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A new species of *Ophiura* (Echinodermata, Ophiuroidea) from Miocene deep-sea deposits in the Pohang Basin, Korea

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Abstract. Dense aggregations of articulated ophiuroids, in external mould preservation, were discovered in the middle Miocene Duho Formation (Yeonil Group) of Pohang City, near the southeast coast of Korea. These specimens are here described as a new species, *Ophiura pohangensis*, which differs from congeners in having long, slender oral papillae, and tiny quadrangular arm comb papillae. The new species constitutes the first well-identified example of the class Ophiuroidea in the fossil record of Korea. Aggregation density of the new species is similar to that of occurrences of both fossil and extant *Ophiura sarsii sarsii* across Japan.

Keywords: Dense aggregations, Duho Formation, Neogene, Ophiuridae, Paleoenvironment, Taxonomy

Introduction

The genus *Ophiura* is among the most speciose in the entire class Ophiuroidea, comprising more than 300 extant and extinct species (e.g. Berry, 1934; Djakonov, 1954; Rasmussen, 1972; Stöhr *et al*., 2018). 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 genus *Ophiura* was included in the family Ophiuridae Müller and Troschel, 1840 (suborder Ophiurina Müller and Troschel, 1840, order Ophiurida Müller and Troschel, 1840). However, these new phylogenetic insights also suggested that *Ophiura* was a polyphyletic complex in need of revision. Since an exhaustive reappraisal of the genus *Ophiura* is beyond the scope of the present study, we here use the genus name in its traditional broad sense, pending a comprehensive revision.

To date, there are only two reports of fossil ophiuroids from Korea. One pertains to a collection of unidentified specimens from the middle Miocene Duho and Hagjeon formations according to Seong *et al*. (2009). The other refers to a set of specimens from the Duho Formation that were assigned to extant species (Lee, 2014), but these identifications are dubious in view of insufficient morphological observations. Recently, dense aggregations of more than 20 specimens of articulated skeletons, in external mould preservation, have been recovered from mudstones of the middle Miocene Duho Formation (Yeonil Group) in Pohang City, near the southeast coast of Korea (Figure 1). On the basis of a detailed morphological analysis, we here erect a new species of *Ophiura* to accommodate these specimens. The new species is compared with its most closely similar extant congener, *Ophiura sarsii sarsii* Lütken, 1855, as well as with 17 other recent species of *Ophiura* that occur around Korea and Japan and a number of fossil forms of Jurassic to Pleistocene age, from Greenland, Europe, the USA and Japan that have previously been placed in the genus *Ophiura*. Finally, the mode of occurrence and aggregation density of the new species are compared with those of occurrences of both extant and fossil *O. sarsii sarsii* across Japan.

Geological setting

A total of 23 specimens preserved as articulated skel-

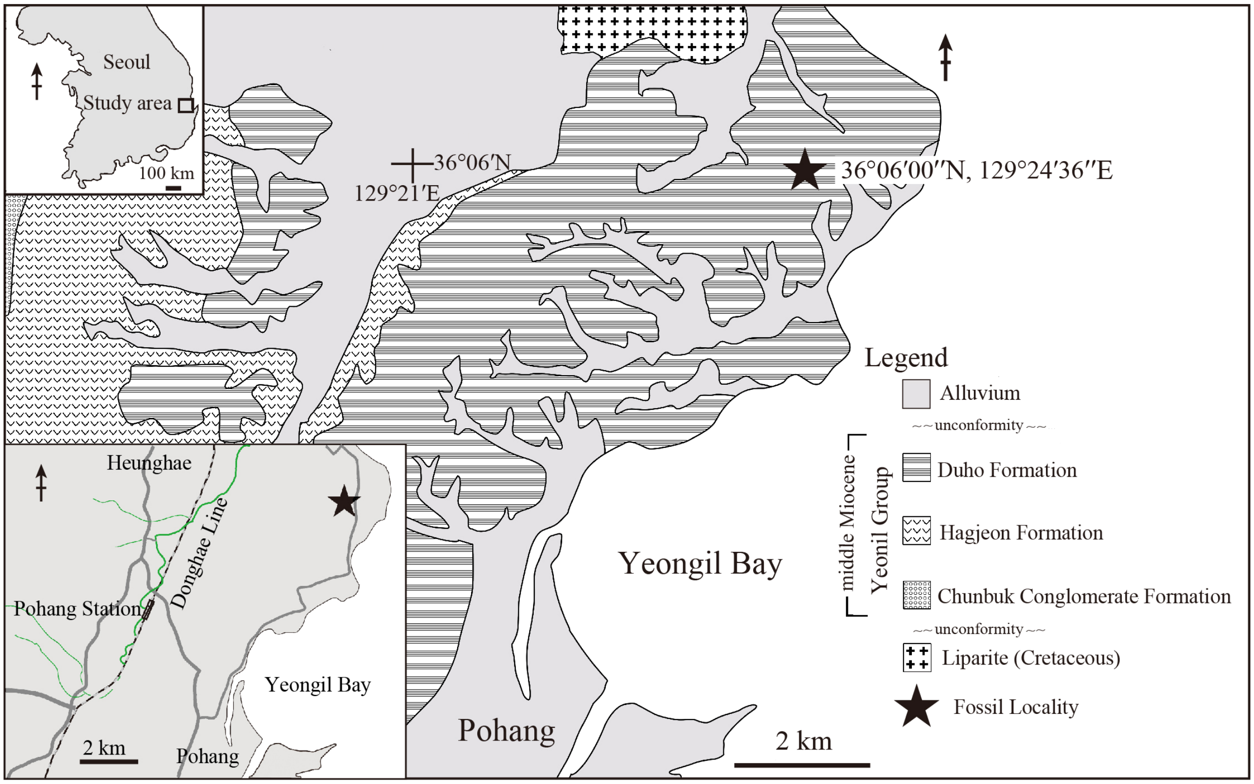

Figure 1. Map showing the position of the locality (marked by star) that has yielded *Ophiura pohangensis* sp. nov. from the middle Miocene Duho Formation (Yeonil Group), placed in a geological and topographic context. The geological map is modified from Yun (1986).

etons, were collected from mudstones of the middle Miocene Duho Formation (Yun, 1986) of the Yeonil Group (Tateiwa, 1924) in the Pohang Basin (Kim, 1970) and exposed at Pohang City, near the southeast coast of Korea, about 8 km northeast of Pohang railway station of the Donghae Line (coordinates 36°06′00″N, 129°24′36″E; see Figure 1). All specimens are preserved as external moulds that lack all original skeletal calcite.

Historically, the stratigraphic subdivision of the Yeonil Group in the Pohang Basin has been controversial (Tateiwa, 1924; Um *et al*., 1964; Kim, 1965; Yoon, 1975; Yun, 1986; Chough *et al*., 1990; Noh, 1994). Here we use the stratigraphic sequence of Yun (1986), because Seong *et al*. (2009) and Lee (2014), who recently reported fossil ophiuroids, supported Yun's stratigraphy. According to Yun (1986), the Yeonil Group can be lithologically subdivided into three formations in ascending order: the Chunbuk Conglomerate Formation (*c*. 500 m thick), the Hagjeon Formation (*c*. 600 m thick) and the Duho Formation (*c*. 300 m thick) (Figure 1).

