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The beginning of a success story: basalmost members of the extant ophiuroid clade from the Silurian of Gotland, Sweden

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Abstract. Due to the fragility of the ophiuroid (brittle star) skeleton, the bulk of the group's fossil record consists of dissociated ossicles preserved as microfossils. In spite of their great potential as basis for taxonomic and phylogenetic studies, however, ophiuroid ossicles from the Paleozoic have received very little attention so far. Here, we provide an exhaustive taxonomic assessment of such fossils retrieved from sieving residues from the Silurian of Gotland, Sweden. This material was used in a previous study to describe two key taxa that allowed constraining the origin of the extant ophiuroid clade. The remaining taxa belonging to that same lineage are described in the present paper. The evidence at hand suggests that the stem of the extant ophiuroid clade was formed by two genera, *Ophiopetagno* and *Ophiolofsson* gen. nov., including six and five species, respectively, and spanning at least the upper Llandovery through upper Ludlow. We conclude that *Ophiopetagno* and *Ophiolofsson* represent sister genera that coexisted through most of the Silurian in the shallow tropical seas of Gotland. They underwent repeated body size reductions in correlation with environmental perturbations, with *Ophiopetagno paicei* eventually giving rise to *Muldaster haakei*; the first member of the living Ophiuroidea. Herein, we also introduce two new clades, Ankhurida clade nov. and Ophiovalida clade nov., and the following eight new species: *Ophiolofsson joelmciveri* gen. et sp. nov., *O. obituary* gen. et sp. nov., *O. immolation* gen. et sp. nov., *O. archspire* gen. et sp. nov., *O. hendersonorum* gen. et sp. nov., *Ophiopetagno bonzo* sp. nov., *O. kansas* sp. nov., *O. doro* sp. nov.; and two probably new species in open nomenclature: *Ophiopetagno* sp. 1, and *Ophiopetagno* sp. 2.

Keywords. Phylogeny, new species, Gotland, Ankhurida, Ophiovalida.

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Introduction

Ophiuroids (or brittle stars) are a major component of modern marine benthic communities and occur in all parts of the world oceans, from the poles to the tropics and from the intertidal to the abyssal (Stöhr *et al.* 2012). Apart from the near-omnipresence on the seafloor, they have recently emerged as a promising model organism to explore large-scale biogeography and evolutionary trends (e.g., Thuy 2013; Woolley *et al.* 2016; Bribiesca-Contreras *et al.* 2017; O'Hara *et al.* 2018). Thanks to recent progress in compiling extensive, converging molecular and morphological datasets, the phylogeny of the living ophiuroids is one of the best known among marine invertebrates (O'Hara *et al.* 2014, 2017; Thuy & Stöhr 2016). Yet, the basalmost Paleozoic nodes, and in particular the origin of the extant ophiuroids, remain poorly known. The incomplete fossil record has contributed to a limited understanding of early ophiuroid evolution.

In terms of stratigraphic completeness and numbers of species, the fossil record of Paleozoic ophiuroids does not significantly lag behind the Mesozoic and Cenozoic ones (Spencer & Wright 1966). Nevertheless, Paleozoic and post-Paleozoic ophiuroids are often treated differently in systematic studies, in spite of unambiguous evidence for a Paleozoic origin of the extant ophiuroids (Hotchkiss & Haude 2000; O'Hara *et al*. 2014; Thuy *et al.* 2015, 2022, 2023) and for the survival of Paleozoic clades into the Mesozoic (Thuy *et al.* 2017). This separation of research traditions is also reflected in the use of different terminologies, even though homologies are often unambiguously established (e.g., ambulacrals versus vertebrae). Although this artificial dichotomy seems justified in some cases, for example, because pairs of ambulacrals are separate in most Paleozoic ophiuroids while being fused to vertebrae in all extant ones, it has not proven beneficial for the understanding of evolutionary trends of the Ophiuroidea Gray, 1840 across the Paleozoic–Mesozoic boundary.

To make matters worse, the vast majority of Paleozoic ophiuroids are known from external molds of articulated skeletons only, a mode of preservation restricted to specific taphonomic conditions, and therefore represent a small sample set of their fossil record (e.g., Donovan 1991). Because ophiuroid skeletons rapidly disintegrate after death, dissociated skeletal parts preserved as microscopic fossils comprise the bulk of their fossil record (e.g., Stöhr *et al.* 2012). Specific types of ophiuroid microfossils are identifiable to species level and available for phylogenetic studies (Thuy & Stöhr 2011, 2016), and there is ample evidence from the Mesozoic that paleobiodiversity estimates are significantly more complete when microfossils are considered (e.g., Thuy 2013; Thuy *et al.* 2018). In spite of their great potential, however, ophiuroid microfossils from the Paleozoic have received very little attention so far (Boczarowski 2001; Hotchkiss *et al.* 2007; Thuy *et al.* 2022, 2023).

We recently used microfossils from the Silurian of Gotland, Sweden, to explore the origin of the extant ophiuroid clade (Thuy *et al.* 2022). The vast number of specimens (more than 1300 skeletal plates), the outstanding preservation of the material and the high stratigraphic resolution allowed us to document negative body size excursions in correlation with three successive extinction events, with the strongest size decrease leading to skeletal modifications typical of modern ophiuroids. For the sake of conciseness, only the two key species, *Ophiopetagno paicei* Thuy, Eriksson & Numberger-Thuy, 2022 and *Muldaster haakei* Thuy, Eriksson & Numberger-Thuy, 2022, comprising the speciation event that gave birth to the modern ophiuroid clade, were formally described. Here, we provide an exhaustive taxonomic assessment of the yet unnamed material involved in the study by Thuy *et al.* (2022). It adds significantly to the Silurian fossil record that is still underrepresented compared to the Ordovician and Devonian equivalents (Gladwell 2018).

