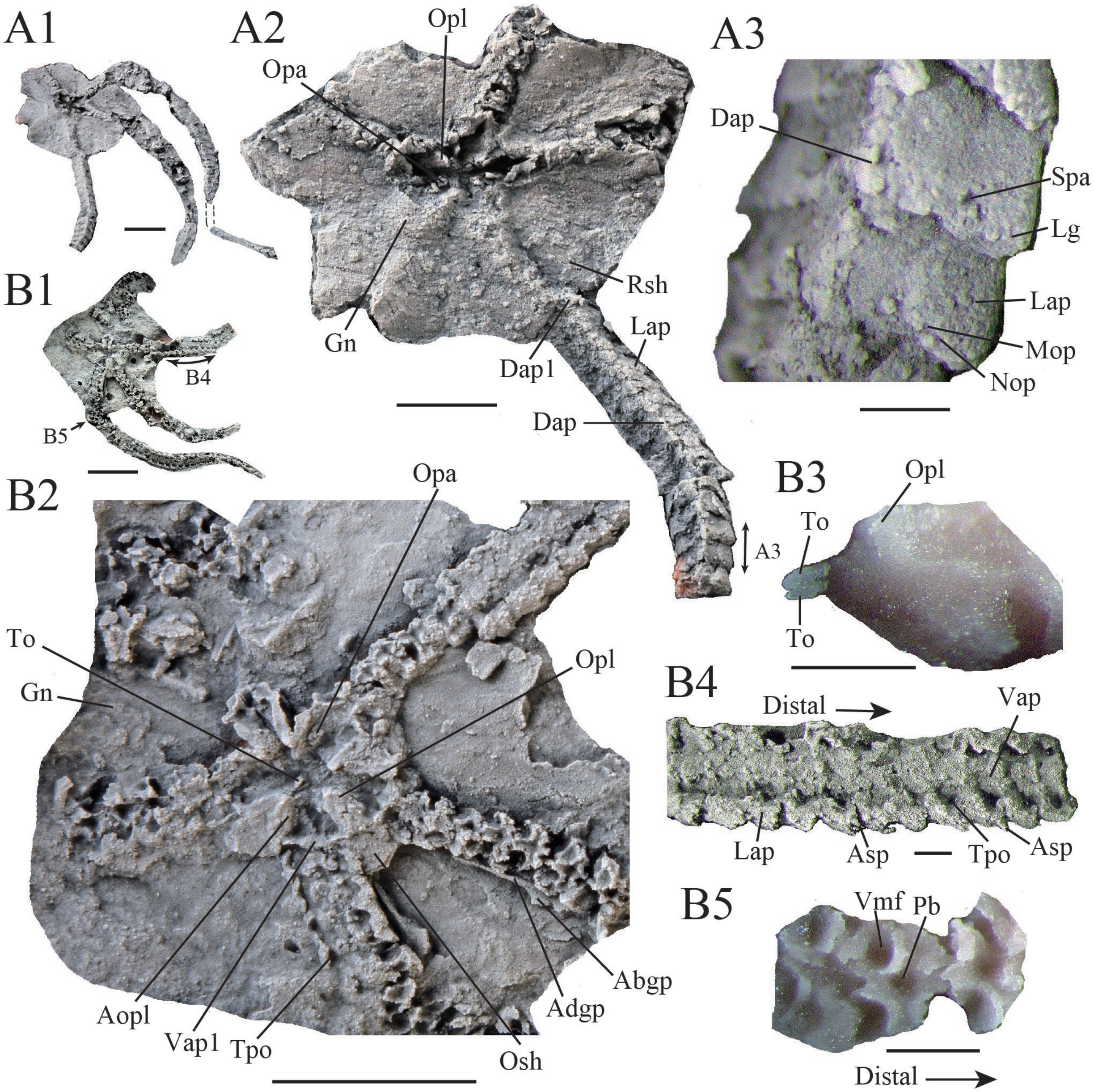

Figure 3. Synthetic resin casts of the holotype of *Triadoleucella meensis* gen. et sp. nov. **A**, VNMN-P-0278 (cast, NMNS PA 20004), dorsal side; A1, entire specimen; A2, disk and proximal arm; A3, enlarged view of mid-arm lateral arm plate; **B**, VNMN-P-0278 (cast, NMNS PA 20004), ventral side; B1, entire specimen; B2, enlarged view of disk; B3, enlarged view of teeth; B4, enlarged view of proximal arm; B5, vertebrae of proximal arm. Abbreviations: Abgp, Abradial genital plate; Adgp, Adradial genital plate; Aopl, adoral plate; Asp, arm spine; Dap, dorsal arm plate; Dap1, first dorsal arm plate; Gn, granule; Lap, lateral arm plate; Lg, Ledge; Mop, muscle opening; Nop, nerve opening; Opa, oral papilla; Opl, oral plate; Osh, oral shield; Pb, podial basin; Rsh, radial shield; Spa, spine articulation; To, tooth; Tpo, tentacle pore; Vap, ventral arm plate; Vap1, first ventral arm plate; Vmf, ventral muscle fossa. Scale bars equal 5 mm (A1, A2, B1, B2) and 1 mm (A3, B3, B4, B5).

Systematic paleontology

Class Ophiuroidea Gray, 1840
Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017
Order Ophioleucida O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017
Family unknown
Genus ***Triadoleucella*** nov.