The Yeonil Group is dated as the middle Miocene on the basis of microfossils (e.g. Kim, 1965, 1984; Lee, 1975; Chough *et al*., 1990; Byun and Yun, 1992; Yi, 1992; Noh, 1994), plants (e.g. Huzioka, 1972; Chun, 2004; Kim, 2005, 2008, 2009, 2010; Kim *et al*., 2017), and mollusks (e.g. Kanehara, 1936a, b; Lee and Yoon, 2004); for the Hagjeon Formation and its equivalents, age assignment relies on foraminifera (*Turborotalia bykovae* and *Globigerina trilocularis*; see Kim, 1965, 1984), on diatoms (*Actinocyclus ingens* and *Denticula hustedtii*; see Lee, 1975), on plants (*Pinus miocenica*, *Keteleeria ezoana* and *Pterocarya asymmetrosa*; see Huzioka, 1972) and on molluscs (*Solemya tokunagai*, *Conchocele bisectoides* and *Acila divaricate*; see Kanehara, 1936a, b); for the Duho Formation, age constraints come from nannoplankton (*Discoaster exilis*; see Yi, 1992) and dinoflagellate cysts (*Dapsilidinium pseudocolligerum* and *Cribroperidinium giuseppei*; see Byun and Yun, 1992).

The depositional environment of the Duho Formation is interpreted to have been a deep-sea setting as based on several lines of evidence: sedimentary facies analysis and benthic foraminifera typical of lower bathyal depths such as *Uvigerina proboscidae* (see Chough *et al*., 1990) indicating a hemi-pelagic environment, as well as fragmentary diatom and siliceous ooze indicative of a pelagic setting (Noh, 1994) and molluscan fossils found near the present ophiuroid-bearing locality, in particular the bivalves *Yoldia sagittaria*, *Acharax tokunagai*, *Nucu-*

lana pennula, *Portlandia* cf. *gratiosa*, *Lucinoma acutilineatum*, *Conchocele bisecta*, *Propeamussium tateiwai*, *Lucina acutilineata*, *Calyptogena* cf. *elongata*, *Panomya simotomensis*, *Mizuhopecten kimurai ugoensis* and others (Kanehara, 1936a, b; Yoon, 1975, 1976; Kim and Yoon, 1978; Lee, 1992; Lee and Yoon, 2004; K. Amano, unpublished data), that are indicative of an offshore setting. Finally, there are trace fossils, such as *Chondrites* (see Kim and Paik, 2013), that indicate deep water.

In order to enable a detailed morphological observation of the ophiuroid specimens, synthetic resin casts were made. Scanning electron microscope (SEM) images were taken for some arm segments, and line drawings were produced with the help of a camera lucida device. The mode of occurrence of the brittle stars was traced on a transparent paper placed on the rock fragments with the specimens. Individuals of extant *Ophiura sarsii sarsii* housed in collections of the National Museum of Nature and Science, Tsukuba (NSMT E-5990 (3/4), 1870) were used for morphological comparisons with fossil material which is kept in the collections of the Kongju National University, Korea (registration numbers KNU 34001–34020), and of the National Museum of Nature and Science, Tsukuba, Japan (access numbers NMNS PA 18688–18690).

Systematic paleontology

Order Ophiurida Müller and Troschel, 1840
Suborder Ophiurina Müller and Troschel, 1840
Family Ophiuridae Müller and Troschel, 1840
Subfamily Ophiurinae Lyman, 1865
Genus ***Ophiura*** Lamarck, 1801
Ophiura pohangensis sp. nov.

Figures 2, 3

Diagnosis.—Oral papillae, inclusive of a single tooth papilla or ventralmost tooth, long and spiniform, separated from each other by small gaps (Figures 2A, B, 3A, B). Arm comb papillae tiny, squarish and in contact with each other (Figures 2C–E, 3C, D). Dorsal and ventral sides of disc covered by comparatively large scales (Figures 2A, C–E, 3A, C–E).

Material.—Set of 23 fully articulated specimens, preserved as external moulds lacking all original skeletal calcite.

Holotype, KNU 34014 (ventral side; Figures 2A, 3A, 5B6, 6B6).

Paratypes, KNU 34005 (ventral side; Figures 2B, 3B, 5A5, 6A5), KNU 34008 (dorsal side; Figures 2C, 3C, 5A8, 6A8), KNU 34018 (dorsal side; Figures 2D, 3D, 5C4, 6C4), and KNU 34020 (dorsal side; Figures 2E, 3E, 5C6, 6C6).

Additional material, 18 specimens: KNU 34001 (Figures 5A1, 6A1), KNU 34002 (Figures 5A2, 6A2), KNU 34003 (Figures 5A3, 6A3), KNU 34004 (Figures 5A4, 6A4), KNU 34006 (Figures 5A6, 6A6), KNU 34007 (Figures 5A7, 6A7), KNU 34009 (Figures 5B1, 6B1), KNU 34010 (Figures 5B2, 6B2), KNU 34011 (Figures 5B3, 6B3), KNU 34012 (Figures 5B4, 6B4), KNU 34013 (Figures 5B5, 6B5), KNU 34015 (Figures 5C1, 6C1), KNU 34016 (Figures 5C2, 6C2), KNU 34017 (Figures 5C3, 6C3), KNU 34019 (Figures 5C5, 6C5), NMNS PA 18688 (Figures 5D1, 6D1), NMNS PA 18689 (Figures 5D2, 6D2), and NMNS PA 18690 (Figures 5D3, 6D3).

Twenty specimens, including the holotype and paratypes, are housed in collections at the Kongju National University, Korea (KNU), while the remaining three specimens are kept at the National Museum of Nature and Science, Tsukuba, Japan (NMNS PA).

Etymology.—Named after Pohang City, which is close to the fossil locality.

Locality and horizon.—Pohang City, near the southeast coast of Korea, from mudstone of the Duho Formation (Yeonil Group), middle Miocene (Yun, 1986).

Measurements.—Disc diameters of holotype (Figures 5B6, 6B6) and paratypes (Figures 5A5, 6B5; 5A8, 6A8; 5C4, 6C4; 5C6, 6C6) are 7.5 mm (holotype) and 8.9 mm, 9.8 mm, 9.4 mm and 8.6 mm (paratypes), respectively. Disc diameters of all specimens examined range between 3.2 and 12.0 mm (mean: 9.3 mm, $N=22$). The ratio of proximal arm width to disc diameter ranges from 0.11 to 0.17 (mean: 0.14, $N=19$). Arm length is 3.0–4.4 times disc diameter (mean: 3.5, $N=9$).