Material and methods

The material described herein was retrieved from the sieving residues of bulk sediment samples collected at various sections (see below) on the island of Gotland. The samples were screen-washed, dried and picked using a dissecting microscope. Selected specimens were cleaned in an ultrasonic bath, mounted on stubs and gold-coated for scanning electron microscopy using a JEOL Neoscope JMC-5000. Type specimens and illustrated material are deposited in the collections of The Swedish Museum of Natural History (Naturhistoriska Riksmuseet: acronym NRM) in Stockholm, Sweden. Because the specimens described are at the base of crown-group ophiuroids, terminology follows Thuy & Stöhr (2011, 2016) and Stöhr *et al.* (2012). For morphological structures not known in extant ophiuroids, terminology follows Gladwell (2018).

Geological setting and stratigraphy

The island of Gotland, situated in the Baltic Sea east of the Swedish mainland (Fig. 1), has been a hotspot for geological and paleontological campaigns for more than two centuries, notably also including research visits by legendary botanist, zoologist and 'the father of modern taxonomy', Carl von Linnaeus (Bassett & Cocks 1974). No wonder this island has received so much attention as it exposes pristine Silurian strata that are now world-famous for their abundance and often excellent preservation of fossils. The reasons for the well-preserved rock succession, which comprise stacked generations of carbonate platforms formed in shallow marine settings, boil down to a combination of the paleolatitudinal setting and post-depositional history.

The exposed succession was formed along the northwestern margin of the intracratonic Baltic Basin during the Silurian Period (e.g., Hede 1960; Baarli *et al.* 2003; Eriksson & Calner 2005). Tectonic overprinting is overall negligible and dolomitization is very rare, which are the primary reasons for the well-preserved entombed biotas found. The current sub-division of the Gotland strata largely dates back to the pioneering work by J. Ernhold Hede, conducted in the early through middle part of the last century (for a summary, see Hede 1960). Using Hede's framework as a stepping-stone, more recent studies have added some units and refined others, which has resulted in the lithostratigraphic subdivision shown in Figs 1 and 2.

The entire Gotland strata have an approximate maximum thickness of 750 m (Jeppsson *et al.* 2006). Due to a very gentle dip towards the southeast, the oldest rocks are exposed in the northwestern part of the island, gradually becoming younger towards the southeast (e.g., Hede 1960; Jeppsson *et al.* 2006). From the oldest to the youngest, the whole succession spans the upper Llandovery Lower Visby Formation through the upper Ludlow Sundre Formation (Figs 1–2; Eriksson & Calner 2005; Jeppsson *et al.* 2006). In addition to this large-scale architecture, the facies belts change along outcrop strike, roughly speaking from more proximally formed limestones in the northeast to sparsely graptolitic, and more distally formed, marls in the southwest (Samtleben *et al.* 1996; Eriksson & Calner 2005). The stratigraphic completeness accompanied by the abundant and excellently preserved fossils and lengthy tradition of paleontological investigations have resulted in very well-known biotas across a wide range of taxa. Moreover, this has facilitated the establishment of a very high-resolution biostratigraphic scheme, primarily based on conodonts (Fig. 2; Jeppsson *et al.* 2006).

Over the last few decades, most of the Phanerozoic systems have seen a wealth of new isotopic data (particularly with regards to $\delta^{13}C$ and $\delta^{18}O$) being produced, and the Silurian is no exception (e.g., Samtleben *et al.* 1996; Cramer *et al.* 2011; Melchin *et al.* 2020). Not only has chemostratigraphy combined with biostratigraphy been instrumental in the clarification of local and global stratigraphic relationships, but it has also shone the light on conspicuous environmental perturbations. The Silurian Period clearly was a dynamic and environmentally unstable time in Earth History, as shown through a whole range of biogeochemical events identified in rocks of that age (e.g., Jeppsson 1990; Jeppsson *et al.* 1995; Johnson 2006; Calner 2008; Cramer *et al.* 2011; Melchin *et al.* 2020). In the Gotland succession alone,

