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Amphiura multispina (Ophiuroidea, Amphiuridae) from the upper Pleistocene Kioroshi Formation in a drill core at Nagareyama, Chiba, central Japan

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Abstract. Over 100 well-preserved dissociated ophiuroid arm ossicles, i.e., lateral arm plates, dorsal arm plates, ventral arm plates, vertebrae and arm spines, were recovered from the upper Pleistocene Kioroshi Formation in the core of borehole GS-NY-1 at Nagareyama, Chiba Prefecture, central Japan. Following comparison with the lateral arm plates of ten extant amphiurid species occurring in the seas around Japan and with previously published fossil taxa in this family, the ossicles from Nagareyama were identified as belonging to the extant species, *Amphiura multispina*. This is the first fossil record of this form and the stratigraphically youngest of the Amphiuridae. The taphonomy and paleoenvironment of the brittle star fossils described are also discussed.

Keywords: extant species, lateral arm plate, ophiuroid, ossicle, paleoenvironment, taphonomy

Introduction

The family Amphiuridae, established by Ljungman (1867) and is currently one of the most species-rich within the class Ophiuroidea (e.g. Matsumoto, 1917; A. M. Clark, 1970; Stöhr *et al*., 2021). Recently, O'Hara *et al*. (2017, 2018) have presented a new phylogeny of the Ophiuroidea using molecular data in line with morphological evidence (Martynov, 2010; Thuy and Stöhr, 2016). In the revised classification based on these novel phylogenetic insights (O'Hara *et al*., 2018), the family Amphiuridae was included in the Superfamily Amphiuroidea Ljungman, 1867 (suborder Gnathophiurina Matsumoto, 1915, order Amphilepidida, O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017). However, the new phylogeny has also suggested that the Amphiuridae is a polyphyletic complex in need of revision and now containing a group of genera and species with strongly divergent morphologies. Since an exhaustive reappraisal of the Amphiuridae is beyond the scope of the present study, we here use the names of genera and species in their traditional broad sense, pending a comprehensive revision.

The fossil record of the Amphiuridae is particularly sparse (Jagt, 2000; Thuy *et al*., 2018), in spite of the considerable present-day diversity and the assumed Mesozoic origin of the family (Stöhr *et al.* 2012; O'Hara *et al*. 2017). Thuy *et al*. (2018) revised extinct material previously included in the Amphiuridae as follows: *Nullamphiura felli* Skwarko, 1963 from the Upper Cretaceous of Australia is based on a virtually unidentifiable specimen, in addition, based on the shape of the spine articulations, *Amphiura cretacea* Spencer, 1907 from the lower Upper Cretaceous of England was transferred to the Ophiotomidae Paterson, 1985, and the articulated body fossils, *Xanthamphiura hauteriviensis* Hess, 1970 from the Lower Cretaceous of Switzerland, *Deckersamphiura inusitata* Jagt and Kutscher, 2000, *in* Jagt (2000) from Upper Cretaceous of the Netherlands and *D. vitea* Jagt, 2001 from Upper Cretaceous of the Netherlands require critical re-assessment taking into account the micromorphology of spine articulations. While, *Amphiura*? *senonensis* Valette, 1915, originally recorded from the Upper Cretaceous of France and subsequently also collected elsewhere in Europe, had tentatively been transferred to *Ophiocoma* L. Agassiz, 1836 by Kutscher and Jagt, *in* Jagt (2000). To date, the only reliable amphiurid fossil taxa are *Amphiura shannoni* Thuy, Numberger-Thuy and Jagt, 2018 and *Amphioplus clementsi* Thuy, Numberger-Thuy and Jagt, 2018, both from the Upper Cretaceous of the eastern USA and based on isolated lateral arm plates, plus records of articulated specimens from the Cenozoic of Japan, in particular *Amphioplus uchigoensis* Ishida, 1992 of Oligocene age

(Ishida, 1992), and four still unidentified genera and species from the Miocene to Pliocene strata (Ishida, 2004).

Recently, in excess of 100 dissociated, yet well-preserved amphiurid arm ossicles (lateral, dorsal and ventral arm plates, vertebrae and arm spines) have been recovered from the upper Pleistocene Kioroshi Formation penetrated in borehole GS-NY-1 in Nagareyama-shi, Chiba Prefecture, central Japan (Nakazawa *et al.*, 2014, 2017) (Figure 1). In order to identify the dissociated ossicles, we have compared them to macerated lateral arm plates of ten extant amphiurid species occurring in the seas around Japan and those of previous records of extinct amphiurids. Here we provide a detailed morphological description of the Nagareyama ossicles and study their taphonomy and paleoenvironmental context.

Material and methods

The material described herein consists of 159 dissociated ophiuroid ossicles, comprising lateral arm plates, vertebrae, arm spines, ventral and dorsal arm plates, all extracted from bulk sediment samples taken from medium-grained sand assigned to upper Pleistocene Kioroshi Formation (Shimousa Group) in drill core GS-NY-1 (Nakazawa *et al.*, 2017). The core was drilled at Nishihatuishi, Nagareyama-shi, Chiba Prefecture, central Japan (co-ordinates 35°52′8.14″N, 139°55′31.40″E; Figure 1). The ophiuroid ossicles were recovered from seven horizons at a depth of 13.40–16.40 m below surface (Sample numbers NY-07 to -13; Figure 2).

Nakazawa *et al.* (2017) analyzed the sedimentary system of the Kioroshi Formation, including data from six drill cores in northern Chiba area, central Japan, on the basis of sequence stratigraphy. In geographical position, the Nagareyama drill core GS-NY-1 is the westernmost of the six cores. Sediments penetrated in this borehole are subdivided into four formations with sequence boundaries; in ascending order these are the Kamiizumi Formation (*c.* 25 m thick), Kiyokawa Formation (*c.* 4 m thick), Kioroshi Formation (*c.* 22 m thick) and Joso Formation (*c.* 3 m thick). In turn, the Kioroshi Formation was subdivided into seven units, using mainly lithological facies and erosion surfaces. Five of these units, in ascending order, Unit I (fluvial facies), Unit II (estuarine facies), Unit IV (central basin facies), Unit V (tidal flood/delta facies) and Unit VII (lagoonal facies), were found in core GS-NY-1. The lower parts of Units I, II, IV is interpreted as incised valley systems, whereas the upper parts of Units V, VII are seen as barrier island systems (Nakazawa *et al.*, 2017) (Figure 2). The brittle star fossils described here were extracted from Unit V, which yielded abundant molluscan shells, well known as the Kioroshi shell bed (dominated by the bivalve *Mactra chinensis* Philippi, 1846 and the echinoid *Scaphechinus mirabilis* A. Agassiz, 1864), and is interpreted as a prograding tidal flood/delta sediment based on lamination structures (Nakazawa *et al*., 2017). Okazaki and Kurozumi (2008) and Okazaki *et al*. (2016) concluded that the fossiliferous layers were deposited on the flank of the delta front. The Kioroshi Formation in the nearby Kashiwa-shi area was interpreted to have been laid down at shallow sublittoral depths (several tens of metres) and yield an admixture of warm- and cold-adapted species among molluscs as well as benthic and planktonic foraminifera (Okazaki *et al*., 2018). The geological age of the Kioroshi Formation is estimated to correspond to marine isotope stage (MIS) 5e (130–117 Ka; Martinson *et al*., 1987) based on correlation with pollen zonation and transgressive stage by oxygen isotope analysis (Nakazawa *et al*., 2017).

Bulk matrix samples were extracted from the core at every 5 cm, resulting in a total of seven sets (Sample numbers NY-07–NY-13; see Figure 2). The sediments were dried for 24 hours at 80 degrees Celsius. For every sample, twenty grams of bulk sediment were extracted and boiled in water. When the sediment particles were sufficiently dispersed, heating was stopped and the sample was washed. The residues were dried in an incubator. Ossicles over 0.125 mm mesh size were handpicked from the residues under a stereo microscope. Selected ossicles were photographed using scanning electron microscopes Hitachi High Technologies TM-1000, and JEOL JSM-6380LV, at the Gunma Museum of Natural History and at the National Museum of Nature and Science, Tsukuba, respectively.