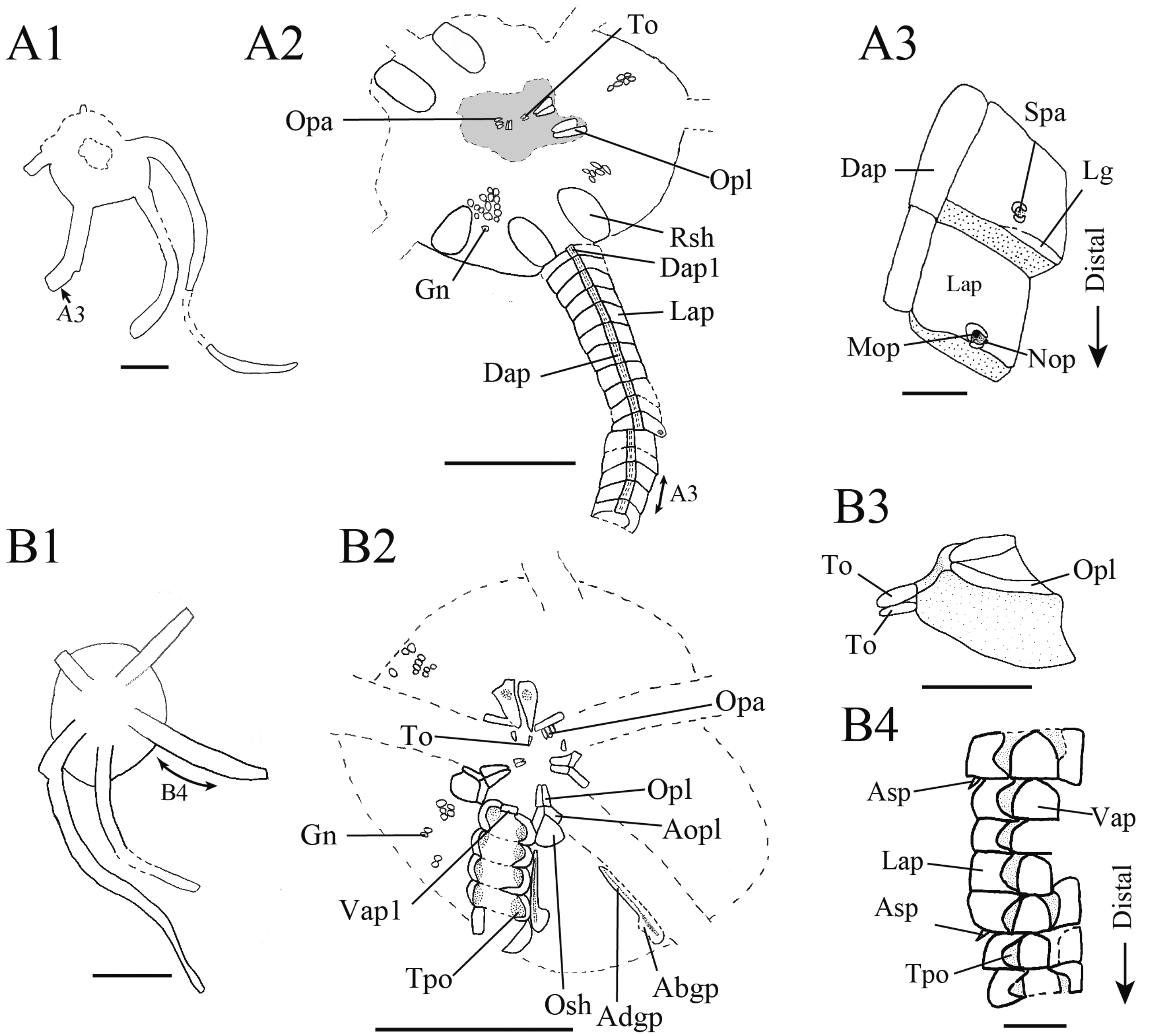

Figure 4. Line drawings of synthetic resin casts of the holotype of *Triadoleucella meensis* gen. et sp. nov. **A**1–**A**3 and **B**1–**B**4 correspond to a part of A1–A3 and B1–B4 in Figure 3, respectively. Abbreviations see Figures 3. Scale bars equal 5 mm (A1, A2, B1, B2) and 1 mm (A3, B3, B4).

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Diagnosis.—Disk low, fragile, relatively large, incorporating five arm segments and covered by relatively large, scattered granules on both dorsal and ventral sides; radial shields moderately large, elongated oval; at least three slender, pointed, contiguous oral papillae *sensu lato*; tentacle pores very large, pointing ventralward and covered by at least two large, operculiform scales; dorsal arm plates elongated, rectangular with sharp radial keel; at least three slender, pointed arm spines, half the length of an arm segment; lateral arm plates rectangular, fragile, with a finely reticulate outer surface stereom.

Type species.—*Triadoleucella meensis* sp. nov., designated herein.

Etymology.—The genus name literally translates as "small ophioleucid from the Triassic".

Triadoleucella meensis sp. nov.