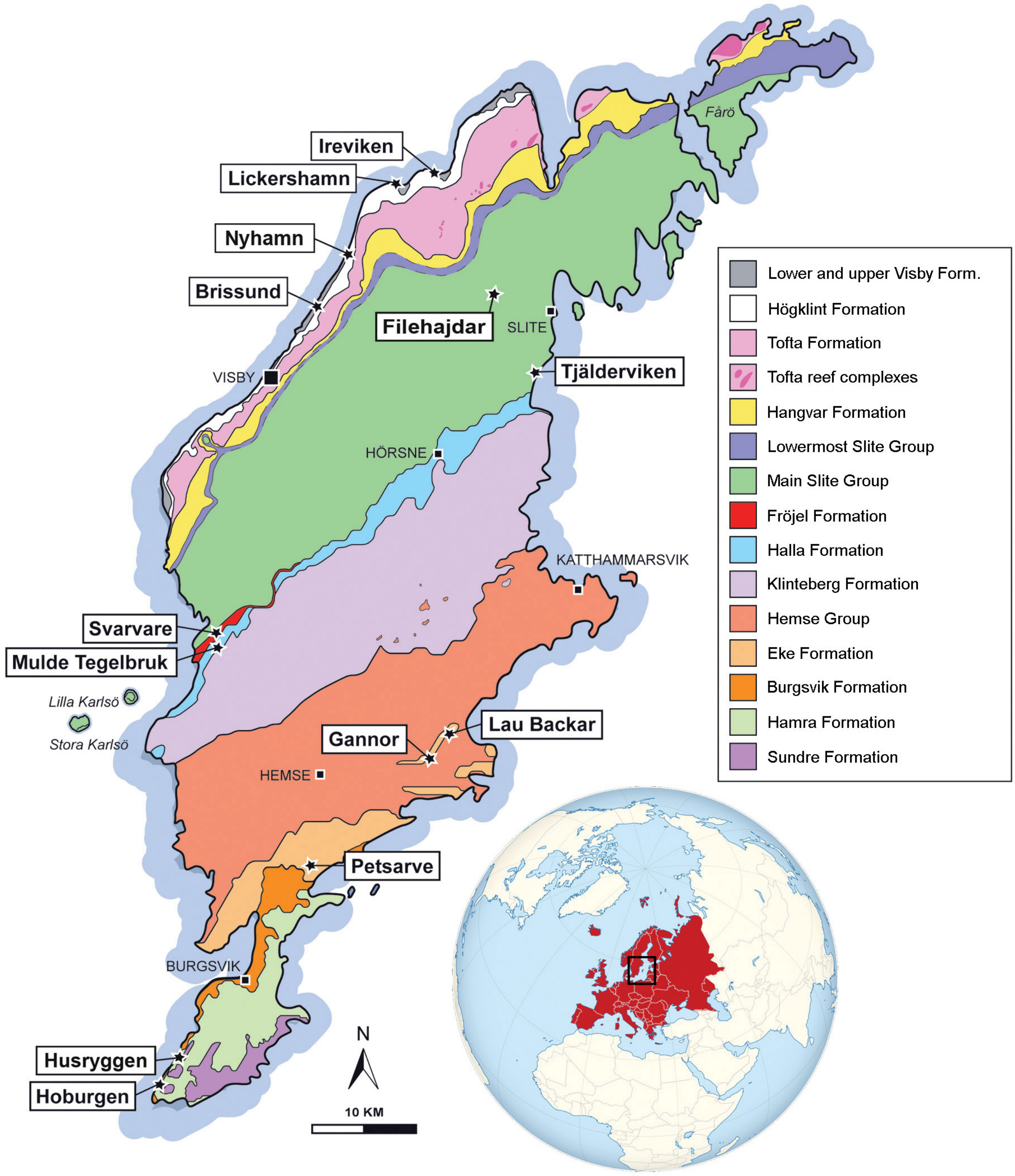

Fig. 1. Geological map of the island of Gotland, Sweden, showing mapped lithological units and localities sampled for ophiuroids. Figure modified from Eriksson & Calner (2005) and Thuy *et al.* (2022).