Portions of arms of 10 extant amphiurid species from the seas around Japan housed in the collections of the National Museum of Nature and Science, Tsukuba, were macerated using household bleach (approximately 5% sodium hypochlorite solution). These are: *Amphioplus* (*Amphioplus*) *macraspis* (NSMT E-4326), *Amphiura arcystata* (NSMT E-1343), *Amphiura* (*Fellaria*) *ecnomiotata* (NSMT E-4391), *Amphiura iridoides* (NSMT E-7388), *Amphiura leptobrachia* (NSMT E-11486), *Amphiura* (*Amphiura*) *luetkeni* (NSMT E-4998), *Amphiura* (*Amphiura*) *micraspis* (NSMT E-4874), *Amphiura multispina* (NSMT E-1490, 6545), *Amphiura* (*Fellaria*) *sinicola* (NSMT E-939), *Amphiura* (*Fellaria*) *vadicola* (NSMT E-1512). Isolated ossicles of these species, observed by scanning electron microscopy, were compared directly with fossil counterparts.

The fossil material extracted from drill core GS-NY-1 is housed in the collections of the National Museum of Nature and Science, Tsukuba (NMNS PA). The fifteen ossicles illustrated in the present paper bear catalogue numbers NMNS PA 20233 up to and including 20247. Terminology of ossicle morphology follows LeClair (1996), Stöhr *et al*. (2012), Thuy and Stöhr (2011, 2016) and Thuy *et al*. (2018). Here we adopt the classification proposed by O'Hara *et al*. (2017, 2018).

Systematic description

Order Amphilepidida O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017
Suborder Gnathophiurina Matsumoto, 1915
Superfamily Amphiuroidea Ljungman, 1867
Family Amphiuridae Ljungman, 1867
Genus ***Amphiura*** Forbes, 1843
Amphiura multispina H. L. Clark, 1915
Figures 3–4

Fossil material examined. – Five dissociated lateral arm plates: NMNS PA 20233 [Figure 3A1, 3] (Sample number NY-09; see Figure 2); NMNS PA 20234 [Figure 3A2, 4] (NY-12); NMNS PA 20235 [Figure 3B1–4] (NY-13); NMNS PA 20236 [Figure 3C1–3] (NY-13) and NMNS PA 20237 [Figure 3C4] (NY-12). Three dissociated dorsal arm plates: NMNS PA 20238 [Figure 4A1–2] (NY-10); NMNS PA 20239 [Figure 4B1–2] (NY-12) and NMNS PA 20240 [Figure 4C1–2] (NY-12). Three dissociated ventral arm plates: NMNS PA 20241 [Figure 4D1–2] (NY-11); NMNS PA 20242 [Figure 4E1–2] (NY-11) and NMNS PA 20243 [Figure 4F1–2] (NY-11). Three vertebrae: NMNS PA 20244 [Figure 4G1–4] (NY-12); NMNS PA 20245 [Figure 4H1–4] (NY-12) and NMNS PA 20246 [Figure 4I1–4] (NY-12). A single arm spine: NMNS PA 20247 [Figure 4J1–4] (NY-09). All material originates from samples collected from Nagareyama drill core GS-NY-1 (NY-07–13, depth 13.40–16.40 m; see Figure 2) within the Pleistocene Kioroshi Formation.

Fifteen figured ossicles (NMNS PA) and the remaining 144 ossicles (61 lateral arm plates, 12 dorsal arm plates, 25 ventral arm plates, 35 vertebrae, 11 arm spines) (Table 1) are kept at the National Museum of Nature and Science, Tsukuba Japan.

Description of fossil ossicles. – Dissociated proximal lateral arm plates (Figure 3A1–4) approximately 3.3 times taller than long, conspicuously sickle-shaped; with pointed dorso-proximal and ventro-proximal tips, distal edge evenly convex, proximal edge evenly concave, devoid of spurs; outer surface with stereom of medium mesh size, without tubercles or otherwise transformed trabecular intersections, but with a narrow crescent-shaped area with more finely meshed stereom in the center of the proximal edge, and similar more finely meshed stereom around the spine articulations; up to eight large spine articulations, freestanding and evenly distributed along the distal edge of the lateral arm plate; ventralmost spine articulations largest, the other ones becoming gradually smaller dorsally; spine articulations (Figure 3A4) horizontal, composed of two parallel, near-equal, massive and fully separated lobes, the dorsal one slightly curved and the ventral one straight; two lobes encompassing nearly equal-sized muscle and nerve openings. Inner side of proximal lateral arm plates (Figure 3A2–3): large oblong depression in the central proximal area of the inner side; three well-defined knobs in the middle of the inner side, one of which in a central position (central knob), round, flat, strongly protruding and composed of densely meshed stereom, the two other knobs (centro-proximal knobs) each consisting of a wide plateau composed of massive stereom at the edge of the large oblong depression in a central proximal position; fourth poorly defined, tiny, flat knob composed of densely meshed stereom close to the ventro-distal edge (ventral knob). Tentacle notch wide and shallow, resulting in a slightly concave ventro-distal edge of the lateral arm plate. Conspicuous elongated perforation close to the ventral edge of the central knob. Narrow and well-defined vertical furrow with at least three elongated perforations. Inner surface composed of relatively coarsely meshed stereom.

Dissociated median lateral arm plates (Figure 3B1–4) approximately 2.5 times taller than long, sickle-shaped; dorsal and ventral edges as in proximal lateral arm plates; outer surface as in proximal arm plates; up to five spine articulations located at distal edge of the median lateral arm plates as in proximal lateral arm plates. Inner side of median lateral arm plates (Figure 3B2–3): depression at centro-proximal portion unclear, probably replaced by area of massive stereom; central knob as in proximal lateral arm plates, centro-proximal knobs merged, ventro-distal knob very tiny or indistinct; vertical furrow indistinct; stereom on inner surface slightly coarser than in proximal lateral arm plates.

Dissociated distal lateral arm plates (Figure 3C1–4) approximately 1.6 times taller than long, the shape of the dorsal and ventral edges as in proximal and median lateral arm plates; outer surface as in proximal and median lateral arm plates; three spine articulations, the ventral one slightly larger than the two dorsal ones; other features as in median arm plates. Inner side of distal lateral arm plates (Figure 3C2–3): vertical furrow indistinct; stereom on inner surface slightly coarser than in median lateral arm plates; centro-proximal knobs merged, small, of irregular shape; ventral knob indistinct; perforation close to the ventral edge of the central knob indistinct; other features as in median lateral arm plates.

Dissociated proximal dorsal arm plates (Figure 4A1-2) are slightly longer than wide, thin, oval shape with the proximal part cut off and slightly concave, the outer surface slightly swollen at the center; the inner side slightly swollen at the center, with a deep longitudinal groove. The stereom of the outer surface is finer than the inner surface. Dissociated median dorsal arm plates (Figure 4B1–2) wider than long, of oval outline with the proximal edge cut off and slightly concave, and with a rounded distal portion; outer surface entirely composed of finely meshed stereom, becoming finer along the edge of the plate. Inner side of median dorsal arm plates (Figure 4B2), slightly swollen at the center, with relatively deep, longitudinal groove; inner surface composed of coarser stereom than outer surface. Dissociated distal dorsal arm plates (Figure 4C1–2) slightly smaller than median ones, slightly wider than long; outline and stereom microstructure as in median dorsal arm plates.

Dissociated proximal ventral arm plates (Figure 4D1) as long as wide, relatively thick, hexagonal, slightly concave at proximal edge, slightly convex at lateral edges, with four pointed angles at proximal side; outer surface entirely composed of finely meshed stereom, becoming finer along the edge of the plate. Inner side of proximal ventral arm plates (Figure 4D2), swollen in the middle; inner surface composed of relatively coarse stereom at the depression in the proximal half of the plate, becoming finer towards the plate edges. Dissociated median ventral arm plates (Figure 4E1–2) smaller, otherwise similar to the proximal ones. Dissociated distal ventral arm plates (Figure 4F1–2) smaller than median ones, slightly concave at lateral edges; shape and stereom microstructure as in median and proximal ones.