Description of holotype.—Ventral side is exposed (Figures 2A, 3A). The disc is thin, circular in outline, covered by thin, relatively large, oval to elongate scales that either abut or overlap. The arms are flat, slender, about four times longer than disc diameter, gradually tapering towards the tip. The oral papillae are placed on the oral plates horizontally in a row, long, slender and spiniform, separated from each other by small gaps. A single tooth is placed at the tip of the oral plates, slender and as long as the oral papillae. The oral plates are robust, rectangular, wider distally, in contact with each other proximally. The adoral shields are elongated, quadrangular, bordering the proximal edges of the oral shield and first lateral arm plates, and in contact with each other proximally. The oral shields are small, about one-quarter of the disc radius, pentagonal, slightly longer than wide or as long as wide, convex at distal edge. The genital slits are narrow, extending from the oral shield to the disc edge, bearing tiny, contiguous scales. The second oral tentacle pores are open largely near the mouth slits with up to three small contiguous peg-like scales on either side. The tentacle pores in three arm segments on the ventral disc are relatively large with two or more small tentacle scales, the

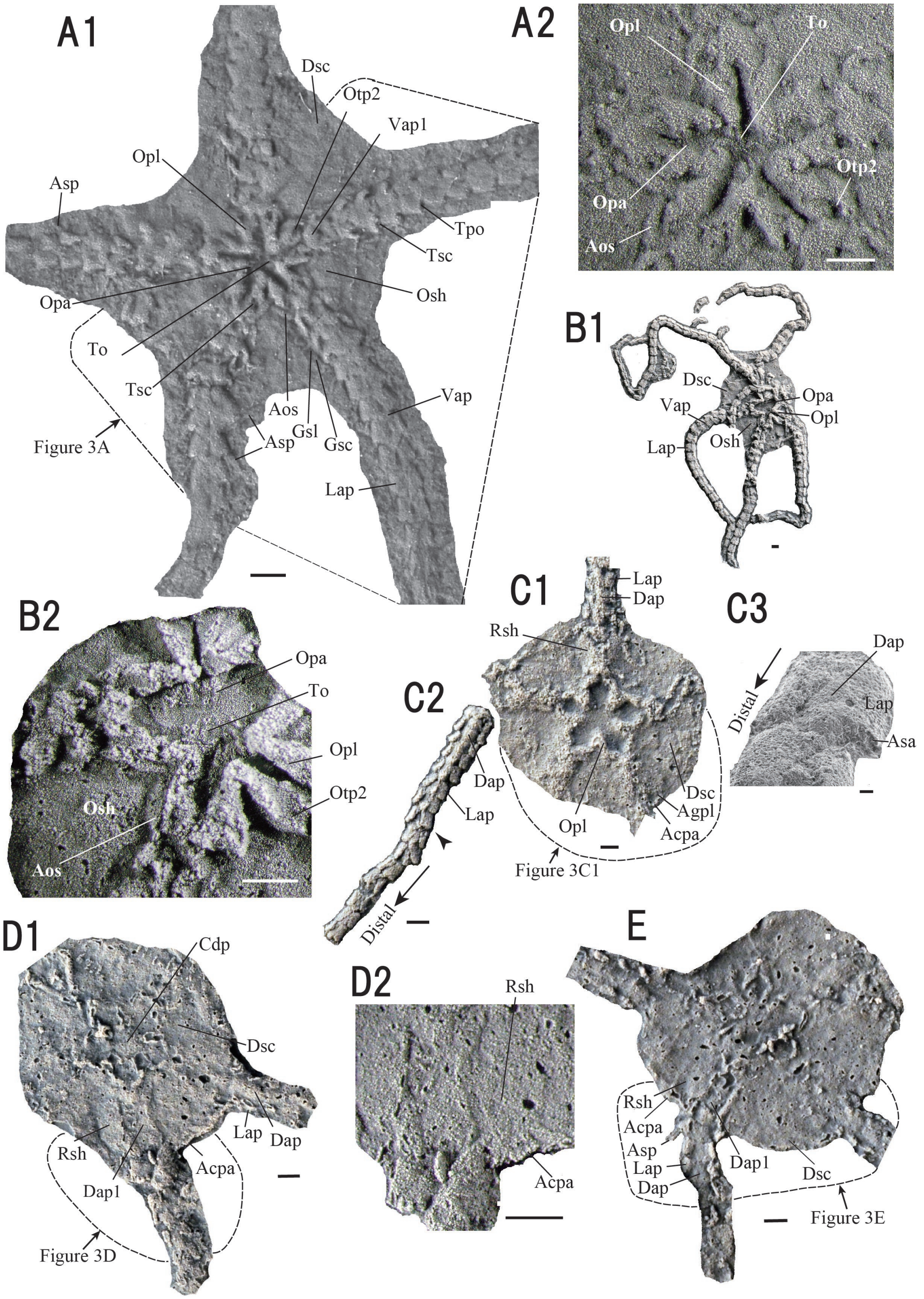

Figure 2. Photographs (A, B, C1, C2, D1, D2, E) and SEM image (C3) of synthetic resin casts of *Ophiura pohangensis* sp. nov. Synthetic resin casts of *Ophiura pohangensis* sp. nov. **A**, KNU 34014, holotype; A1, ventral side of the disc and proximal arms; A2, enlarged view of the mouth frame; **B**, KNU 34005, paratype; B1, ventral side of a complete specimen; B2, enlarged view of the mouth frame; **C**, KNU 34008, paratype; C1, dorsal side of disc and proximal arm segments; C2, a more complete arm; C3, an arm segment (indicated by an arrow tip in C2); **D**, KNU 34018, paratype; D1, dorsal side of disc and proximal arms; D2, enlarged view of disc edge; **E**, KNU 34020, paratype, dorsal side of disc and proximal arms. Abbreviations: Acpa, arm comb papilla; Agpl, abradial genital plate (arm comb plate); Aos, adoral shield; Asa, arm spine articulation; Asp, arm spine; Cdp, central disc plate; Dap, dorsal arm plate; Dap1, first dorsal arm plate; Dsc, disc scale; Gsc, genital scale; Gsl, genital slit; Lap, lateral arm plate; Opa, Oral papilla; Opl, oral plate; Osh, oral shield; Otp2, second oral tentacle pore; Rsh, radial shield; To, tooth; Tpo, tentacle pore; Tsc, tentacle scale; Vap, ventral arm plate; Vap1, first ventral arm plate. Scale bars equal 1 mm (A, B, C1, C2, D, E) and 0.1 mm (C3).