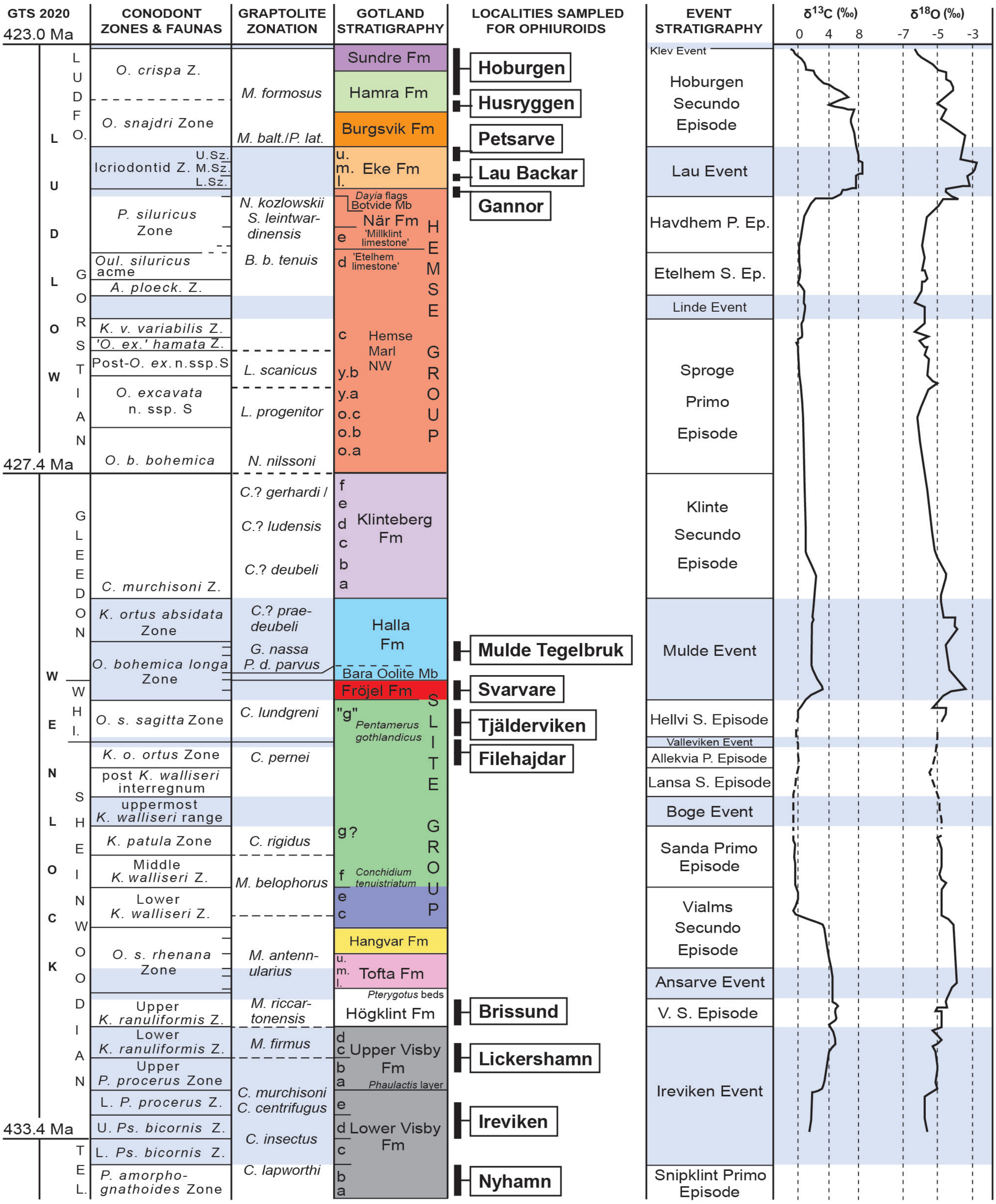

Fig. 2. Stratigraphic framework of Gotland, with the stratigraphic positions of localities sampled for ophiuroids alongside identified Silurian events (modified from Eriksson & Calner 2005, with chronostratigraphic ages after Melchin *et al.* 2020).

high-resolution studies primarily based on conodonts and subsequently complemented by isotopic work, have enabled the identification of up to eight such events; the most prominent ones being the Ireviken Event, the Mulde Event, and the Lau Event (Fig. 2; e.g., Jeppsson 1990, 1998, 2005; Samtleben *et al.* 1996; Jeppsson *et al.* 2006). The three latter events are associated with rapid and profound shifts in the oxygen and carbon isotope signatures, faunal reorganisations (including profound extinctions and organism malformations, but also taxonomic originations), sedimentary facies restructurings, and have subsequently been shown to have a geographically very widespread, if not global, occurrence on Earth (e.g., Jeppsson 1998; Jeppsson *et al.* 2006; Calner 2008; Eriksson *et al.* 2009; Munnecke *et al.* 2012; Melchin *et al.* 2020; Thuy *et al.* 2022).

Sampled localities

The bulk sediment samples yielding the ophiuroid remains described herein were collected at the following thirteen sections, listed below in ascending stratigraphic order (see also Figs 1 and 2):

Nyhamn

Llandovery Series, Telychian Stage, *Pterospathodus amorphognathoides* Walliser, 1964 conodont Zone, Lower Visby Formation (units a and b). Ophiuroid sample is from unit a or b of the Lower Visby Fm. Locality references, e.g., Laufeld (1974), Bergman (1989).

Ireviken

Llandovery and Wenlock series, Telychian and Sheinwoodian stages, *Pterospathodus amorphognathoides* through Upper *Kockellela ranuliformis* (Walliser, 1964) conodont zones, Lower Visby Formation through Högklint Formation (unit a). Ophiuroid sample is from the middle–upper portion of the Lower Visby Formation. Locality references, e.g., Laufeld (1974), Bergman (1989).

Lickershamn

Wenlock Series, Sheinwoodian Stage, Lower *Pterospathodus procerus* (Walliser, 1964) through Upper *Kockellela ranuliformis* conodont zones, Lower Visby Formation (unit e) through Högklint Formation (unit b). Ophiuroid sample is from the middle part of the Upper Visby Formation. Locality references, e.g., Laufeld (1974), Bergman (1989).

Brissund

Wenlock Series, Sheinwoodian Stage, Upper *Kockellela ranuliformis* conodont Zone, Högklint Formation “undifferentiated”. Locality references, e.g., Riding & Watts (1991), Watts & Riding (2000).

Filehajdar

Wenlock Series, Sheinwoodian Stage, *Kockellela ortus ortus* (Walliser, 1964) conodont Zone (possibly also lowermost part of overlying *Ozarkodina sagitta sagitta* Zone), Slite Group (unit i). Locality references, e.g., Sivhed (1990), Jerre (1994).

Tjälderviken

Wenlock Series, Whitwell Stage, *Ozarkodina sagitta sagitta* (Walliser, 1964) conodont Zone, Slite Group (upper part – “*Pentamerus gothlandicus* beds” or equivalents). For locality references, see Tjeldersholm (Laufeld 1974; Bergman 1989).

Svarvare

Wenlock Series, Whitwell Stage, *Ozarkodina bohemica longa* Jeppsson, 2003 conodont Zone, Slite Group, Fröjel Formation, Gannarve or Svarvare member. Locality references, e.g., Laufeld (1974), Larsson (1979), Bergman (1989).

Mulde Tegelbruk

Wenlock Series, Gleedon Stage, *Ozarkodina bohemica longa* conodont Zone, Halla Formation, Mulde Brick clay member. *Gothograptus nassa–Pristioprion dubius* graptolite Interregnum, Mulde Event, fauna 4. Locality references, e.g., Laufeld (1974), Larsson (1979), Bergman (1989).

Gannor

Ludlow Series, Ludfordian Stage, uppermost part of the *Polygnathoides siluricus* Branson & Mehl, 1933 conodont Zone or lowermost part of the Lower Icriodontid conodont subzone sensu Jeppsson (2005), Hemse Group, När Formation, Botvide Member or the lowermost Eke Formation. Locality references, e.g., Laufeld (1974), Bergman (1989).

Lau Backar

Ludlow Series, Ludfordian Stage, uppermost part of the Lower Icriodontid conodont subzone sensu Jeppsson (2005), Eke Formation. Locality references, e.g., Laufeld (1974), Bergman (1989).

Petsarve

Ludlow Series, Ludfordian Stage, Upper Icriodontid conodont subzone sensu Jeppsson (2005), Eke Formation, upper part. Locality references, e.g., Laufeld (1974), Bergman (1989).