Dissociated proximal to distal vertebrae (Figure 4G1–4, H1–4, I1–4) of zygospondylous type; at the distal side, zygosphene small, as high as wide, drop-shaped; zygocondyles small, balloon-shaped, of equal width and height, round dorsally, pointed ventrally. At the proximal side, median sockets triangular with round corners, pointed ventrally, of equal width and height; surrounding ridges slightly detached from each other ventrally. Median saddle short, rod-like, pointed dorsally. At the dorsal side, dorsal edges of distal muscle fossae distalwards converging and projecting, forming a keel-like structure; dorso-proximal muscle fossae collapsed, forming a proximal depression-like structure; dorso-distal muscle fossae wide, without conspicuous groove. At the ventral side, ambulacral grooves deep and with protruding lateral sides; ventro-distal muscle fossae with deep groove.

Dissociated proximal to median arm spines (Figure 4J1–4) conical, tumid, laterally compressed, with blunt tip; outer surface composed of finely meshed stereom, becoming slightly rougher around lateral edges. Articulation with lateral arm plates slightly protruding, with curved elongated groove and two small perforations, one irregular, large, the other one round, small.

Discussion

The dissociated ossicles from the Nagareyama drill core GS-NY-1 comprise lateral, dorsal and ventral arm plates, vertebrae, and arm spines. Among these ossicles, the lateral arm plates have a particularly character-rich morphology, thus allowing for a detailed identification down to species level (e.g. Thuy and Stöhr, 2011). Therefore, as a first step, we compared the fossil lateral arm plates with those of closely related extant and extinct taxa.

The lateral arm plates described herein can be assigned to the family Amphiuridae because they show the following features: 1) spine articulations with two smooth, separated, parallel, slightly curved dorsal and ventral lobes; 2) a sickle-shaped general outline with conspicuously pointed dorsal tips; 3) an area of finely meshed stereom at centro-proximal edges of the outer surface; 4) three knobs on the inner side (Thuy and Stöhr, 2011; O'Hara *et al*., 2018).

The genus- and species-level spectrum of amphiurid lateral arm plate morphologies has not yet been explored in detail (Thuy *et al*., 2018). To make matters worse, the major extant genera within the family are polyphyletic in their current species composition (O'Hara *et al*., 2017). Therefore, we compared the fossil lateral arm plates from the Nagareyama core with macerated lateral arm plates of 10 species of extant amphiurids inhabiting the seas around Japan, in addition to the three species for which Thuy and Stöhr (2011) provided illustrations and descriptions of lateral arm plate morphologies. Furthermore, we compared the material described herein with the lateral arm plates of previously recorded extinct amphiurids.

Comparisons with extant amphiurid species. —The number of arm spines is among the main characters used in species-level identification keys of Amphiuridae, with spine numbers varying between three and ten (e.g. Matsumoto, 1917). In view of the fact that lateral arm plates from the Nagareyama core have up to eight spine articulations, we focused on extant species with five or more spine articulations (e.g. Matsumoto, 1917; Murakami, 1942).

Amphiura multispina (Figure 5; disk diameter, 9.1 mm, NSMT E-1490), dissociated proximal to distal lateral arm plates (ratios of height/width of proximal, median, distal portions, 3.3, 2.6, 1.7, respectively) agree with the fossil ones described herein in every aspect (Figure 3).

Amphioplus (*Amphioplus*) *macraspis* (H. L. Clark, 1911) (Figure 6A; disk diameter, 11.4 mm, NSMT E-4326), dissociated proximal lateral arm plates with five spine articulations, differing from the present fossil specimens in having a slightly wider sickle-shape (ratio of height/width 2.6), an indistinct vertical furrow on the inner side, a protruding ventral knob, and a smaller perforation at ventral edge of the central knob.

Amphiura (*Amphiura*) *micraspis* H. L. Clark, 1911 (Figure 6B; disk diameter, 9.1 mm, NSMT E-4874), dissociated proximal lateral arm plates with five spine articulations, differing from the present fossil specimens in having a very wide sickle-shape (ratio of height/width 1.6), a long and narrow crescent-shaped area composed of finely meshed stereom in the centro-dorsal part of the proximal edge, lined by bands of more massive stereom distally, a smaller central knob and an indistinct ventral knob on the inner side, and in lacking a vertical furrow on the inner side.

Amphiura iridoides Matsumoto, 1917 (Figure 6C; disk diameter, 4.0 mm, NSMT E-7388), dissociated proximal lateral arm plates with five spine articulations, differing from the present fossil specimens in having a very wide sickle-shape (ratio of height/width 1.6), a wide band of massive stereom proximally bordering the row of spine articulations, and roughly meshed stereom on the inner side, and in lacking a vertical furrow on the inner side.

Amphiura leptobrachia Murakami,1942 (Figure 6D; disk diameter, 4.7 mm, NSMT E-11486), dissociated proximal lateral arm plates with six spine articulations, differing from the present fossil specimens in having a very wide sickle-shape (ratio of height/width 1.5), a conspicuous long, crescent-shaped area composed of finely meshed stereom in the centro-dorsal part of the proximal edge, a broad band of massive stereom proximally bordering the row of spine articulations, and coarse-meshed stereom on the inner side, and in lacking a vertical furrow on the inner side.

Amphiura (*Amphiura*) *luetkeni* Duncan, 1879 (Figure 6E; disk diameter, 3.3 mm, NSMT E-4998), dissociated proximal lateral arm plates with six spine articulations, differing from the present specimens in having a very wide sickle-shape (ratio of height/width 2.0), a relatively wide crescent-shaped area of finely meshed stereom at the centro-proximal edge, and relatively coarsely meshed stereom on the inner side, and in lacking a vertical furrow.

Amphiura arcystata H. L. Clark, 1911 (Figure 6F; disk diameter, 6.3 mm, NSMT E-1343), dissociated proximal lateral arm plates with six spine articulations, resembling the specimens described in the present paper in the tall shape (ratio of height/width 3.3), but differing in having large spine articulations ventrally and dorsally, an indistinct vertical furrow with a few perforations, and an indistinct ventral knob.

Amphiura (*Fellaria*) *vadicola* Matsumoto, 1915 (Figure 6G; disk diameter, 6.5 mm, NSMT E-1512), dissociated proximal lateral arm plates with six spine articulations, differing from the present specimens in having a relatively wider sickle-shape (ratio of height/width 2.5), an indistinct vertical furrow, a small pointed centro-distal knob, and wide and flat centro-proximal and ventral knobs.

Amphiura (*Fellaria*) *sinicola* Matsumoto, 1941 (Figure 6H; disk diameter, 7.3 mm; NSMT E-939), dissociated proximal lateral arm plates with six spine articulations, resembling the fossil specimens described herein in having a tall sickle-shaped outline (ratio of height/width 3.3), a vertical furrow with small perforations on the inner side, but differing in having a centro-distal knob with a curved tip and a flat and elongated centro-proximal knob on the inner side, a ventralmost spine articulation composed of thicker lobes, and slightly more coarsely meshed stereom on the inner and outer surfaces.

Amphiura (*Fellaria*) *ecnomiotata* H. L. Clark, 1911 (Figure 6I; disk diameter, 6.7 mm; NSMT E-4391), dissociated proximal lateral arm plates with eight spine articulations, of a similar, tall sickle-shaped outline (ratio of height/width 3.3), but differing from the fossil specimens described herein in having an indistinct vertical furrow with small perforations, a large trapezoidal centro-proximal knob with rounded corners, a protruding ventral knob, a ridge-like central knob composed of finely meshed stereom, and a protruding small knob at the dorsal edge (dorsal knob) on the inner side, a much larger ventralmost spine articulation, and larger muscle openings in the spine articulations.