Figures 3–6, 8, 9

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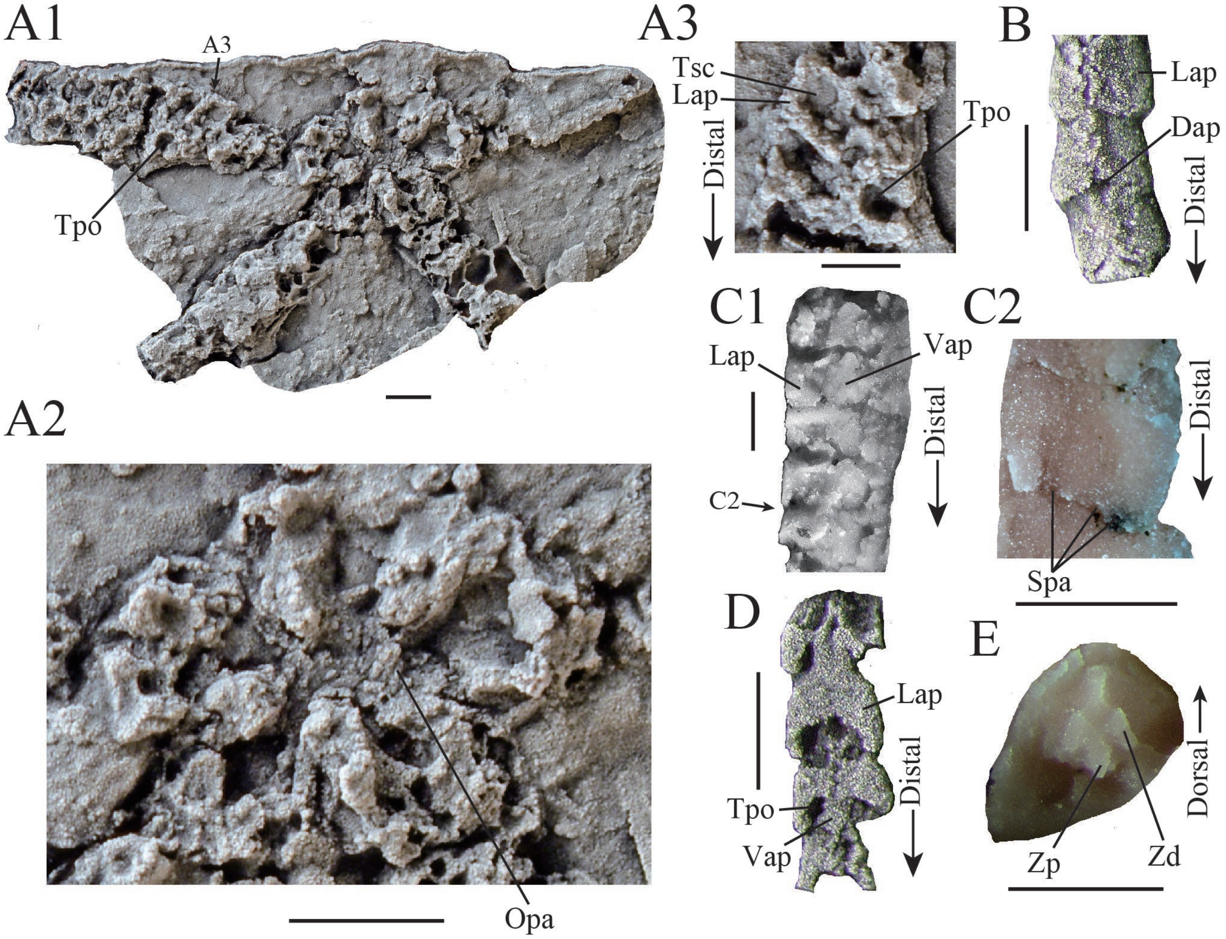

Figure 5. Synthetic resin casts of paratypes of *Triadoleucella meensis* gen. et sp. nov. **A**, VNMN-P-0279 (cast, NMNS PA 20005; A1, ventral side of disk and proximal arms; A2, enlarged view of jaw apparatus; A3, arm segments in disk; **B**, VNMN-P-0280 (cast, NMNS PA 20006), dorsal side of distal arm; **C**, VNMN-P-0281 (cast, NMNS PA 20007); C1, ventral side of mid arm; C2, enlarged view of lateral arm plate; **D**, VNMN-P-0282 (cast, NMNS PA 20008), ventral side of distal arm; **E**, VNMN-P-0283 (cast, NMNS PA 20009); distal part of a vertebra. Abbreviations: Tsc, tentacle scale; Zd, zygocondyle; Zp, zygosphene. The other abbreviations see Figure 3. Scale bars equal 1 mm.

Diagnosis.—As for genus.

Material.—Type material comprises three fully articulated specimens, and 25 articulated arms, preserved as external molds without any original skeletal calcite.

The holotype is VNMN-P-0278: for the cast, NMNS PA 20004, dorsal side (Figures 3A, 4A, 8A1, 9A1), ventral side (Figures 3B, 4B, 8B1, 9B1).

Paratypes are VNMN-P-0279 (cast, NMNS PA 20005; ventral side, Figures 5A, 6A, 8C1, 9C1), VNMN-P-0280 (cast, NMNS PA 20006; dorsal side of distal arm segments, Figures 5B, 6B, 8A2, 9A2), VNMN-P-0281 (cast, NMNS PA 20007; ventral side of articulated proximal to mid-arm, Figures 5C, 6C, 8D1, 9D1), VNMN-P-0282 (cast, NMNS PA 20008; ventral side of articulated distal arm, Figures 5D, 6D, 8D2, 9D2), VNMN-P-0283 (cast, NMNS PA 20009; dorsal side of articulated mid to distal arm, Figures 5E, 8B2, 9B2), VNMN-P-0284 (dorsal side; Figures 8E, 8F, 9E, 9F).

Additional material comprises 21 articulated arms deposited at Vietnam National Museum.

Etymology.—Species named after the type locality of the species, the Me area in northern Vietnam.