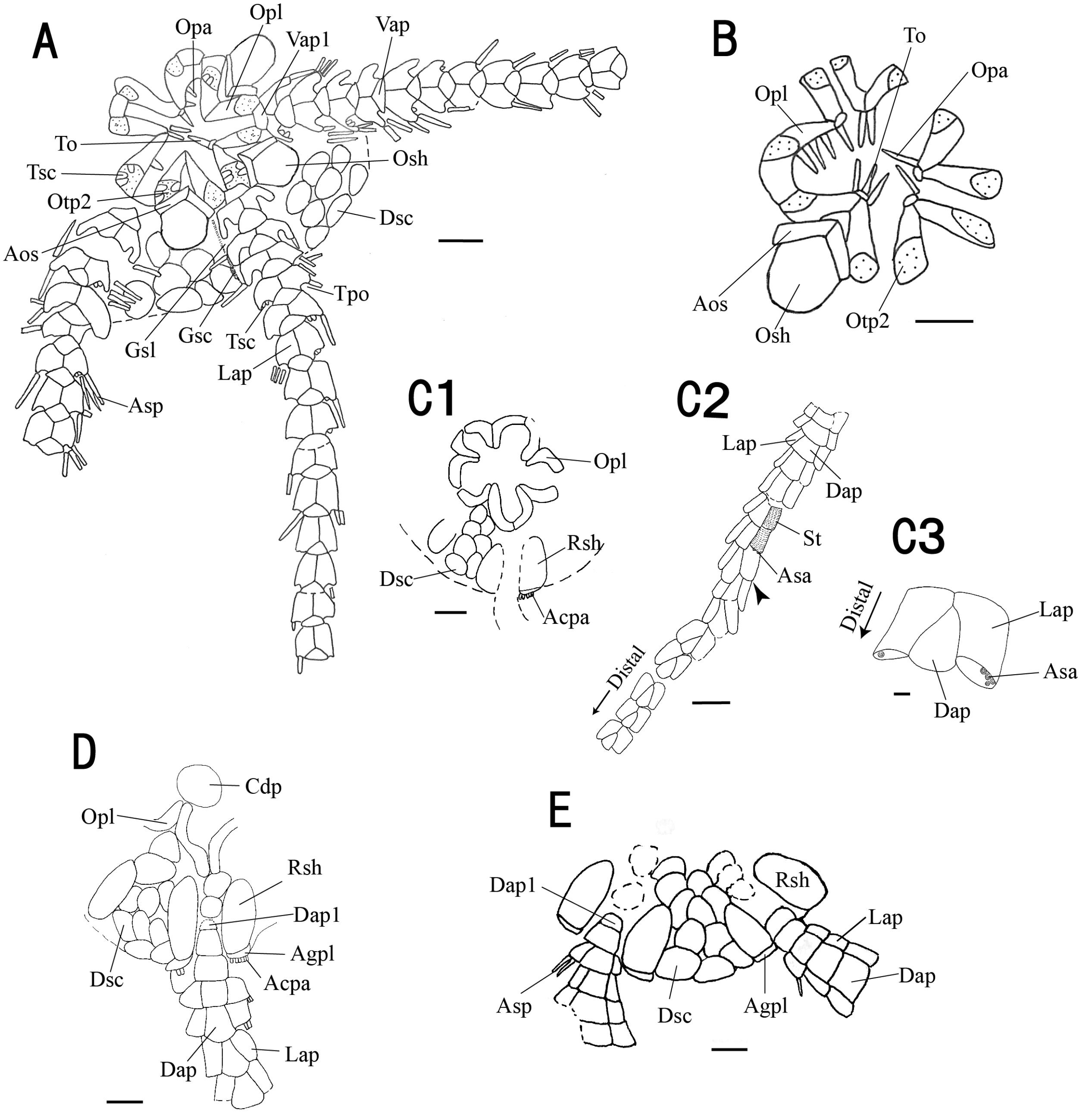

Figure 3. Line drawings of synthetic resin casts of *Ophiura pohangensis* sp. nov. Figures **A**–**E,** correspond to a part of A–E in Figure 2, respectively. Abbreviations: St, striation; see Figure 2 for the others. Scale bars equal 1 mm (A, B, C1, C2, D, E) and 0.1 mm (C3).

following pores gradually becoming smaller. The first ventral arm plates are small, trapezoidal, wider than long, the following ventral arm plates being triangular or rhombic, about twice as wide as long, separated from the most proximal arm segments onwards; up to three arm segments are within the disk on the ventral side. The lateral arm plates on the ventral side are short, squarish in the most proximal arm segments; the middle to distal plates are elongate. They meet on the mid-line of all arm segments. There are three arm spines in proximal arm segments. They are slender, pointed at the tip, approximately of the same length as or a little longer than the proximal to middle arm segments, appressed or at a low angle to lateral arm plates.

Paratypes.—KNU 34005 (Figures 2B, 3B) is an articulated specimen exposing the ventral side. The oral papil-

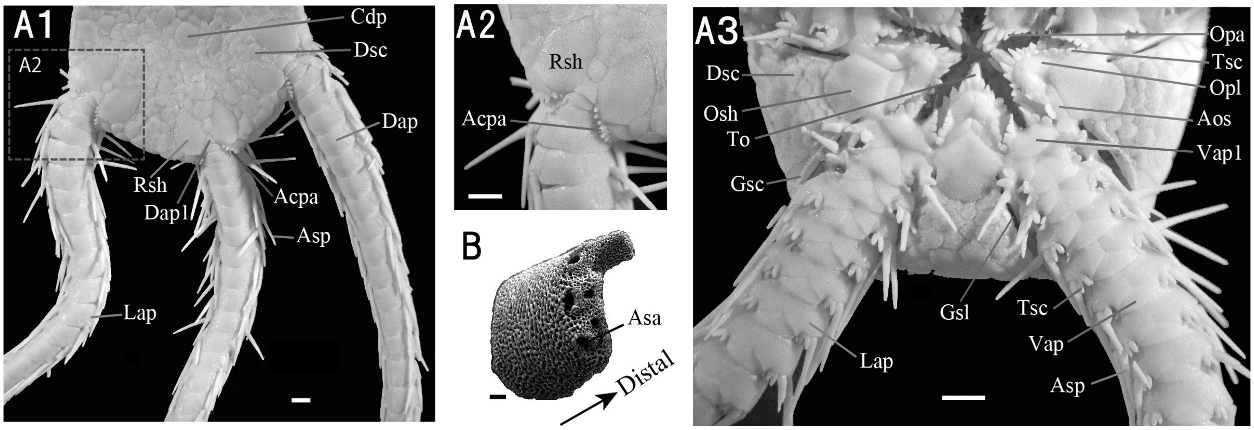

Figure 4. Photographs (A) and SEM image (B) of recent *Ophiura sarsii sarsii*. **A**, NSMT E-5990 (3/4); A1, dorsal side of disc and arms; A2, enlarged view of disc and proximal arm; A3, ventral side of disc and proximal arms; **B**, NSMT E-1870, outer surface of lateral arm plate. Scale bars equal 1 mm (A) and 0.1 mm (B). See Figure 2 for abbreviations.

lae and a single tooth are better preserved than in the holotype specimen. There are up to five oral papillae. The oral papillae and a single tooth are more than three times longer than broad. The oral shields differ from those of the holotype in being slightly more pentagonal with slightly pointed corners laterally and in being slightly longer than in the holotype specimen, accounting for about one-third of the disc radius.