Amphiura chiajei Forbes, 1843 (Thuy and Stöhr, 2011, Figure 12, 1–3), dissociated proximal lateral arm plates with five spine articulations, resembling the material described herein in having a vertical furrow with small perforations on the inner side, but differing in having a distinct, deep central perforation, an indistinct central knob and a relatively flat centro-proximal knob on the inner side.

Amphiura filiformis (O. F. Müller, 1776) (Thuy and Stöhr, 2011, Figure 12, 4), dissociated proximal lateral arm plates with six spine articulations, resembling the specimens described herein in having a relatively tall sickle-shaped outline, but differing in having an indistinct vertical furrow, and a small central knob and flat centro-proximal knob on the inner side.

Amphiura sundevalli (Müller and Troschel, 1842) (Thuy and Stöhr, 2011, Figure 12, 7), dissociated proximal lateral arm plates with six spine articulations, resembling the specimens described herein in having a tall sickle-shaped outline and a vertical furrow, but differing in having a tiny central knob and equal-sized spine articulations.

Comparisons with fossil species of Amphiuridae. — Only few extinct species can be unambiguously referred to the Amphiuridae (Jagt, 2000; Thuy *et al*., 2018), the best known being of Late Cretaceous age. Although it seems very unlikely that the specimens described herein belong to a species previously known from the Cretaceous, we wish to provide comparisons for the sake of completeness.

Amphiura shannoni Thuy, Numberger-Thuy and Jagt, 2018 from the Upper Cretaceous, USA (Thuy *et al*., 2018, Fig. 7a–c), dissociated proximal lateral arm plates with ten spine articulations, agreeing with the specimens described herein in having a tall, sickle-shaped outline and a vertical furrow with small perforations, but differing in having spine articulations with a strong ventralward increase in size, and small knobs at inner side.

Amphioplus clementsi Thuy, Numberger-Thuy and Jagt, 2018 from the Upper Cretaceous, USA (Thuy *et al*., 2018, Fig. 7d–f), dissociated proximal lateral arm plates with three spine articulations, differing from the present specimens, in having a wide sickle-shape outline, a much smaller number of spine articulations, and in lacking a vertical furrow.

Amphiura? *plana* Kutscher and Jagt, *in* Jagt, 2000 from the Upper Cretaceous, Germany (Kutscher and Jagt, 2000, Pl. 29, fig. 1–5), dissociated proximal lateral arm plates with six spine articulations, differing from the present specimens in having a wide sickle-shaped outline.

In the light of the comparisons made above, we conclude that the fossil lateral arm plates from the Nagareyama drill core GS-NY-1 described herein can be identified as *Amphiura multispina*. In addition to the lateral arm plates, the other ossicles described in this study, i.e., dorsal arm plates, ventral arm plates, vertebrae, arm spines (Figure 4), are also closely similar to those of extant *Amphiura multispina* (Figure 7), corroborating this assignment. Following its original description by H. L. Clark (1915), *Amphiura multispina* was redescribed in detail by Fujita *et al.* (2011) and illustrated with color photographs. Here, we now add a detailed description of dissociated arm ossicles of *A. multispina*.

The fossil record of the Amphiuridae is notoriously sparse (Jagt, 2000; Thuy *et al*., 2018). The only unambiguous amphiurid taxa to date are *Amphiura shannoni* Thuy, Numberger-Thuy and Jagt, 2018 and *Amphioplus clementsi* Thuy, Numberger-Thuy and Jagt, 2018 from Upper Cretaceous of USA (both based on dissociated lateral arm plates), as well as records of articulated amphiurid fossils from Japan, in particular *Amphioplus uchigoensis* Ishida, 1992 from the Oligocene Asagai Formation, Fukushima (Ishida, 1992), and four unidentified genera and species from four formations: the upper Miocene Hongo Formation of Yamagata, the Plio-Pleistocene Hijikata Formation of Shizuoka, the Pleistocene Nobori Formation of Kochi and the lower Pleistocene Kiwada Formtion of Chiba (Ishida, 2004). Thus, *Amphiura multispina* from the upper Pleistocene Kioroshi Formation in Nagareyama drill core GS-NY-1 significantly adds to the fossil record of the Amphiuridae. It represents the youngest fossil record of the family and the first fossil example of an extant amphiurid species.

The mode of occurrence of *Amphiura multispina* in the Nagareyama drill core GS-NY-1 provides insights into the taphonomy of the assemblage. Ophiuroids disarticulate within days after death in a normal marine environment (Brett *et al*., 1997; Kerr and Twitchett, 2004). The remains retrieved from the Nagareyama drill core GS-NY-1 were completely disarticulated, but extremely well preserved, mostly lacking signs of fragmentation and abrasion, and including all major components of the arm skeleton (Figures 3, 4). This suggests that the dead animals fell apart prior to burial, and that the dissociated ossicles were barely moved by currents, if at all.

Ossicles of *Amphiura multispina* from Nagareyama drill core GS-NY-1 were not found in the muddy sediments of the central basin facies (Unit IV), but in the medium-grained sands of the tidal flood/delta facies (Unit V) (Figure 2, Table 1). Extant individuals of *Amphiura multispina* have been recorded from eight localities around Japan, from the south (Kyushu, 32˚51.0'N) to the north (Miyagi Prefecture, 38˚40.1'N), and mainly at depths of 10–90 m, on a muddy sand to gravel substrate (H. L. Clark, 1915; Fujita *et al*., 2011; unpublished collection data of National Museum Nature and Science, Tsukuba, Japan). Based on the reconstruction of the sedimentary environment and paleodepth of the Kioroshi Formation (Okazaki *et al*., 2018), the paleohabitat of ancient *A. multispina* falls within the bathymetric, geographic and substrate-related range of its modern equivalents.

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School Science Research Club", Yoshimi Kubota (National Museum of Nature and Science) for advice as to the method of keeping the fossil ossicle specimens, and Gunma Museum of Natural History for help in scanning electron microscopy. John W. M. Jagt (Natuurhistorisch Museum, Maastricht, the Netherlands) and Sabine Stöhr (Swedish Museum of Natural History) greatly improved an earlier draft of this manuscript.

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Explanation of Figures and Table

Figure 1. Map showing the position of the locality (marked by a star) of the Nagareyama drill core GS-NY-1 that has yielded dissociated ossicles of *Amphiura multispina* from the Kioroshi Formation.

Figure 2. Columnar section of the levels penetrated in the Nagareyama borehole GS-NY-1, showing the horizons of fossil occurrences (modified from Nakazawa *et al*., 2017).

Figure 3. Fossil dissociated lateral arm plates of *Amphiura multispina* from the Kioroshi Formation in Nagareyama drill core GS-NY-1. **A**, proximal lateral arm plates; A1, 3 (NMNS PA 20233), A2, 4 (NMNS PA 20234). **B**, median lateral arm plates; B1–4 (NMNS PA 20235). **C**, distal lateral arm plates; C1–3 (NMNS PA 20236), C4 (NMNS PA 20237). A1, B1, C1 in external view, A2, B2, C2 in internal view, A3, B3, C3 in proximal view and A4, B4, C4 in distal view. All lateral arm plates are shown with their dorsal side upward. Abbreviations; adr; adradial; Ck, central knob; Cpk, centro-proximal knob; di, distal; Mo, muscle opening; No, nerve opening; Pf, perforation; Sa, spine articulation; Tn, tentacle notch; Vf, vertical furrow; Vk, ventral knob. Scale bars equal 0.1 mm.