Husryggen

The Husryggen area comprises several mapped geological localities spanning the Ludlow Series, Ludfordian Stage, *Ozarkodina snajdri* (Walliser, 1964) through *O. crispa* (Walliser, 1964) conodont zones, uppermost Burgsvik Formation through lowermost Hamra Formation. Ophiuroid sample is from a slope section east of the road running parallel to the beach, ca 300 m north of the Hoburgen restaurant/café; most likely basal part of the Hamra Formation. Locality references, e.g., Laufeld (1974), Larsson (1979), Bergman (1989).

Hoburgen

The Hoburgen area comprises several mapped geological localities spanning the Ludlow Series, Ludfordian Stage, *Ozarkodiana snajdri* through *O. crispa* conodont zones, uppermost Burgsvik Formation through the Sundre Formation. Ophiuroid sample is from weathered material within a cave adjacent to the so-called Hoburgsgubben (“Hoburg man”) sea stack; Hamra or Sundre Formation. Locality references, e.g., Laufeld (1974), Larsson (1979), Bergman (1989).

Results

Systematic paleontology

Note that in our latest study on the origin of the extant ophiuroid clade (Thuy *et al.* 2022), we performed a phylogenetic analysis of the Ophiuroidea, considering representatives of both the extinct Paleozoic groups and the living forms. To our knowledge, this was the first attempt at a total-group phylogeny. The high resolution and good support values of the resulting tree has prompted us to revise high-level ophiuroid classification in the present paper and suggest names for some of the relevant clades.

The most widely cited subdivision of the Ophiuroidea (e.g., Fell 1960; Spencer & Wright 1966) was introduced by Matsumoto (1913, 1929) based on whether the ambulacral grooves are covered or not (Matsumoto’s original subclasses Myophiuroida Matsumoto, 1915 and Oegophiuroida Green, 1895, respectively). Our phylogeny, however, suggests that the ophiuroids with covered ambulacral grooves (with or without ventral arm plates) are nested in a clade of taxa with an open ambulacral groove, thus corroborating previous assumptions of a paraphyletic Oegophiuroida (Simms *et al.* 1993). Therefore, our phylogeny supports a fundamental subdivision of the Ophiuroidea based on whether the ambulacrals are opposite or alternating. Matsumoto (1913, 1929) used this character to subdivide the oegophiuroid infraclass Protophiurida Matsumoto, 1913 into the orders Lysophiurida Gregory, 1896 and Zeugophiurida Matsumoto, 1929. We adopt Matsumoto's names for the oegophiuroid orders because they have a long citing history (e.g., Spencer & Wright 1966) and fit very well etymologically but we use them at a higher systematic level: 1) the subclass Lysophiuroidea (from greek-derived 'lys' meaning 'loose' or 'dissolved') and 2) the subclass Zeugophiuroidea (from Greek-derived 'zeug' meaning 'joined in pairs'). For classification below the subclass level, we fully adopt the scheme proposed by O'Hara *et al.* (2018) that includes: Matsumoto's (1913) infraclass Metophiurida (comprising all ophiuroids with ventral arm plates and both or either of radial shields and genital plates), and subclass Myophiuroidea Matsumoto, 1915 (comprising all ophiuroids with ventral arm plates). However, the latter represents a node between the subclass Zeugophiuroidea and the infraclass Metophiurida. Thus, while our phylogeny endorses the validity of the Myophiuroidea, it should be treated as a clade outside formal Linnean categories.

Herein, we introduce formal names for two additional nodes between the subclass Zeugophiuroidea and the infraclass Metophiurida. This is done first for practical reasons in order to avoid lengthy paraphrasing and/or non-memorable working designations when navigating across the stem of the extant ophiuroid clade, and second, because of their pivotal and well-documented position within the ophiuroid evolutionary history. Diagnoses, etymologies and all further details of the two new clades are provided below.

Phylum Echinodermata Bruguière, 1791
Subphylum Asterozoa von Zittel, 1895
Class Ophiuroidea Gray, 1840

Subclass **Zeugophiuroidea** Matsumoto, 1913 stat. nov. (raised to subclass level)

Diagnosis

Ophiuroids with ambulacrals joined in pairs, whether fused or not.

Clade **Ankhurida** clade nov.

Diagnosis

Zeugophiuroid ophiuroids with ambulacral halves firmly merged and with lateral arm plates showing a tentacle notch.

Etymology

From 'ankh', the ancient Egyptian hieroglyphic symbol for 'life', because the node in question represents the deepest known in the clade including the living ophiuroids.

Taxa included

Ophiolofsson gen. nov., *Ophiopetagno* Thuy, Eriksson & Numberger-Thuy, 2022 and all members of the clade Ophiovalida clade nov. (see below).

Remarks

We propose the new clade name Ankhurida clade nov. to designate a basalmost node in the evolutionary history of living ophiuroids. This node marks the earliest divergence within the clade encompassing all extant ophiuroids, and it is the sister group to an extinct clade consisting of the families Furcasteridae Stürtz, 1899, Eospondylidae Spencer & Wright, 1966, and Onychasteridae Miller, 1889. For the latter three families, in spite of the limited number of taxa represented in our phylogeny (Thuy *et al.* 2022), it is noteworthy that our tree topology favors a close relationship between the three, as previously suggested (Hotchkiss & Glass 2012).

Genus ***Ophiolofsson*** gen. nov.
urn:lsid:zoobank.org:act:8F0B9C56-6C24-4AB3-B752-55E3F7EAE41C

Type species

Ophiolofsson obituary gen. et sp. nov., by present designation.