KNU 34008 (Figures 2C, 3C) is an articulated specimen exposing the dorsal side and preserving one long arm. The disc is circular in outline, covered with scales similar to those of the holotype specimen. The arms are low arch-shaped. The radial shields are slightly shorter than half the disc radius. The abradial genital plates (arm comb plates) have up to five contiguous, squarish, tiny arm comb papillae on their distal edge (Figures 2C1, 3C1). The proximal dorsal arm plates are trapezoidal, contiguous, about twice as wide as long, with a convex distal edge. The dorsal arm plates from the middle of the arm to the tip are trapezoidal, gradually becoming longer and narrower; triangular with rounded distal edge, separated from each other in distal arm segments (Figures 2C2, 3C2). The lateral arm plates on the dorsal side have fine vertical striations on the surface (Figure 3C2), are short, squarish in the most proximal arm segments; the middle to distal plates are elongate, quadrangular. They are separated from each other in proximal to middle arm segments, but in contact with each other proximally in distal arm segments (Figures 2C2, 3C2). The arm spine articulations are present on the distal edge of the lateral arm plates. They have a row of three larger rounded muscle openings surrounded by a low wall, and up to two paired smaller nerve openings under them (Figures 2C3, 3C3).

KNU 34018 (Figures 2D, 3D) is an articulated specimen exposing dorsal side. The radial shields are elongated-oval, more than half the disc radius, approximately twice as long as wide, separated by two or three rounded scales proximally and two dorsal arm plates distally. Central disc plates are large and circular.

KNU 34020 (Figures 2E, 3E) is an articulated specimen exposing the dorsal side. The radial shields are almost as long as half the disc radius. The abradial genital plates (arm comb plates) are elongated, quadrangular. The first dorsal arm plates are small, triangular with rounded corners proximally, wider than long.

Discussion

The new species is assigned to the genus *Ophiura* on account of having a thin disc covered by imbricating to abutting scales with large central disc plates, separated radial shields, slender, gradually tapering arms, contiguous trapezoidal dorsal arm plates, contiguous tiny arm comb papillae, large second oral tentacle pores near the mouth slit with scales, contiguous tiny genital scales, appressed tapering arm spines, non-contiguous wide ventral arm plates, and an additional pair of circular arm spine articulations on the distal end of the lateral arm plates, similar to the extant genus *Ophiura* (Figures 2–4).

Comparisons to extant taxa.—Our comparison of the new species to modern species of *Ophiura* from around Korea and Japan has revealed that it is most closely similar to *O. sarsii sarsii* (Figure 4). Differences pertain to the long and slender oral papillae and the tiny, contiguous rectangular arm comb papillae.

The new species also differs from the following extant congeners that occur in the region, namely *O. aequalis*

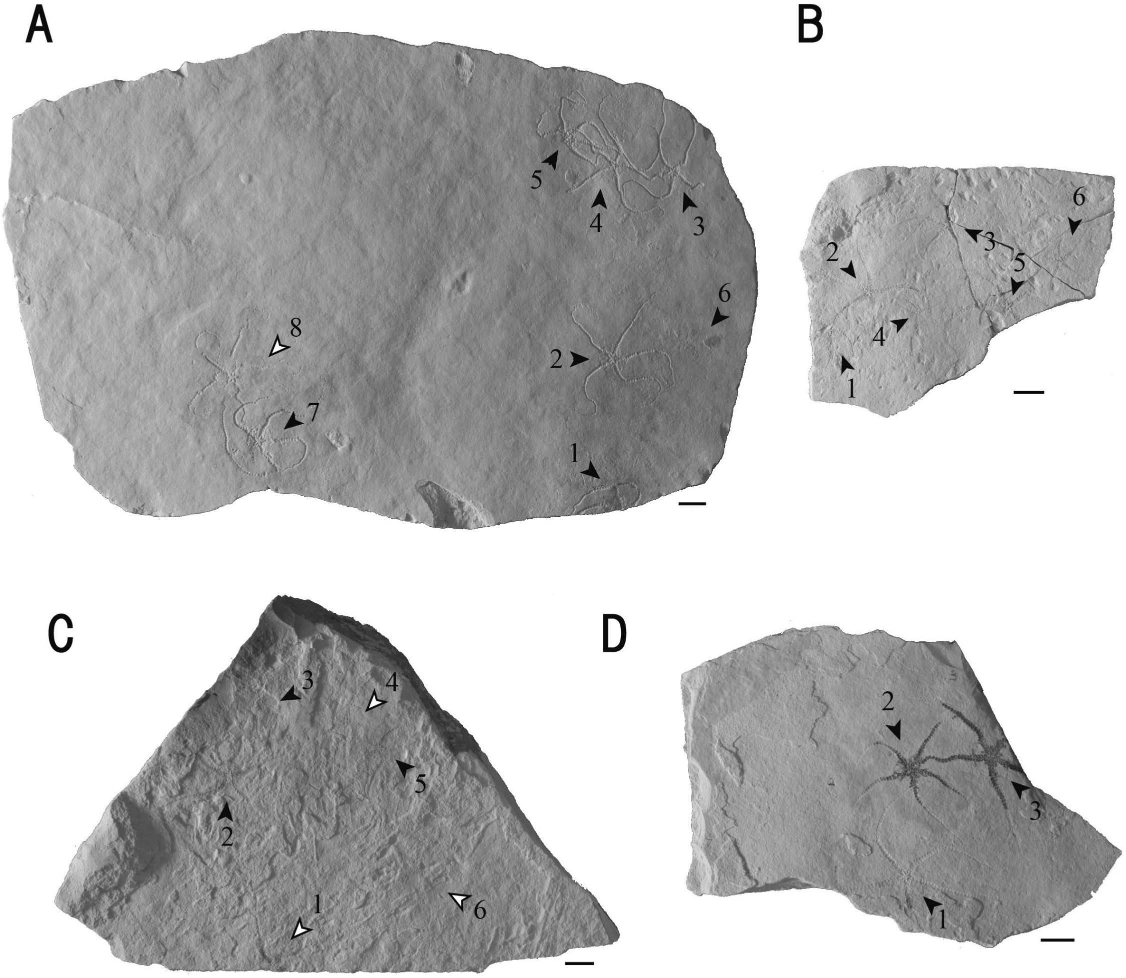

Figure 5. Bedding plane of matrix slabs with *Ophiura pohangensis* sp. nov. **A,** 1–8, KNU 34001–34008; **B,** 1–6, KNU 34009–34014; **C,** 1–6, KNU 34015–34020; **D,** 1–3, NMNS PA 18688–18690. Specimens arrowed in black and white illustrate ventral and dorsal sides, respectively. Scale bars equal 1 cm.