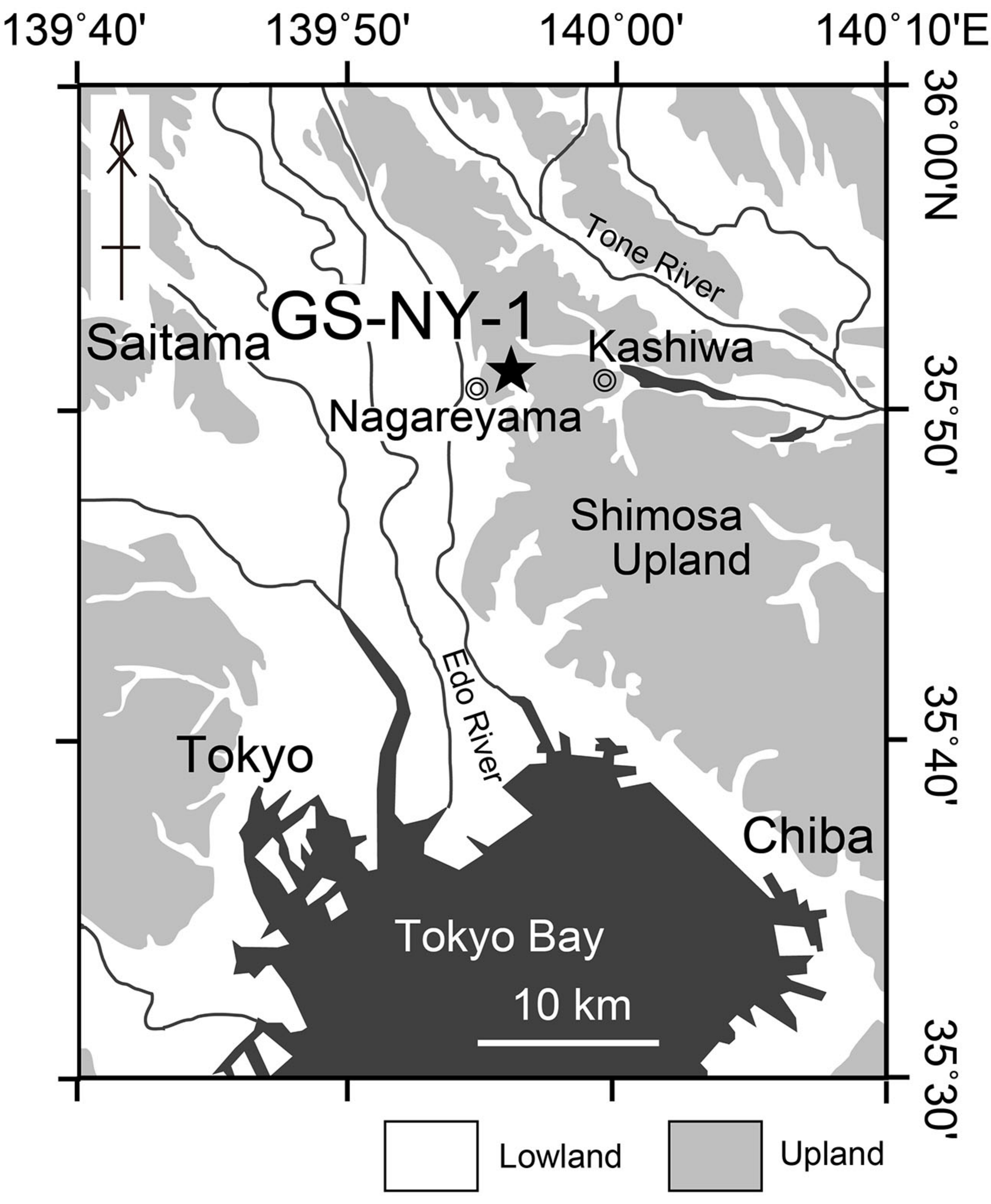
Figure 4. Fossil dissociated arm ossicles of *Amphiura multispina* from the Kioroshi Formation in the Nagareyama drill core GS-NY-1. **A**–**C**, dorsal arm plates: A (NMNS PA 20238), proximal part, B (NMNS PA 20239), median part, C (NMNS PA 20240), distal part; A1, B1, C1 in external view and A2, B2, C2 in internal view. **D**–**F**, ventral arm plates: D (NMNS PA 20241), proximal part, E (NMNS PA 20242), median part, F (NMNS PA 20243), distal part; D1, E1, F1 in external view and D2, E2, F2 in internal view. **G**–**I**, vertebrae: G (NMNS PA 20244), proximal part, H (NMNS PA 20245), median part, I (NMNS PA 20246), distal part; G1, H1, I1 in dorsal view, G2, H2, I2 in ventral view, G3, H3, I3 in proximal view and G4, H4, I4 in distal view. **J,** arm spine (NMNS PA 20247): J1, wide side, J2, narrow side, J3, proximal side, J4, tip side. Abbreviations: Ag, ambulacral groove; Ddmf, dorso-distal muscular fossa; do, dorsal; Ke, keel; Msa, median saddle; Mso, median socket; pr, proximal; Prd; proximal depression; Vdmf, ventro-distal muscular fossa; Zd, Zygocondyle; Zp, zygosphene. Scale bars equal 0.1 mm.

Figure 5. Dissociated lateral arm plates of an extant specimen of *Amphiura multispina* (NSMT E-1490). **A**, proximal lateral arm plates: **B**, median lateral arm plates: **C**, distal lateral arm plates. A1, B1, C1 in external view, A2, B2, C2 in internal view, A3, B3, C3 in proximal view and A4, B4, C4 in distal view. All lateral arm plates are shown with their dorsal side upward. Abbreviations as in Figure 3. Scale bars equal 0.1 mm.

Figure 6. Dissociated lateral arm plates of extant amphiurid taxa. **A**, *Amphioplus* (*Amphioplus*) *macraspis* (NSMT E-4326); **B**, *Amphiura* (*Amphiura*) *micraspis* (NSMT E-4874); **C**, *Amphiura iridoides* (NSMT E-7388); **D**, *Amphiura leptobrachia* (NSMT E-11486); **E**, *Amphiura* (*Amphiura*) *luetkeni* (NSMT E-4998); **F**, *Amphiura arcystata* (NSMT E-1343); **G**, *Amphiura* (*Fellaria*) *vadicola* (NSMT E-1512); **H**, *Amphiura* (*Fellaria*) *sinicola* (NSMT E-939); **I**, *Amphiura* (*Fellaria*) *ecnomiotata* (NSMT E-4391). A1, B1, C1, D1, E1, F1, G1, H1, I1 in external view, A2, B2, C2, D2, E2, F2, G2, H2, I2 in internal view, A3, F3, G3, H3, I3 in proximal view and A4, B3, C3, D3, E3, F4, G4, H4, I4 in distal view. All lateral arm plates are shown with their dorsal side upward. Abbreviations as in Figure 3. Scale bars equal 0.1 mm.

Figure 7. Dissociated arm ossicles of extant specimens of *Amphiura multispina* (A, C, G–I, NSMT E-6545, B, D–F, J, NSMT E-1490). **A**–**C**, dorsal arm plates: A, proximal part, B, median part, C, distal part: A1, B1, C1 in external view and A2, B2, C2 in internal view. **D**–**F**, ventral arm plates: D, proximal part, E, median part, F, distal part; D1, E1, F1 in external view and D2, E2, F2 in internal view. **G**–**I**, vertebrae: G, proximal part, H, median part, I, distal part; G1, H1, I1 in dorsal view, G2, H2, I2 in ventral view, G3, H3, I3 in proximal view and G4, H4, I4 in distal view. **J,** arm spines: J1, wide side, J2, narrow side, J3, proximal side, J4, tip side. Abbreviations as in Figure 4. Scale bars equal 0.1 mm.

Table 1. Number of dissociated arm ossicles of *Amphiura multispina* retrieved from the Nagareyama drill core GS-NY-1.