Locality and horizon.—Only known from the type locality: Loc 01 of Komatsu *et al.* (2017) in the Doi Cat Quarry, approximately 1 km from Me Town, Ninh Binh Province, northern Vietnam. Lower part of Upper Triassic Suoi Bang Formation. Upper Triassic Suoi Bang Formation.

Measurements.—Holotype (Figures 3A1, 3A2, 4A1, 4A2): disk diameter 11.4 mm, proximal arm width 2.0

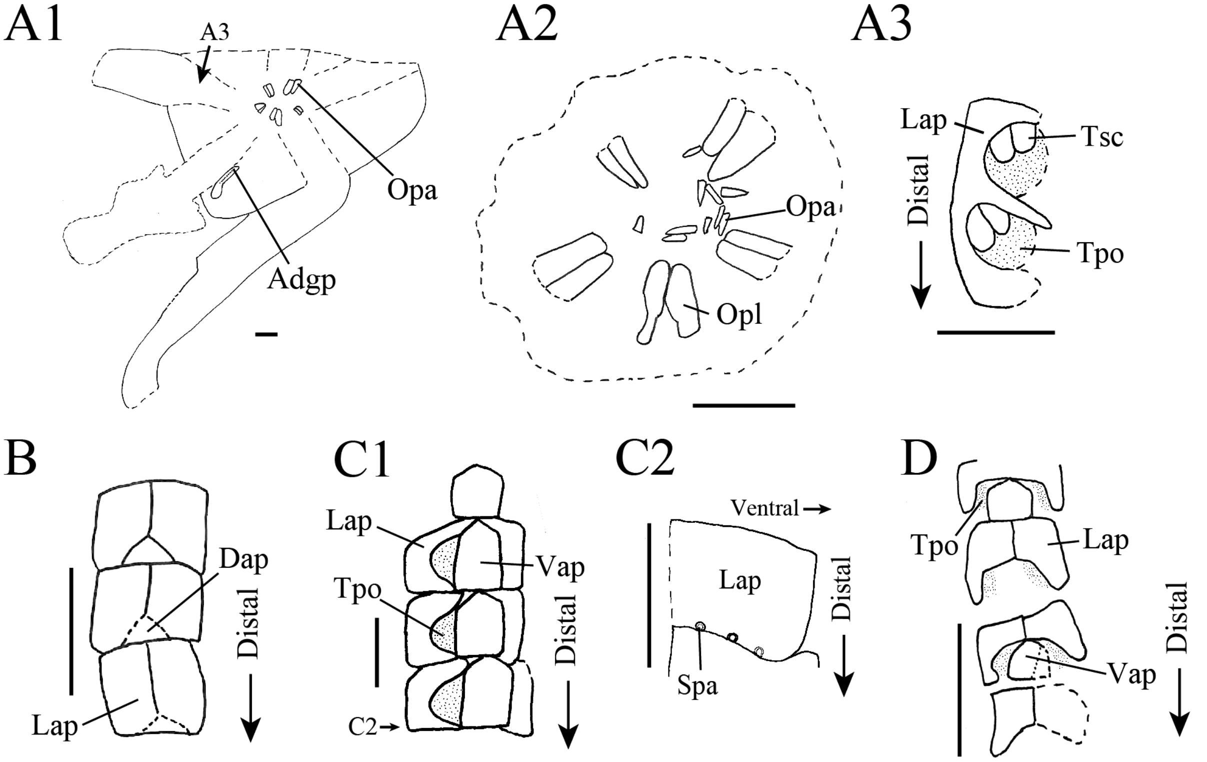

Figure 6. Line drawings of synthetic resin casts of paratypes of *Triadoleucella meensis* gen. et sp. nov. **A**–**D**, largely correspond to A–D in Figure 5. Abbreviations see Figures 3 and 5. Scale bars equal 1 mm.

mm and arm length 22.1+ mm. Paratype (VNMN-P-0279; cast, NMNS PA 20005: Figures 5A1, 6A1): disk diameter 12.9 mm, proximal arm width 2.3 mm and arm length 6.7+ mm. Paratype (VNMN-P-0284, Figures 8E, 8F, 9E, 9F): disk diameter 20.2 mm, proximal arm width 2.2 mm and arm length 10.0+ mm. The length of dissociated arms is 6.2–21.6 mm, on average, 11.1 mm (n = 25).

Description of holotype.—Articulated specimen preserved as external mold, with disk and long arms, exposing both the dorsal (VNMN-P-0278; cast, NMNS PA 20004: Figures 3A1–3A3, 4A1–4A3) and the ventral sides (VNMN-P-0278; cast, NMNS PA 20004: Figures 3B1–3B5, 4B1–4B4). The disk is fragile, flat, rounded pentagonal in outline, relatively large, incorporating the first five arm segments. The dorsal side of the disk and the ventral interradii are covered by thin, round scales bearing relatively large, scattered granules. The radial shields are moderately large, equaling approximately half the disk radius in length; they are elongated oval, about half as wide as long, separated from each other, with the distal-adradial portion exposed.

The jaw apparatus is dorsally exposed in the broken central part of the disk, showing the proximal tips of the oral plates bearing slender teeth in a single vertical row. The ventral side of the disk shows small, rounded-triangular oral shields about one-sixth of the disk radius, as long as wide and with a slightly convex distal edge. A madreporite is not discernible. The oral shields are proximally encompassed by small, quadrangular, relatively wide adoral shields that broadly meet in front of the oral shield. The oral plates are slender, form relatively short oral slits, and are bordered by at least three small, slender, contiguous pointed oral papillae *sensu lato* in a single row (Figures 3A2, 4A2, 3B2, 4B2). The teeth are small, slender, pointed, slightly wider than the oral papillae *sensu lato* and arranged in a single, short, vertical row (Figures 3B2, 3B3, 4B2, 4B3). The second oral tentacle pore opens superficially within the mouth slit but is not enclosed by extra rows of papillae. The adradial genital plates are elongated, extending from the distal edge of oral shields to disk edge. The abradial genital plate is approximately one third shorter than the adradial one and has a slightly concave distal tip.