Diagnosis

Ankhurid ophiuroid with thick, rounded lateral arm plates showing articulations for ambulacral groove spines, lacking a ventro-proximalwards protruding ventral portion, and having and a well-defined, strongly prominent vertebral articulation knob situated directly at the dorsal edge of the lateral arm plate; vertebrae roughly cylindrical; lateral sides with large, oval articulation surface proximally, matching vertebral articular knob on inner side of lateral arm plates; distal side with large, dorsally converging zygocondyles; water vessel canal running entirely within vertebra, distally enclosed by large zygosphene.

Etymology

Genus name honoring Swedish ‘metal painter’ Pär Olofsson in recognition of his artistic talent and ability to integrate complex anatomical features in remarkable scientific accuracy into his art pieces, making them disturbingly vivid. Gender: masculine.

Other species included

Ophiolofsson joelmciveri gen. et sp. nov., *O. immolation* gen. et sp. nov., *O. archspire* gen. et sp. nov., and *O. hendersonorum* gen. et sp. nov.

Remarks

Ophiolofsson gen. nov. and *Ophiopetagno* are the two basalmost representatives of the extant ophiuroid clade Ankhurida clade nov. currently known. They are also the only ankhurids with ambulacral groove spine articulations, resulting in a unique combination of ancestral and derived characters not found in any other known ophiuroid. Closest similarities are shared with the lateral arm plates of the basal zeugophiuroid genera *Lapworthura* Gregory, 1897 (Gladwell 2018) and *Hallaster* Stürtz, 1886 (Spencer 1925). The lateral arm plates of those two genera, however, lack tentacle notches, a ventro-distalwards protruding ventral portion and an outer surface ornamentation. In addition, their ambulacrals are, albeit opposing, not fused into vertebrae. Lateral arm plates of furcasterids, eospondylids and onychasterids all lack a tentacle notch and share a particular type of spine articulation strongly differing from the simple opening seen in the lateral arm plates of *Ophiolofsson* and *Ophiopetagno*. The latter two genera can thus be readily distinguished from all other currently known ophiuroids.

The lateral arm plates of *Ophiolofsson* gen. nov. differ from those of *Ophiopetagno* in being thicker, having a much smaller ventro-distalwards protruding ventral portion and a strongly prominent vertebral articulation knob located directly at the dorsal edge, altogether leading to a lateral arm plate shape that appears less strongly wrapped around the vertebra. Since these differences are consistently found across various species, we consider them to be genus diagnostic.

Ophiolofsson joelmciveri gen. et sp. nov.
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Figs 3A–D, 7

Diagnosis

Species of *Ophiolofsson* gen. nov. with lateral arm plates of rounded rectangular outline, with a convex dorsal edge; outer surface with a moderately coarse, dense tuberculation, up to three large, round spine articulations in the ventral half of the distal edge; up to five small, weakly protruding ambulacral groove spine articulations.

Etymology

Species named after prolific British author and music journalist, Joel McIver, for his unique ability to convey the cultural importance and impact of music.

Type material

Holotype

SWEDEN • Gotland, Nyhamn; NRM PAL Ec38322.

Paratype

SWEDEN • same data as for holotype; MnhnL NRM PAL Ec38323.

Type locality and stratum

Llandovery Series, Telychian Stage, *Pterospathodus amorphognathoides* conodont Zone, Lower Visby Formation (units a and b); Nyhamn, Gotland, Sweden.

Description

Holotype (Fig. 3A–B)

NRM PAL Ec38322 is a dissociated proximal lateral arm plate, approximately 1.3 times as long as high, with very weakly convex dorsal and ventral edges and straight distal edge; proximal edge slightly oblique, with very weak central incision and semi-circular depression dorsally and ventrally bordered by poorly defined, slightly prominent but not protruding oval knobs; outer surface with trabecular intersections enlarged into medium-sized, irregular tubercles, resulting in coarse overall appearance; tuberculation on entire outer surface except for depressed area near proximal edge; three large, approximately equidistant lateral arm spine articulations (LSA) freestanding in vertical row at some distance from distal edge; dorsalmost spine articulation at some distance from dorsal edge of lateral arm plate, with dorsal third of lateral arm plate devoid of spine articulations; ventralmost spine articulation at ventral edge of lateral arm plate; two central spine articulations largest; spine articulations consisting of single opening encompassed by elevated ring; ventral edge of lateral arm plate with very weakly visible protrusions of ambulacral groove spine articulations (AGSA). Inner side of lateral arm plate (Fig. 3B) with large, well-defined vertebral articulation knob with slightly depressed centre and situated directly at dorso-proximal corner of lateral arm plate; inner distal edge slightly depressed and separated from remaining inner surface by vertical ridge; large but relatively shallow tentacle notch (TN) on inner side; ventral edge of lateral arm plate without incision for tentacle notch but with four weakly developed ambulacral groove spine articulations.

Paratype (supplements)

NRM PAL Ec38323 (Fig. 3C–D) is a dissociated median to distal lateral arm plate approximately 1.5 times as long as high; overall, similar to holotype, but with convex distal edge, resulting in more rounded general outline; three spine articulations similar to those of holotype but with dorsalmost one missing; ventral edge of lateral arm plate with stronger protrusions of ambulacral groove spine articulations. Inner side as in holotype but with five instead of four ambulacral groove spine articulations.

Remarks

Ophiolofsson joelmciveri gen. et sp. nov. differs from its congeners in having large, round lateral spine articulations at some distance from the distal edge and restricted to the ventral part of the distal portion of the lateral arm plate. The closest similarities are shared with the stratigraphically close *Ophiolofsson obituary* gen. et sp. nov. However, there are distinctions: *Ophiolofsson obituary* features larger and vertically elongated spine articulations, a slightly coarser outer surface tuberculation, a concave dorsal edge, and larger, more pronounced ambulacral groove spine articulations.