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Nagareyama
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Edo River
Tokyo
Chiba
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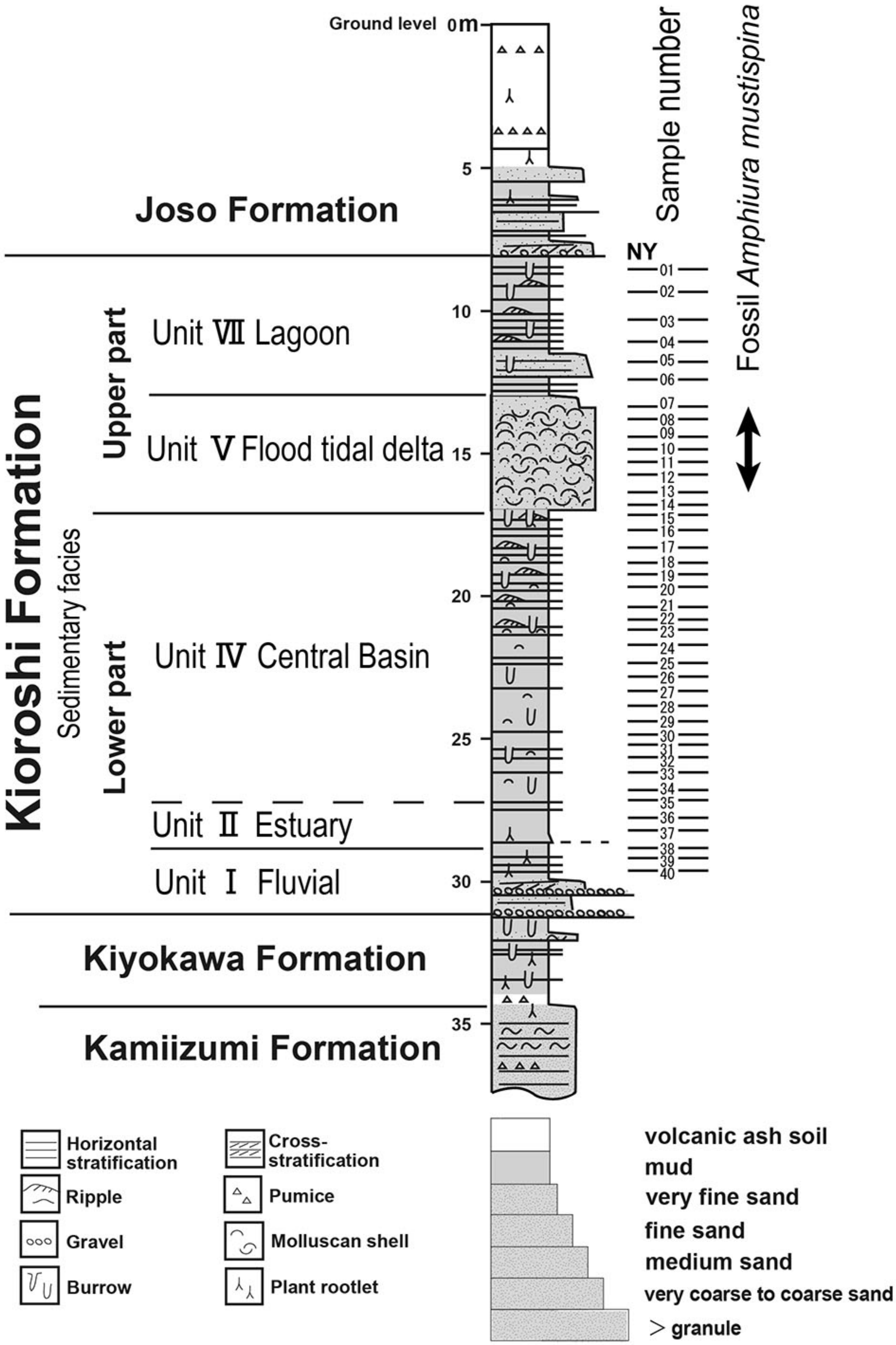
10 km
Lowland
Upland