The arms are slender and gradually taper toward the tip. The dorsal arm plates are squarish with a sharp radial keel. The proximalmost dorsal arm plates are as long as wide or slightly longer. They become gradually more elongate toward the tip of the arms and are in contact in all pre-

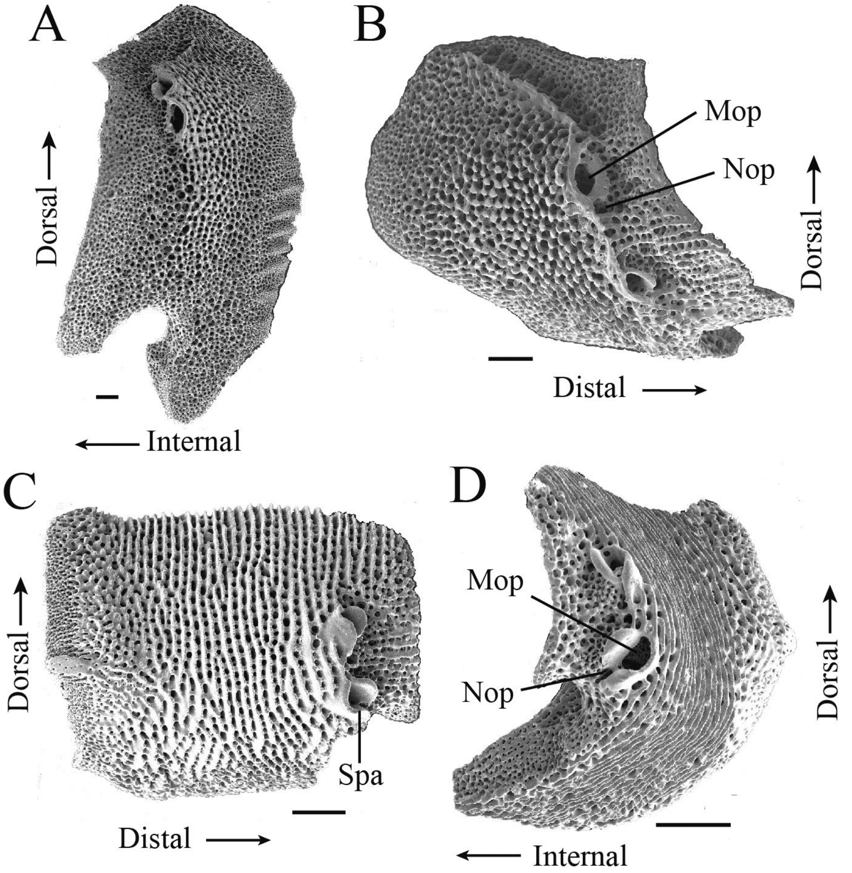

Figure 7. SEM images of proximal lateral arm plates of two extant species of Ophioleucida, *Ophiernus adspersus adspersus* Lyman, 1883 (Ophiernidae) NSMT E-11836 (**A**, **B**) and *Ophioleuce seminudum* Koehler, 1904 (Ophioleucidae) NSMT E-3101 (**C**, **D**). Abbreviations see Figure 3. Scale bars equal 0.1 mm.

served segments. The ventral arm plates are pentagonal, with a slightly convex distal edge, slightly concave lateral edges and a pointed proximal tip. The proximalmost ventral arm plates are rectangular, approximately 1.5 times wider than long. Successive ventral arm plates become gradually more elongate. They are in contact in proximal to median arm segments. The tentacle pores are very large and point ventralward. They are covered by at least two large, operculiform tentacle scales.

The lateral arm plates are fragile and of rectangular outline. Their outer surface stereom shows a fine reticulation. Their ventral edge is deeply incised by a large tentacle notch. Close to the distal edge of the lateral arm plates there are at least three small spine articulations, distally bordered by a narrow, lowered, thin ledge. The spine articulations are irregularly rhombic and consist of a large muscle opening ventrally bordered by a smaller nerve opening, and distally and proximally encompassed by slender, C-shaped lobes (Figures 3A3, 4A3). The ventralmost spine articulation seems to be the largest. The arm spines are small, conical, pointed, half the length of an arm segment (Figures 3B4, 4B4). Some arm segments expose the vertebrae (Figure 3B5), which show large ventro-proximal muscle fossae and large podial basins.

Description of paratypes.—VNMN-P-0279 (cast, NMNS PA 20005; Figures 5A1–5A3, 6A1–6A3, 8C1, 9C1) is an articulated specimen with disk and proximal arms exposing the ventral side. The oral papillae *sensu lato* and the teeth are small, slender and pointed as in the holotype. A number of dissociated papillae in the mouth opening suggests that there were more than three oral papillae *sensu lato*. The tentacle scales of the arm segments incorporated in the disk are slightly better preserved than in the holotype and corroborate their large size and operculiform shape.