Occurrence

Nyhamn and Ireviken.

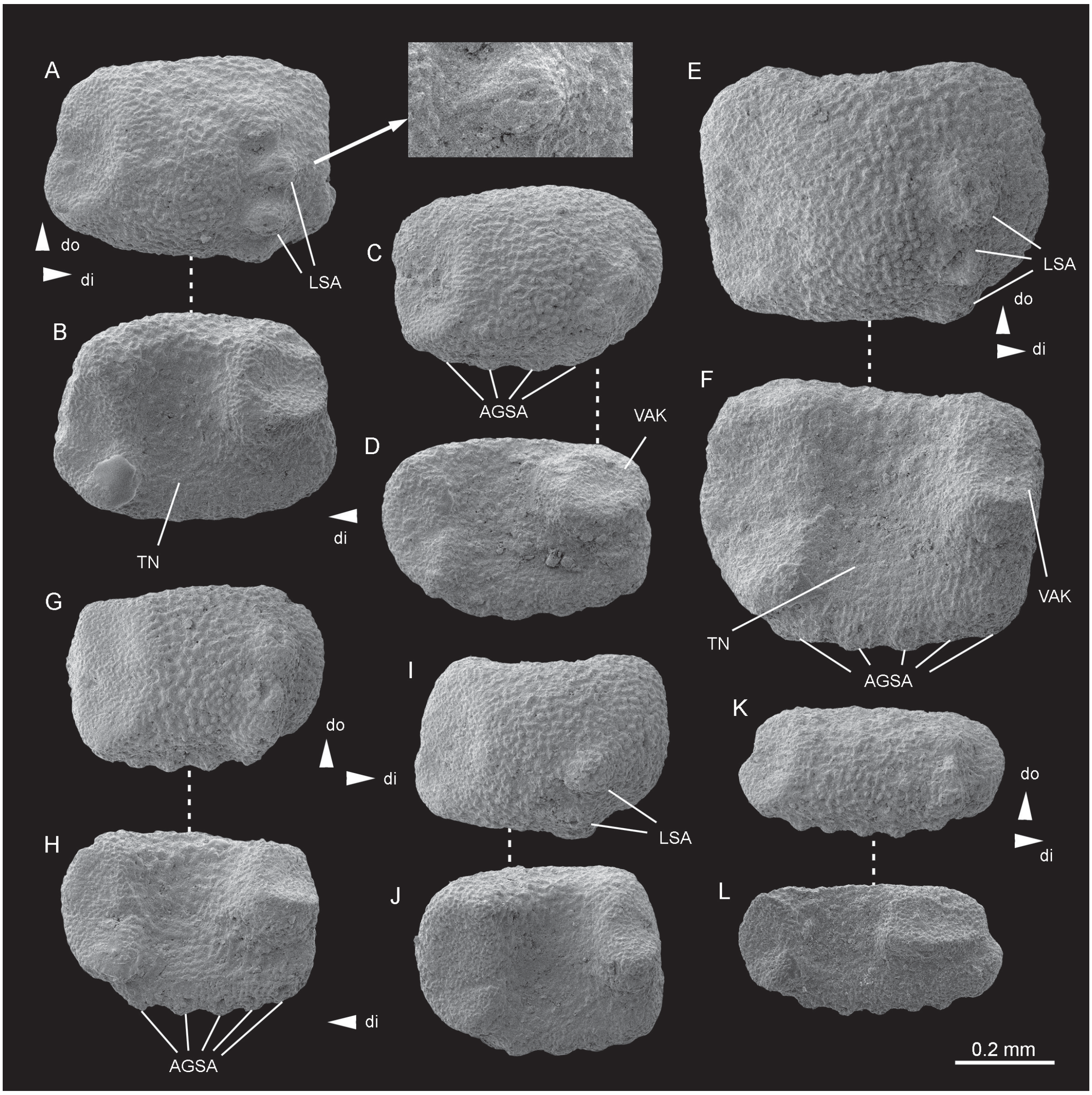

Fig. 3. Dissociated lateral arm plates of ophiuroids from the Silurian of Gotland. **A–B**. *Ophiolofsson joelmciveri* gen. et sp. nov., holotype, NRM PAL Ec38322, proximal lateral arm plate in external (A) and internal (B) views. **C–D**. *O. joelmciveri*, paratype, NRM PAL Ec38323, median to distal lateral arm plate in external (C) and internal (D) views. **E–F**. *Ophiolofsson obituary* gen. et sp. nov., holotype, NRM PAL Ec38324, median to proximal lateral arm plate in external (E) and internal (F) views. **G–H**. *O. obituary*, paratype, NRM PAL Ec38325, proximal lateral arm plate in external (G) and internal (H) views. **I–J**. *O. obituary*, paratype, NRM PAL Ec38326, proximal median lateral arm plate in external (I) and internal (J) views. **K–L**. *O. obituary*, paratype, NRM PAL Ec38327, distal lateral arm plate in external (K) and internal (L) views. Abbreviations: AGSA = ambulacral groove spine articulations; di = distal; do = dorsal; LSA = lateral spine articulations; TN = tentacle notch; VAK = vertebral articular knob.

Ophiolofsson obituary gen. et sp. nov.

urn:lsid:zoobank.org:act:78904D7E-CE55-4F89-8E26-16E70DB74B82
Figs 3E–L, 7

Diagnosis

Species of *Ophiolofsson* gen. nov. with rounded trapezoidal lateral arm plates with a slightly concave dorsal edge; outer surface with a coarse, dense tuberculation; up to three very large, vertically elongate spine articulations in ventral portion of distal edge; up to five large, strongly protruding ambulacral groove spine articulations.