Lyman, 1878, *O. bathybia* H. L. Clark, 1911, *O. calyptolepis* H. L. Clark, 1911, *O. cryptolepis* H. L. Clark, 1911, *O. flagellata* (Lyman, 1878), *O. imbecillis* (Lyman, 1878), *O. kinbergi* (Ljungman, 1866), *O. leptoctenia* H. L. Clark, 1911, *O. micracantha* H. L. Clark, 1911, *O. ooplax* (H. L. Clark, 1911), *O. paucisquama* Matsumoto, 1917, *O. quadrispina* H. L. Clark, 1911, *O. sarsii vadicola* Djakonov, 1954, in having long, spiniform oral papillae, tiny, contiguous quadrangular arm comb papillae and relatively large disc scales.

Although *Ophiura albata* (Lyman, 1878), *O. atacta* H. L. Clark, 1911, *O. irrorata irrorata* (Lyman, 1878) and *O. monostoecha* H. L. Clark, 1911 have quadrangular arm comb papillae, they differ from the new species in having short arm spines, short oral papillae and larger quadrangular arm comb papillae.

Comparisons to fossil taxa.—Up to now, there were only two records of fossil ophiuroids from Korea. Lee (2014) recorded more than 1,500 articulated specimens of brittle stars from the middle Miocene Duho Formation in the Pohang Basin (Korea) and assigned them to two species, *Ophiura sarsii* Lütken, 1855 and *O. leptoctenia* H. L. Clark, 1911. These identifications, however, are dubious because they were not based on detailed observations of the morphology of these specimens. Seong *et al.* (2009) noted additional occurrences of articulated ophiuroid specimens from the middle Miocene Hagjeon and Duho formations, but did not provide any identification. Specimens from the Hagjeon Formation possibly belong to the family Ophiacanthidae on account of the long arm spines and noded arm segments (see Seong *et al.*, 2009, p. 370, fig. 2). Both previously published records from the Duho Formation by Lee (2014, p. 31, fig. 6) and Seong *et al.* (2009, p. 371, fig. 3) could be conspecific with the

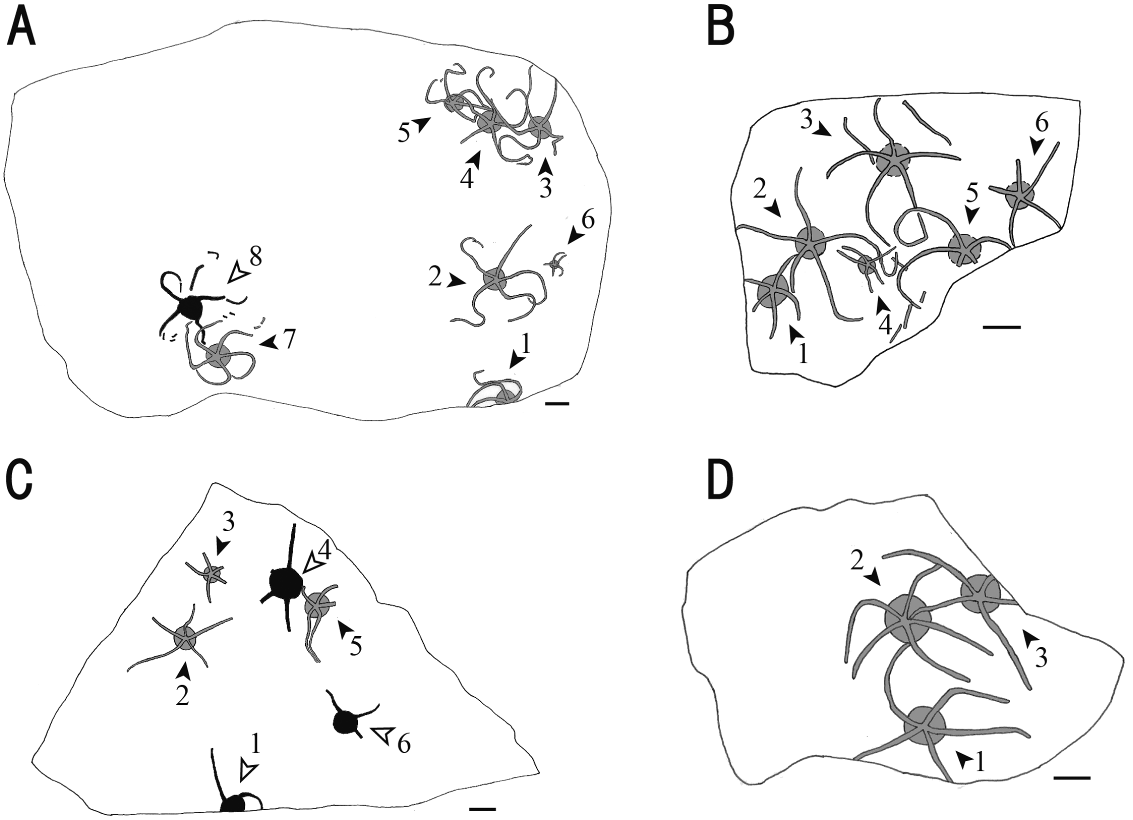

Figure 6. Line drawings of the bedding plane of matrix sample with *Ophiura pohangensis* sp. nov. Specimen numbers are the same as in Figure 5. Scale bars equal 1 cm. Specimens arrowed in black and white illustrate ventral and dorsal sides, respectively.

specimens described herein because of similarities in overall shape of discs and arms.

The following fossil taxa once assigned to *Ophiura*, have since been transferred to other genera: *Ophiura serrata* Roemer, 1840, *Ophioglypha gracilis* Valette, 1915 and *Ophiura parvisentis* Spencer, 1907 are now accepted as *Ophiotitanos serrata* (Roemer, 1840) (see Stöhr *et al*., 2018). In addition, *Ophiura*? *hagenowi* Rasmussen, 1950, which was listed as *Stegophiura*? *hagenowi* by Jagt (2000), has recently been assigned to *Ophiopeza* Peters, 1851 by Ishida *et al*. (2018).

The following 24 Jurassic-Pleistocene species are still assigned to *Ophiura*. For that reason, we compare them here to the present species from the Duho Formation and at the same time briefly assess the validity of the assignment to *Ophiura.*

Ophiura? *astonensis* Hess, 1964 from the Pliensbachian (Lower Jurassic) of Worcestershire (England) is based on disarticulated lateral arm plates (Hess, 1964). It differs from the new species in having a row of six arm spine articulations on the distal end of lateral arm plates, and tiny arm spines. A preliminary examination of the original material by one of us (BT) has revealed that the holotype (The Natural History Museum, London, NHMUK E 52996; see Hess, 1964, p. 768, fig. 17) belongs to a different species than the other specimens (see Hess, 1964, p. 766, figs. 15, 16). The holotype has basal ophiodermatid affinities whereas the remaining specimens show arm spine articulations that are typically found in the superfamily Ophiolepidoidea.