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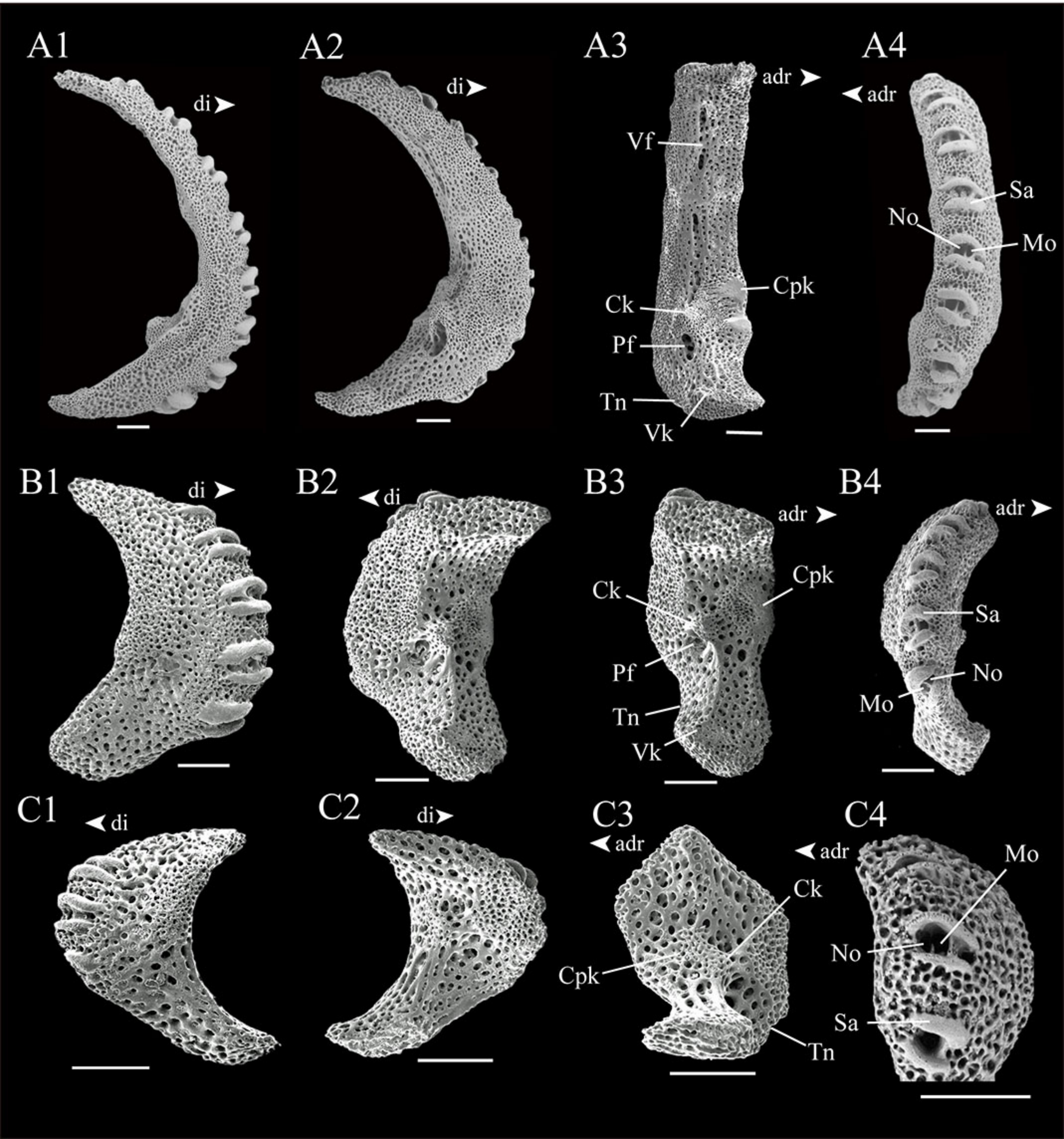
Fossil Amphiura mustispina
Joso Formation
Kioroshi Formation
Sedimentary facies
Upper part
Lower part
Unit Ⅶ Lagoon
Unit Ⅴ Flood tidal delta
Unit Ⅳ Central Basin
Unit Ⅱ Estuary
Unit Ⅰ Fluvial
Kiyokawa Formation
Kamiizumi Formation
Horizontal stratification
Cross-stratification
Ripple
Pumice
Gravel
Molluscan shell
Burrow
Plant rootlet
volcanic ash soil
mud
very fine sand
fine sand
medium sand
very coarse to coarse sand
> granule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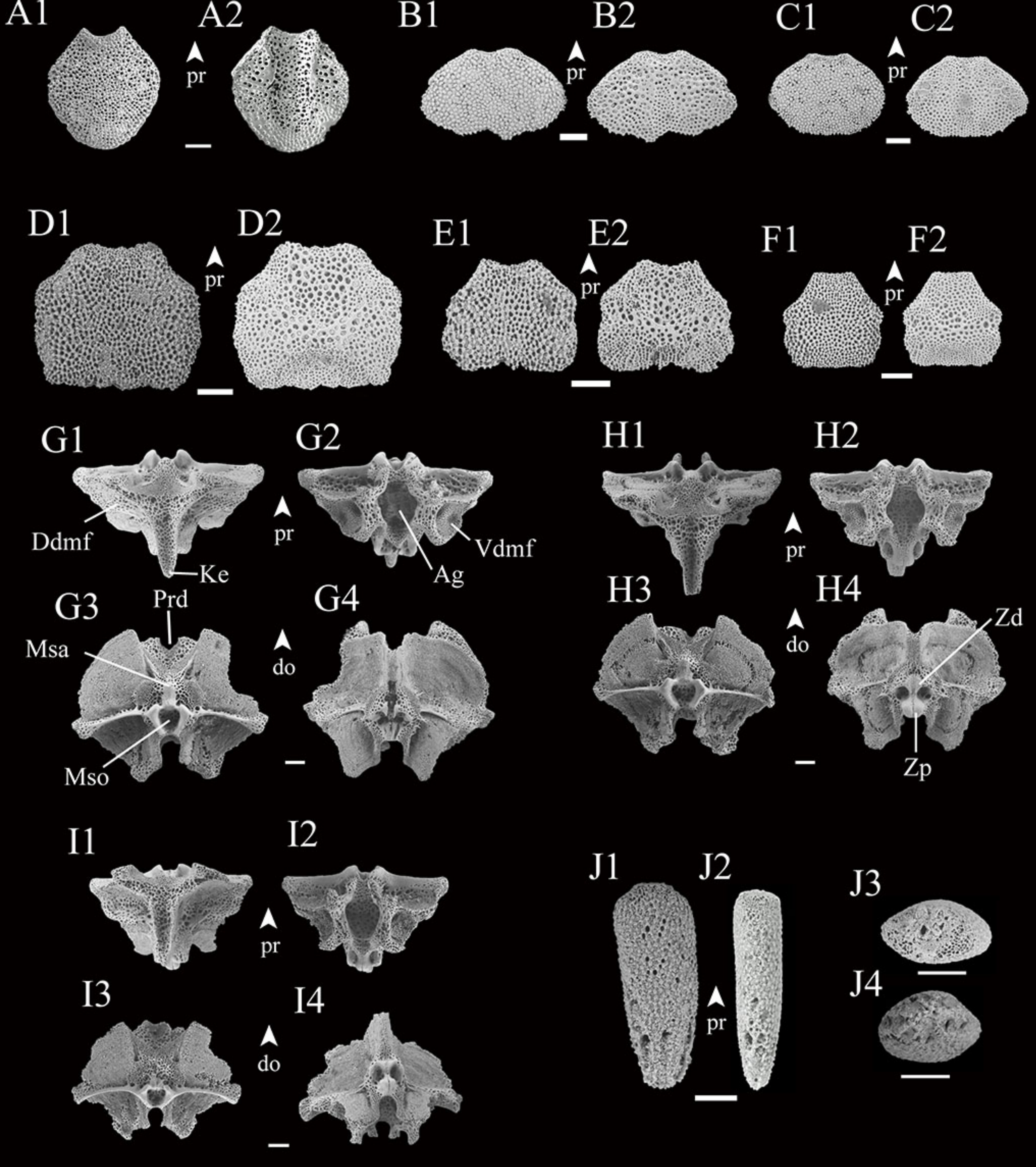
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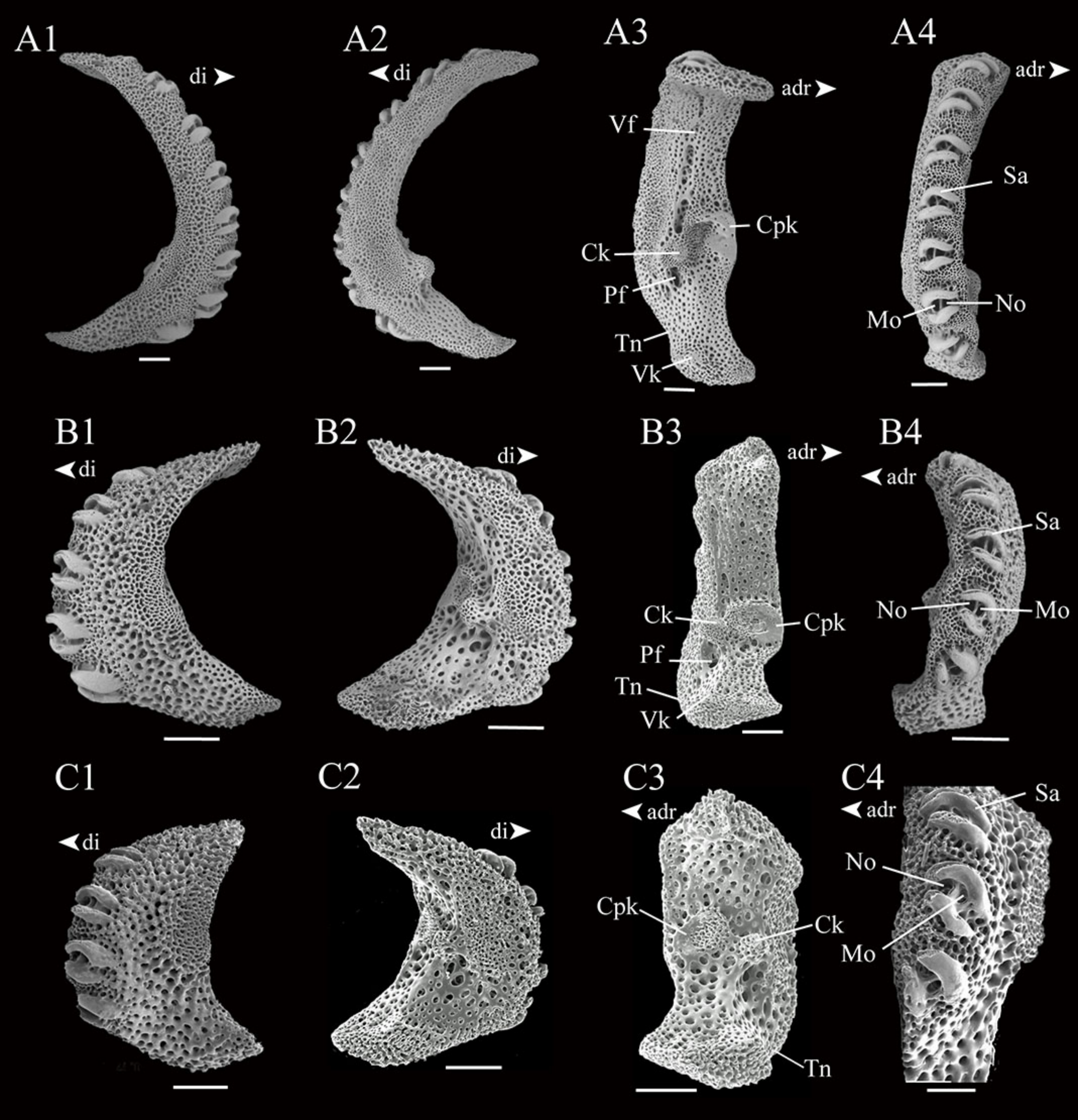