VNMN-P-0280 (cast, NMNS PA 20006; Figures 5B, 6B, 8A2, 9A2) is an articulated arm fragment preserving eight arm segments, with a total length of 7.3 mm. It exposes the dorsal side of distal arm segments in which the lateral arm plates meet dorsally. The dorsal arm plates

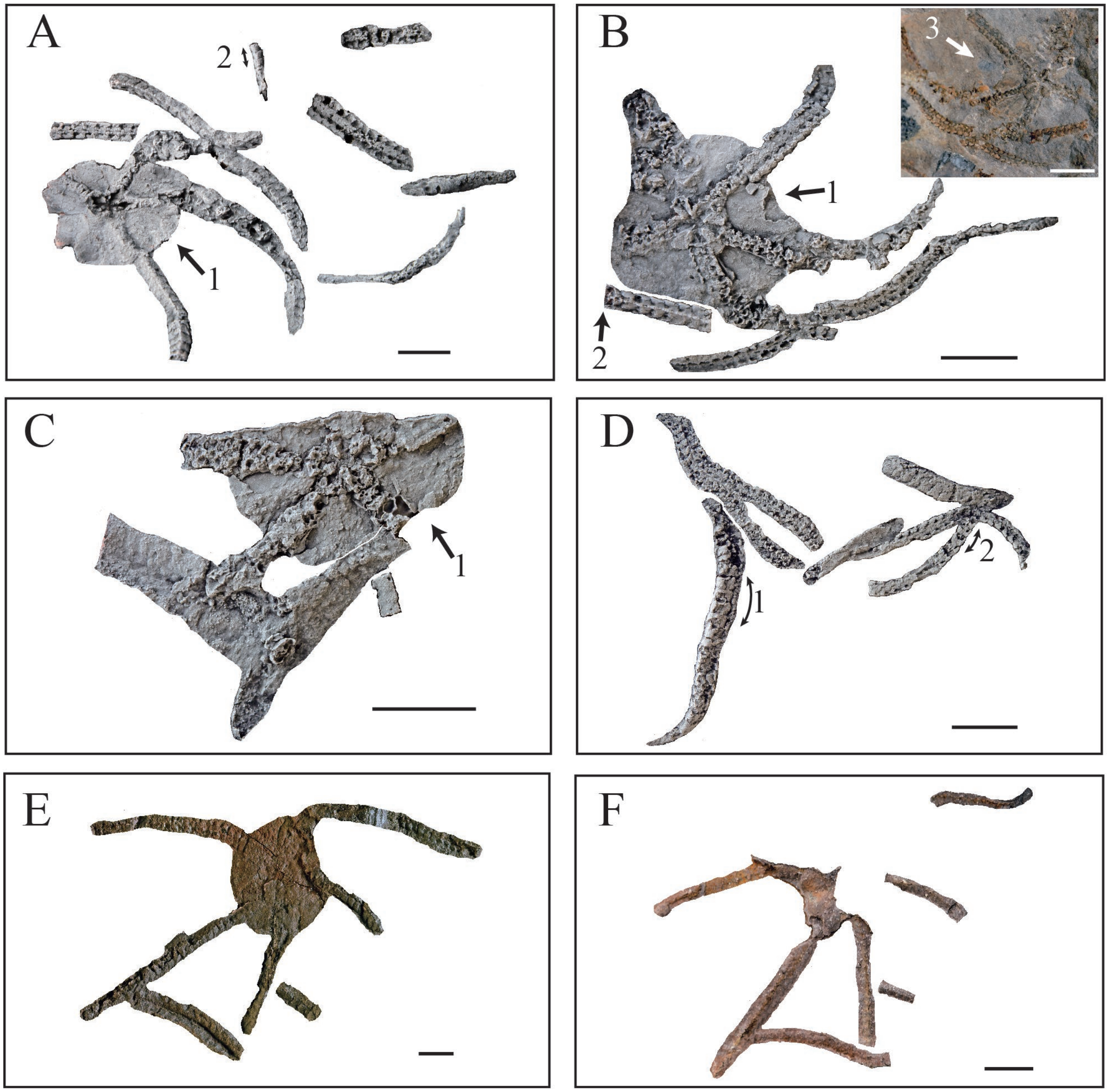

Figure 8. Mode of occurrence of *Triadoleucella meensis* gen. et sp. nov. **A**1, VNMN-P-0278 (cast, NMNS PA 20004), dorsal side; **A**2, VNMN-P-0280 (cast, NMNS PA 20006); **B**1, VNMN-P-0278 (cast, NMNS PA 20004), ventral side; **B**2, VNMN-P-0283 (cast, NMNS PA 20009); **B**3, VNMN-P-0278 (original sample of B1 with surrounding matrix); **C**1, VNMN-P-0279 (cast, NMNS PA 20005); **D**1, VNMN-P-0281 (cast, NMNS PA 20007); **D**2, VNMN-P-0282 (cast, NMNS PA 20008); **E**, **F**, VNMN-P-0284, divided into two parts (E, horizontal section, dorsal side; F, outer surface, dorsal side). Synthetic resin casts (A–D) and matrix samples (B3, E, F). Scale bars equal 5 mm.

are lost and were probably reduced to small, triangular rudiments in the distal tip of the arm segment judging from the voids left.

VNMN-P-0281 (cast, NMNS PA 20007; Figures 5C1, 5C2, 6C1, 6C2, 8D1, 9D1) is an articulated arm fragment preserving 22 arm segments, with a total length of 15.5 mm. It exposes the ventral and lateral sides of median arm segments. The ventral arm plates and spine articulations in the median plates are slightly better preserved than in the holotype specimen. The ventral arm plates are pentagonal, slightly longer than wide (Figures 5C1, 6C1). The spine articulations are similar to those of the holotype. There are at least three spine articulations evenly spaced close to the distal edge of the lateral arm plates (Figures 5C2, 6C2).