Ophiura tinurtiensis Valette, 1929 from the Aalenian–Bajocian (Middle Jurassic) of Tournus (Saône-et-Loire, France), comprising the dorsal and ventral sides of articulated individuals (Valette, 1929), differs from the new species in having elongated quadrangular ventral and dorsal arm plates. The generic placement of *O. tinurtiensis* cannot be comprehensively assessed without a detailed examination of the specimens, but assignment to *Ophiura* may be ruled out due to the lack of typical diagnostic features of that genus, in particular the genital papillae that cover the dorsal side of the arm base and distally pointing tentacle notches.

Ophiura utahensis (Clark and Twitchell, 1915) from the Jurassic of San Rafael River near Castledale (Utah, USA), consisting of the articulated dorsal side of disc and arms (Clark and Twitchell, 1915), differs from the new species in having long arm spines, fine disc scales and small radial shields. This species shows greatest affinities with members of the superfamily Ophionereidoidea, thus probably precluding assignment to *Ophiura*.

Ophiura texana (W. B. Clark, 1893) from the upper Albian (Lower Cretaceous) Denison Formation of Texas (USA) is based on the ventral side of disc, ventral and dorsal sides of articulated arm segments (Berry, 1941). It differs from the new species in having hexagonal ventral arm plates and wider dorsal arm plates. Assignment to *Ophiura* is dubious; greatest affinities are shared with species of the Ophiolepidoidea.

Ophiura graysonensis (Alexander, 1931) from the Grayson Marl Member of the Denison Formation (Lower Cretaceous) of Texas (USA), consisting of the dorsal and ventral sides of articulated body fossils (Alexander, 1931; Berry, 1941), differs from the new species in having tiny arm spines and pentagonal ventral arm plates. This species probably belongs to the Ophiolepidoidea.

Ophiura straini Cornell, Lemone and Norland, 1991 from the Comanche Series (Albian, Lower Cretaceous) at Cerro de Cristo Rey (New Mexico, USA) is based on articulated dorsal and ventral sides of disc and proximal arms (Cornell *et al*., 1991). It differs from the new species in having disc scales of variable size, trapezoidal proximal dorsal arm plates that are longer than wide, minute arm spines and equilateral triangular radial shields. Assignment to *Ophiura* can probably be ruled out on account of the absence of the diagnostic features of that genus.

Ophiura travisana Berry, 1941 from the Upper Cretaceous Kemp Clay (Navarro Group) of Texas (USA), consisting of disarticulated dorsal arm plates, ventral arm plates, radial shields, oral shields, vertebrae, lateral arm plates, arm spine, genital plates and adoral shields (misidentified as comb plates) (Berry, 1941), differs from the new species in having cordiform oral shields, widely rectangular dorsal arm plates with rounded corners and pentagonal ventral arm plates. The lateral arm plates of *O. travisana* have a ventrally pointed tentacle notch, thus probably precluding assignment to *Ophiura*.

Ophiura bridgerensis (Meek, 1873) from the Cretaceous of Montana (USA) is based on a dorsal disc and proximal arms, but was never illustrated (Meek, 1873). It differs from the new Korean species in having short arm spines and hexagonal dorsal arm plates. The generic assignment of this species remains dubious pending a detailed examination of the type material.

Ophiura achatae Rasmussen, 1972 from the upper Danian (lower Paleocene) Agatdal Formation of Nugssuaq (Greenland), consisting of articulated arm fragments (Rasmussen, 1972), differs from the new species in having very wide dorsal arm plates and abutting ventral arm plates.

Ophiura wetherelli Forbes, 1852 from the lower Eocene (Ypresian) London Clay of Highgate (London, England) is based on an articulated skeleton (Rasmussen, 1972), which differs from the new species in having small disc scales of various sizes, short arm spines, short conical oral papillae and trapezoidal dorsal arm plates with a swollen distal edge.

Ophiura furiae Rasmussen, 1972 from the lower Eocene (Ypresian) Mo-Clay Formation of the Island of Fur (Denmark), consisting of body fossils showing dorsal and ventral sides (Rasmussen, 1972), has slender oral papillae, dorsal arm plates and ventral arm plates that are somewhat similar to those of the new species. It differs, however, in having very short arm spines, fine disc scales and radial shields that are in contact distally.

Ophiura bognoriensis Rasmussen, 1972 from the lower Eocene (Ypresian) Astarte Bed and Starfish Bed (Lower Clay) of Bognor Regis (Sussex, England), consisting of articulated body fossils showing the dorsal side and arm fragments showing both dorsal and ventral sides (Rasmussen, 1972), has short arm comb papillae that are in part similar to those of the new species. It differs, however, in having short arm spines (two- thirds of arm segments), very wide dorsal arm plates proximally and fine disc scales.

Ophiura hendleri Blake and Aronson, 1998 from the upper Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula), consisting of articulated dorsal and ventral discs and proximal arms (Blake and Aronson, 1998), differs from the new species in having many small disc scales, short oral papillae, triangular radial shields and large oral shields.

Ophiura bartonensis Rasmussen, 1972 from the upper Eocene (Bartonian) Lower Barton Beds of Hampshire (England), consisting of articulated body fossils at dorsal and ventral sides (Rasmussen, 1972), has dorsal and ventral arm plates somewhat similar to those of the new species. Differences pertain to the long arm comb papillae, large oral shields and very large marginal disc scales.

Ophiura costata Rasmussen, 1972 from the upper Eocene (Bartonian) Middle Barton Beds of Hampshire (England; Rasmussen, 1972) is based on asteroid remains (Stöhr *et al*., 2011).

Ophiura carpelloides Rasmussen, 1972 from the upper Eocene (Bartonian) Middle Barton Beds of Hampshire (England) is based on disarticulated lateral arm plates, ventral arm plates, dorsal arm plates, radial shields, oral shields, genital plates, vertebrae and oral plates (Rasmussen, 1972). It differs from the new species in having square ventral arm plates, hexagonal dorsal arm plates and no striation on the surface of the lateral arm plates. The shape of the lateral arm plates is unusual for *Ophiura* and calls for a revision of the generic placement of this species.

Ophiura davisi Rasmussen, 1972 from the upper Eocene (Bartonian) Middle Barton Beds of Hampshire (England), consisting of disarticulated lateral arm plates, ventral arm plates, oral shields and vertebrae (Rasmussen, 1972), differs from the new species in having trapezoidal ventral arm plates, taller arm segments, triangular oral shields, a row of four arm spine articulations on the distal edge of the lateral arm plates, and no striation on the surface of the lateral arm plates. The shape of the lateral arm plates probably precludes assignment to *Ophiura*.

Ophiura? *sternbergica* Kutscher, 1980 from the Oligocene 'Sternberger Gestein' of Magdeburg (eastern Germany), consisting of articulated arm segments, disarticulated genital plates, lateral arm plates, ventral arm plates, oral shields and vertebrae (Kutscher, 1980), differs from the new species in having rhombic dorsal arm plates and rhombic or pentagonal ventral arm plates.