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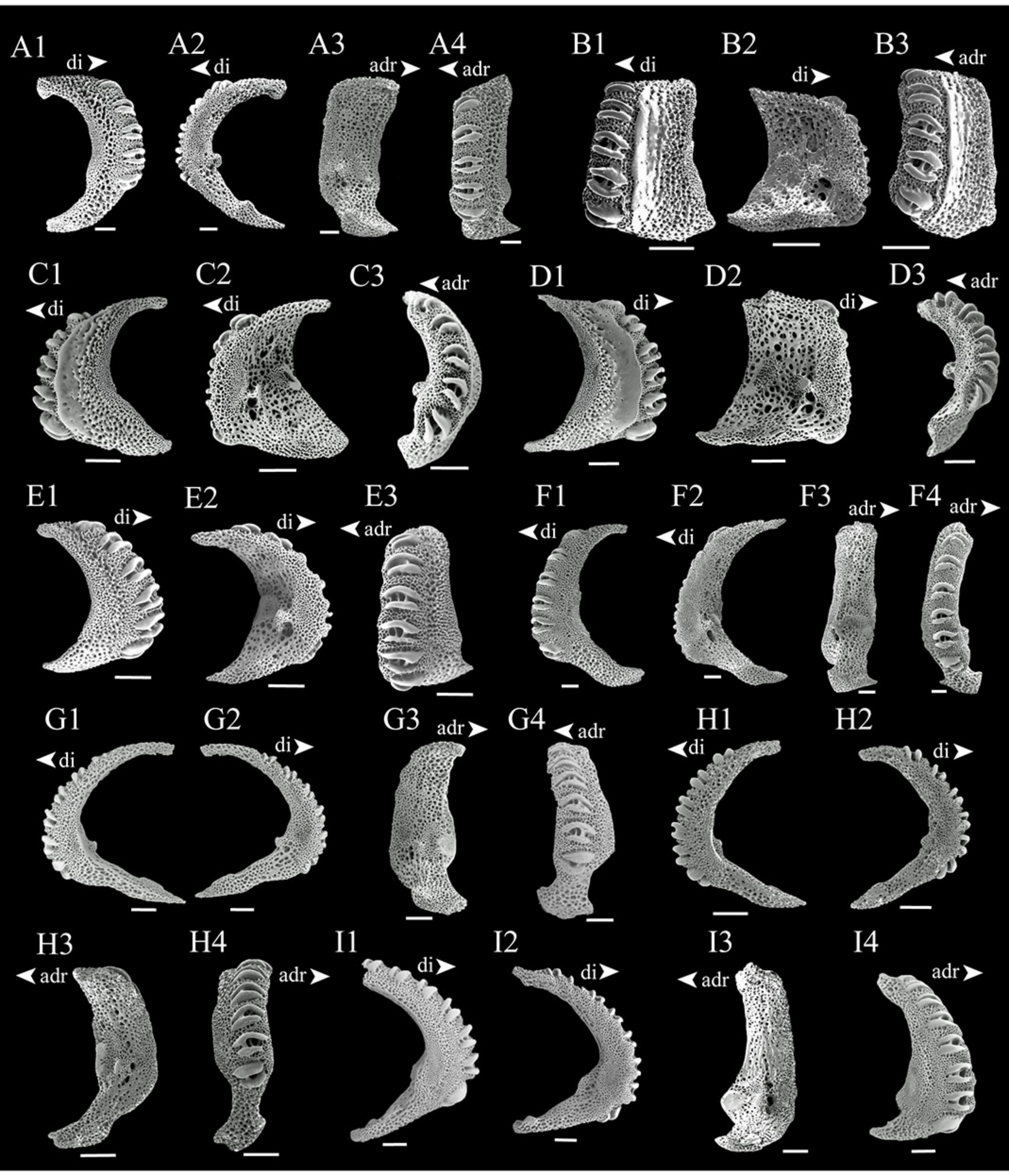

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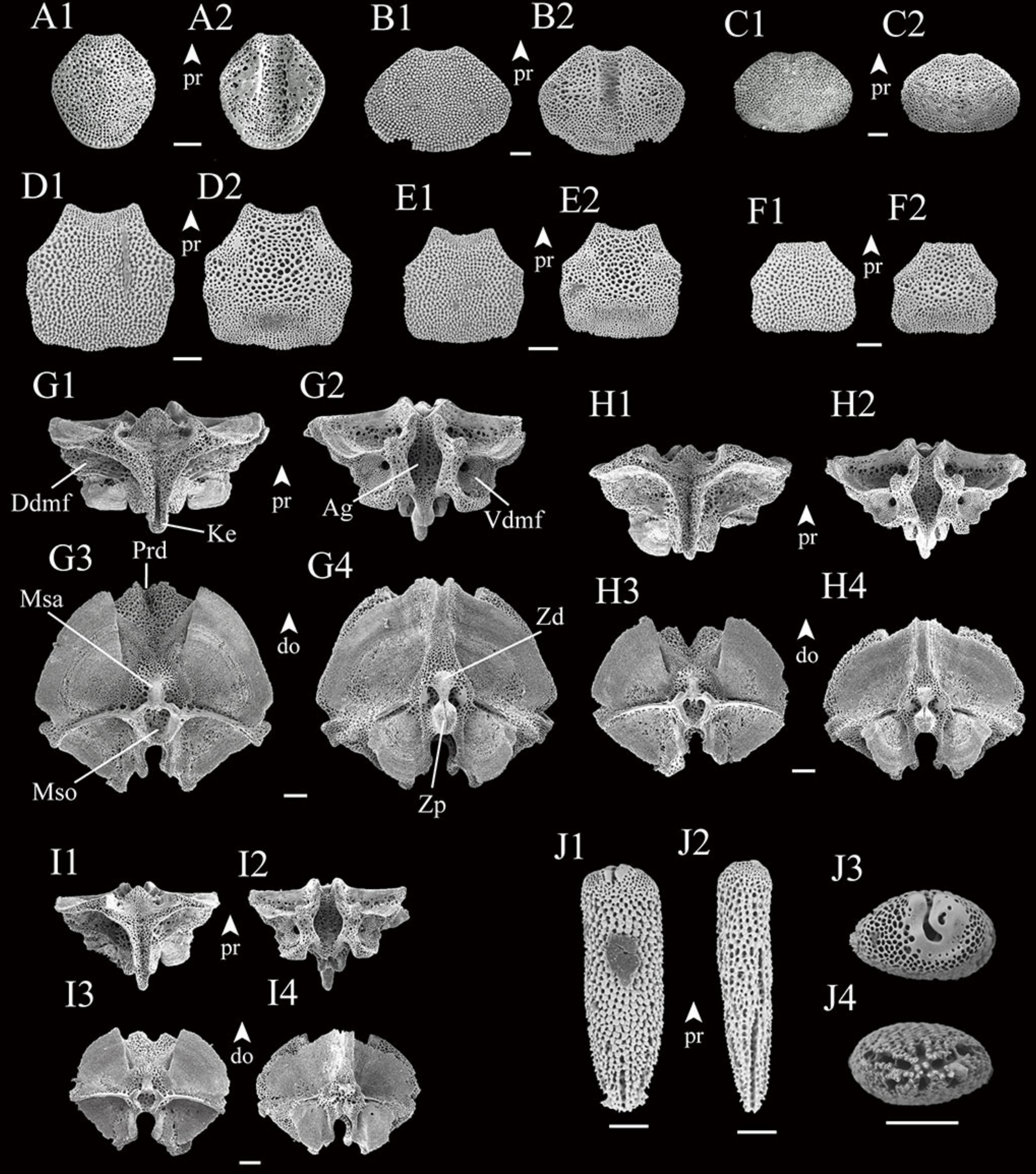

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Table 1. Number of dissociated arm ossicles of *Amphiura multispina* retrieved from the Nagareyama drill core GS-NY-1.

Sample no.	Depth (m)	Lateral arm plates	Dorsal arm plates	Ventral arm plates	Vertebrae	Arm spines	Total
NY-07	13.40–13.45	4	0	0	3	0	7
NY-08	13.80–13.85	1	0	0	1	0	2
NY-09	14.35–14.40	8	2	4	4	2	20
NY-10	14.80–14.85	15	4	5	7	0	31
NY-11	15.35–15.40	14	5	18	7	4	48
NY-12	15.75–15.80	18	4	1	13	3	39
NY-13	16.35–16.40	6	0	0	3	3	12
	Total	66	15	28	38	12	159