VNMN-P-0282 (cast, NMNS PA 20008; Figures 5D,

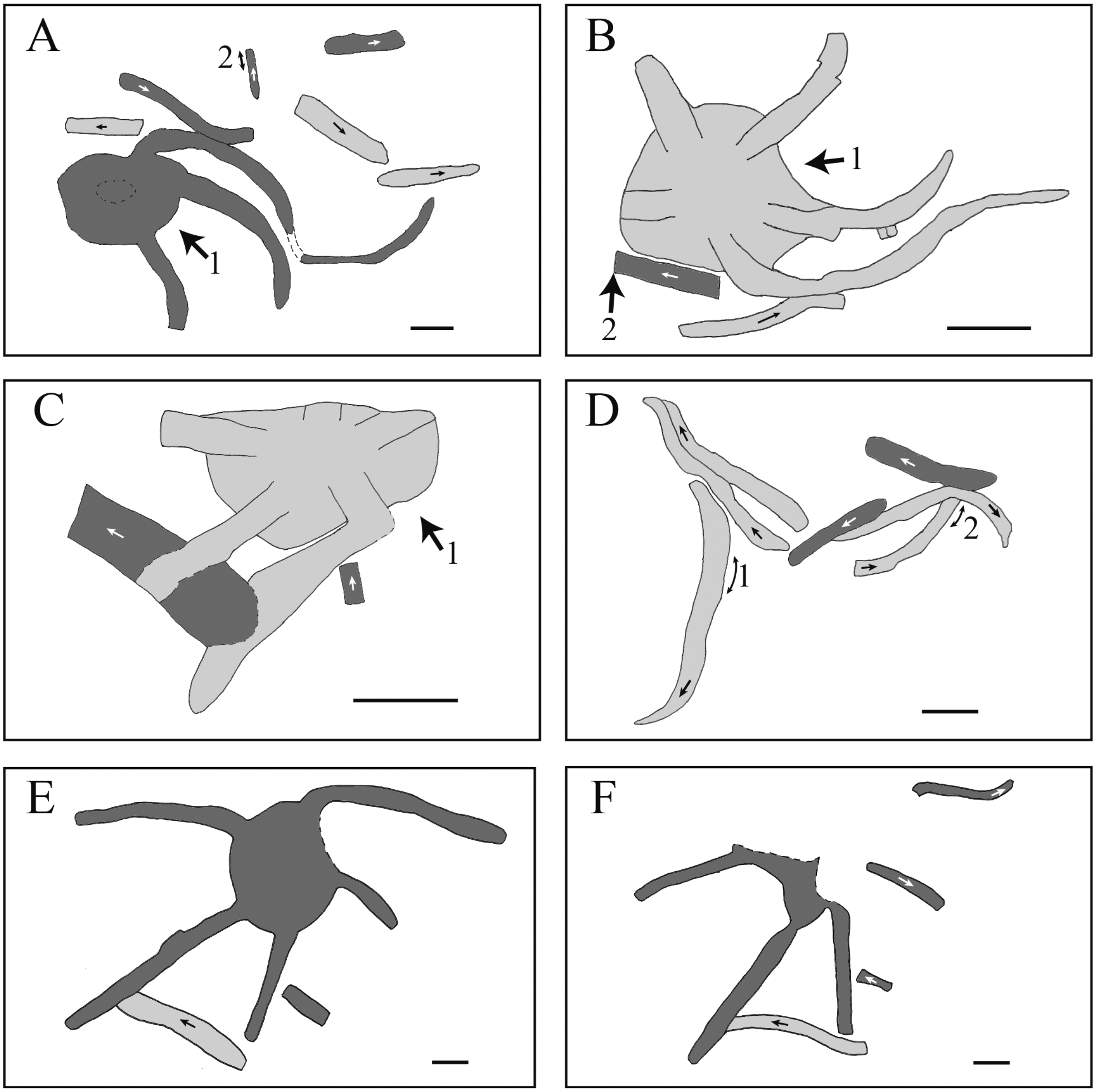

Figure 9. Line drawings of mode of occurrence of synthetic resin casts (**A**–**D**) and a matrix sample (**E**, **F**) of *Triadoleucella meensis* gen. et sp. nov. Specimens shown in gray and dark gray illustrate ventral and dorsal sides, respectively. Arrows indicate the distal direction. Specimen numbers are the same as in Figure 8. Scale bars equal 5 mm.

6D, 8D2, 9D2) is an articulated arm fragment preserving 13 arm segments, with a total length of 8.6 mm. It exposes the ventral side of median to distal arm segments. The ventral arm plates of the distal arm segments are small, pentagonal, approximately 1.5 times longer than wide and separated by the lateral arm plates. The tentacle pores are large.

VNMN-P-0283 (cast, NMNS PA 20009; Figures 5E, 8B2, 9B2) is an articulated arm fragment preserving eight arm segments, with a total length of 6.7 mm. It exposes the dorsal side of median to distal arm segments. Some segments are partly dissociated, exposing the distal side of a vertebra. The articulation is of the zygospondylous type, with dorsalward-converging zygocondyles and a short zygosphene. The vertical shaft on the dorsal side is slender and tall.

VNMN-P-0284 (Figures 8E, 8F, 9E, 9F) is separated into two parts, an articulated skeleton preserving the disk and five arms, and exposing the dorsal side. Some of the arms are more complete than those in the holotype, indicating a length of at least two times the disk diameter.