Ophiura? sp. (*sensu* Kutscher, 1985) from the middle Oligocene of Magdeburg (eastern Germany) is known only from a single lateral arm plate (Kutscher, 1985). The plate is thicker than those of the new species.

Ophiura marylandica Berry, 1934 from the Miocene Mary's Member of Maryland (USA), consisting of the dorsal and ventral sides of articulated body fossils (Berry, 1939), has tiny arm comb papillae similar to those of the new species, but differs in having tiny oral papillae, larger radial shields and wider quadrangular dorsal arm plates that are in contact.

Ophiura? *parviformis* Küpper, 1954 from the lower 'Badenian' (Langhian, middle Miocene) of Barden (Austria), consisting of disarticulated lateral arm plates, ventral arm plates, dorsal arm plates and vertebrae (Küpper, 1954), does not belong to *Ophiura* or the euryophiurids in general, judging from arm spine articulation and lateral arm plate shape. It rather belongs to the order Amphilepidida.

Ophiura? *vindobonensis* Küpper, 1954 from the 'Badenian' (Langhian, middle Miocene) of Barden (Austria) is based on disarticulated lateral arm plates, ventral arm plates, dorsal arm plates and vertebrae (Küpper, 1954). It does not belong to *Ophiura* but instead shows features in common with the superfamily Ophiodermatoidea.

Records of *Ophiura sarsii sarsii* Lütken, 1855 range from the uppermost middle Miocene to Pleistocene of Japan of the following formations: the uppermost middle Miocene to lowermost upper Miocene Itahana Formation of Gunma Prefecture (Ishida *et al*., 2004), the upper middle Miocene Wakkanai Formation and the lower Pliocene Koetoi Formation of Hokkaido (Ishida and Fujita, 2001), the upper Miocene to lower Pliocene Noguchi and Furukuchi formations, and the upper Miocene Hongo Formation of Yamagata Prefecture (Ishida *et al*., 1999), the upper Miocene Ogawa Formation of Nagano Prefecture (Ishida *et al*., 1998a), the lower Pliocene Nakawatari Formation of Yamagata Prefecture (Ishida *et al*., 2002), the upper Pliocene Higashigawa Formation of Niigata Prefecture (Ishida, 2004), the upper Pliocene Hachioji Formation of Niigata Prefecture (Ishida and Kurita, 1998), the Pliocene Hijikata Formation of Shizuoka Prefecture (Ishida *et al*., 1996), and the Pleistocene Ichijuku Formation of Chiba Prefecture (Ishida and Inoue, 1993). These fossil records are all based on articulated skeletons. This taxon differs from the new species, in having small disc scales, longer arm spines and wider arms.

Ophiura paucilepis Stöhr, Jagt and Klompmaker, 2011 from the lower Zanclean to mid-Piacenzian (Pliocene) Oosterhout Formation of Mill-Langenboom (Noord-Brabant, the Netherlands) is based on the dorsal and ventral sides of articulated body fossils (Stöhr *et al*., 2011). It differs from the new species in having shorter arm spines, longer oral shields, wider dorsal arm plates and shorter oral papillae.

Mode of occurrence.—Specimens of *Ophiura pohangensis* sp. nov. from the Duho Formation occur in dense aggregations in four pieces of matrix, mostly with the ventral side (19 out of 23 specimens) exposed on the bedding plane (Figures 5, 6). The arms are long and slightly to strongly bent. Almost all are articulated, although most arm spines, oral papillae and tentacle scales are dissociated. Most individuals were not in contact or overlap with each other. Ophiuroids disarticulate rapidly within days after death in a normal marine environment (Brett *et al*., 1997; Kerr and Twitchett, 2004), but may remain articulated for several months in cold water (Kerr and Twitchett, 2004). Some fossil individuals of *Ophiura sarsii sarsii* have been shown to display escape posture from sediment cover, with arms bending symmetrically and with tilted discs (Ishida *et al*., 1998a, 2004; Ishida, 1999, 2004; Ishida and Fujita, 2001). However, the present specimens do not demonstrate such postures (Figures 5, 6). Consequently, specimens of *O. pohangensis* sp. nov. may have been preserved more or less intact in cold water for a while after death, rather than having been smothered.

Extant *O. sarsii sarsii* occurs in high densities on the deep-sea floor around northern Japan. Individuals are generally not in contact with each other (Fujita and Ohta, 1989). The mode of occurrence of the present specimens of *O. pohangensis* sp. nov. is similar to that of the extant specimens of *O. sarssii sarsii*, suggesting that the present specimens are autochthonous. The aggregation densities measured on the surface area of the four matrix slabs amount to 506 individuals/m^2 (on average: 213 individuals/m^2-calculated from 8 individuals/375 cm^2; Figures 5A, 6A), 930 individuals/m^2 (calculated from 6 individuals/64.5 cm^2; Figures 5B, 6B), 439 individuals/m^2 (calculated from 6 individuals/136.5 cm^2; Figures 5C, 6C), 441 individuals/m^2 (calculated from 3 individuals/68 cm^2; Figures 5D, 6D). The densities of the extant *O. sarsii sarsii* at 152–623 m water depth around northern Japan have been reported as 442 individuals/m^2 off Aomori Prefecture, 554 individuals/m^2 off Iwate Prefecture, 308 individuals/m^2 off Iwate Prefecture, 27 individuals/m^2 off Akita Prefecture, 112 individuals/m^2 off Kyoto Prefecture and 161 individuals/m^2 off Shimane Prefecture (Fujita and Ohta, 1990). In addition, fossil *O. sarsii sarsii* from twelve formations in northern Japan, considered to represent mainly deposition in lower sublittoral to upper bathyal zones, also reportedly occurred in dense aggregations both as autochthonous and allochthonous assemblages (Ishida and Inoue, 1993, 1995; Ishida *et al.*, 1996; Ishida and Kurita, 1998; Ishida *et al.*, 1998a; Ishida and Fujita, 1999; Ishida *et al.*, 1999; Ishida and Fujita, 2001; Ishida *et al.*, 2002; Ishida, 2004; Ishida *et al.*, 2004). Densities in autochthonous occurrences were reported as 150 individuals/m^2 in the upper Miocene Hongo Formation of Yamagata Prefecture (Ishida and Fujita, 1999), 585 individuals/m^2 in the upper Pliocene Hachioji Formation of Niigata Prefecture (Ishida and Kurita, 1998), 645 individuals/m^2 in the middle Pleistocene Ichijuku Formation of Chiba Prefecture (Ishida and Inoue, 1995), and 540 individuals/m^2 in the Pliocene Hijikata Formation of Shizuoka Prefecture (Ishida *et al.*, 1996, 1998b). Aggregation density of *O. pohangensis* sp. nov. is similar to those of living and fossil *O. sarsii sarsii* around Japan. The estimated paleo-depth of the new species also falls into the range of both extant and fossil *O. sarsii sarsii*.

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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. Y. I., T. F. and A. M. identified the fossils. G. N. and J. K. collected the fossils and surveyed the site. All authors contributed to the writing of the manuscript.