Discussion

The ophiuroids described in the present paper appear superficially similar to most other slender-armed, short-spined ophiuroids of Triassic age, and in particular to members of the genera *Aplocoma* d'Orbigny, 1852 and *Arenorbis* Hess, 1970. A more detailed examination, however, has revealed a highly distinctive combination of characters in the new form, namely a relatively large, low, fragile disk covered by scattered granules, a bar-shaped abradial genital plate with a concave distal tip, slender arms with large, ventralward-pointing tentacle pores, rectangular dorsal arm plates, and fragile lateral arm plates with small, irregularly rhombic spine articulations (Figures 3, 4). This combination of characters is exclusively found in the extant order Ophioleucida as defined by O'Hara *et al*. (2018). Similarities in lateral arm plate microstructure and arm spine articulation to Recent members of the Ophioleucida (Figure 7) are particularly compelling. We therefore assign the fossils described in the present paper to the Ophioleucida.

Affinities at the family level, however, are less clear-cut, because the fossils show characters that are found in both the Ophiernidae O'Hara, Stöhr, Hugall, Thuy and Martynov, 2018 and the Ophioleucidae Matsumoto, 1915. To make matters worse, the former, as currently defined, is monotypic, with *Ophiernus* Lyman, 1878 showing a highly specialized morphology, including bristle-shaped arm spines, vertebrae with radiating rib-like structures on distal muscle fossae, and lateral arm plates with rib-like spurs on the outer proximal edge (Figure 7A; O'Hara *et al*., 2018), probably related to an active swimming behavior (Hendler and Miller, 1991). This, together with the estimated Early Mesozoic age of the Ophiernidae (O'Hara *et al*., 2017, 2018) indicates that *Ophiernus* is only a small, extant part of a formerly much more diverse morphological spectrum. At present, we cannot determine if the present fossils belong to one of the two extant ophioleucid families, or should be assigned to an extinct family within the order.

The fossil record of the Ophioleucida is relatively sparse. The most exhaustively known extinct genera are *Ophiopinna* Hess, 1960 from the Middle Jurassic of France, *Eirenura* Thuy, 2011 from the Lower Jurassic of Europe, and *Sinosura* Hess, 1964 from the Lower to Upper Jurassic of Europe. *Sinosura* and *Ophiopinna* differ from the Vietnamese fossils in several respects, among others, in the well-developed vertical striation of the lateral arm plates. In addition, *Ophiopinna* shows large, feather-like arm spines in median arm segments, attached to specialized articulations. *Eirenura* has more spine articulations, smaller dorsal arm plates and a significantly different arrangement of oral papillae *s.l.* Only three Cretaceous ophioleucid records are known to date: *Ophioleuce sanmigueli* Thuy, Gale, Stöhr and Wiese, 2014 from the Aptian of Spain, an unnamed ophioleucid record from the Aptian of the Blake Nose escarpment (Thuy *et al*., 2012) and *Sinosura jasmundensis* Kutscher and Jagt, 2000. All three are based on dissociated lateral arm plates with a well-developed vertical striation, thus clearly differing from the lateral arm plates of the material described herein.

In view of the fact that they significantly differ from all fossil and Recent ophioleucid taxa known to date, we assign the ophiuroids described in the present paper to a new genus and species *Triadoleucella meensis*. It represents the first Triassic record of the Ophioleucida and thus significantly expands the temporal range of that order.

The mode of occurrence of *Triadoleucella meensis* allows insights into the taphonomy of the assemblage. The material comprises three fully articulated individuals that preserve long portions of their fragile arms and even the most delicate skeletal components, such as disk granules and oral papillae, in their original anatomical context (Figures 8, 9). In addition to the three complete skeletons, the material includes 25 long, fragmentary, yet fully articulated arm fragments. Because ophiuroids disarticulate rapidly within hours or days after death in a normal marine environment (Brett *et al*., 1997; Kerr and Twitchett, 2004), the degree of articulation of the ophiuroids described in the present paper suggests effective burial prior to or very soon after death. The orientation of the disks and arm fragments seems to be random with respect to the dorsal or the ventral side facing upward. This observation, together with the fragmented, yet fully articulated preservation of the skeletons, suggests strong mechanical stress during or prior to burial. Since the depositional setting of the ophiuroids described herein was below storm wave base, we speculate that burial was caused by a downslope mudflow.

Acknowledgments

We wish to thank Hung Ba Nguyen (Vietnam National Museum of Nature, Hanoi) for his assistance in the geological survey. John W. M. Jagt (Natuurhistorisch Museum, Maastricht, the Netherlands) and Andreas Kroh (Natural History Museum Vienna, Austria) greatly improved an earlier draft of this manuscript. This study was financially supported by Grants-in-Aid for Scientific Research (KAKENHI) from the Japan Society for the Promotion of Science (19K04059 to T. K.) and Sakura Science Exchange Program, JST (S2019F0531337 to T. K., H. T. T. and Y. I., and by the Project for Collecting

Paleontological Specimens in Vietnam (BSTMV.28/15-18 to H. T. T. and H. D. D.).

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Author contributions

We declare that none of the material in this manuscript has been published or is under consideration for publication elsewhere. B. T., L. D. N-T. and Y. I. identified the fossils, T. F. commented in comparison with extant species, Y. S. discussed the geological age of the fossil site and T. K., H. T. T., H. D. D. and M. T. N. collected the fossils and surveyed the site. All authors contributed to the writing of the manuscript.