Etymology

Species named after American death metal pioneers, Obituary, who were fundamental in developing the death metal genre, and appropriately, *O. obituary* gen. et sp. nov. represents a basal species in the *Ophiolofsson* lineage.

Type material

Holotype
SWEDEN • Gotland, Brissund; NRM PAL Ec38324.

Paratypes
SWEDEN • 3 specs; same data as for holotype; NRM PAL Ec38325 to NRM PAL Ec38327.

Type locality and stratum

Wenlock Series, Sheinwoodian Stage, Upper *Kockellela ranuliformis* conodont Zone, Högklint Formation “undifferentiated”; Brissund, Gotland, Sweden.

Description

Holotype (Fig. 3E–F)
NRM PAL Ec38324 is a dissociated median to proximal lateral arm plate, approximately 1.3 times as long as high, with nearly straight dorsal edge and strongly convex distal edge; proximal edge weakly convex, without central incision and with shallow, poorly defined, semi-circular depression ventrally bordered by a poorly defined, weakly prominent oval knob; outer surface with coarse tuberculation composed of enlarged trabecular intersections covering entire outer surface except for depressed area at proximal edge; three very large, vertically elongate, equidistant lateral arm spine articulations in vertical to slightly oblique row at some distance from distal edge, freestanding and prominent; dorsalward increase in size of spine articulations; dorsalmost spine articulation separated from dorsal edge of lateral arm plate by one quarter to one fifth of lateral arm plate height; spine articulations consisting of single opening encompassed by coarse, elevated ring; ventral edge of lateral arm plate slightly convex, with strong protrusions of ambulacral groove spine articulations. Inner side of lateral arm plate with very large, sharply defined and prominent vertebral articulation knob at dorso-proximal corner of lateral arm plate; centre of knob slightly depressed. Inner distal edge of lateral arm plate (Fig. 3F) slightly elevated and separated from remaining outer surface by low, moderately well-defined vertical ridge; large, well-defined tentacle notch distally sharply bordered by ridge of distal edge; ventral edge of lateral arm plate devoid of incision for tentacle notch but with five large, conspicuous, nearly equidistant ambulacral groove spine articulations.

Paratype (supplements)
NRM PAL Ec38325 (Fig. 3G–H) is a dissociated proximal lateral arm plate approximately 1.2 times as long as high; well in agreement with holotype but with slightly concave dorsal edge; lateral arm spine

articulations as in holotype; ventral edge with only very weak protrusions of ambulacral groove spine articulations. Inner side as in holotype but with four slightly smaller, less strongly protruding ambulacral groove spine articulations.

NRM PAL Ec38326 (Fig. 3I–J) is a dissociated median lateral arm plate similar to holotype but slightly longer and with spine articulations restricted to the ventral half of the plate. Inner side as in holotype.

NRM PAL Ec38327 (Fig. 3K–L) is a dissociated distal lateral arm plate approximately two times as long as high; well in agreement with holotype except for more strongly concave proximal edge; outer surface ornamentation and lateral arm spine articulations as in holotype; ventral edge with five conspicuous protrusions of ambulacral groove spine articulations. Inner side as in holotype.

Remarks

Ophiolofsson obituary gen. et sp. nov. is distinguished from other species by its large, vertically elongated spine articulations, arranged in an oblique row along the ventral section of the distal part of the lateral arm plate. It furthermore differs from the morphologically similar and stratigraphically close *Ophiolofsson joelmciveri* gen. et sp. nov. in having a slightly coarser outer surface tuberculation and larger and more strongly protruding ambulacral groove spines. Remarkably, the two occurrences of *O. obituary* described in the present paper differ in average plate size while maintaining an otherwise identical morphology: the lateral arm plates of *O. obituary* from Lickershamn are significantly larger than their Brissund counterparts. This observation agrees with the size decrease described by Thuy *et al.* (2022) coinciding with the Ireviken Event.

Occurrence

Brissund and Lickershamn.

Ophiolofsson immolation gen. et sp. nov.

urn:lsid:zoobank.org:act:CF27D28D-2B22-449F-AC48-8F9468B09640
Figs 4A–D, 7

Diagnosis

Species of *Ophiolofsson* gen. nov. with lateral arm plates of almost oval outline; outer surface with a fine tuberculation; up to three small, weakly developed lateral spine articulations in a continuous row along the distal plate edge; up to five moderately large, but weakly developed ambulacral groove spine articulations.

Etymology

Species named after legendary American death metal band, Immolation, who came onto the scene slightly later than the above-mentioned Obituary.

Type material

Holotype

SWEDEN • Gotland, Tjälderviken; NRM PAL Ec38328.

Paratype

SWEDEN • same data as for holotype; NRM PAL Ec38329.

Type locality and stratum

Wenlock Series, Whitwell Stage, *Ozarkodina sagitta sagitta* conodont Zone, Slite Group (upper part – "*Pentamerus gothlandicus* beds" or equivalents); Tjälderviken, Gotland, Sweden.

Description

Holotype (Fig. 4A–B)

NRM PAL Ec38328 is a dissociated proximal lateral arm plate approximately 1.3 times as long as high; dorsal edge very weakly convex, distal edge convex and proximal edge straight without central incision; narrow, poorly defined and distalwards concave depressed area at proximal edge; outer surface of lateral arm plate with fine, densely packed tubercles consisting of weakly enlarged trabecular intersections covering entire outer surface except for depressed area at proximal edge; three small lateral arm spine articulations, freestanding and weakly prominent spine articulations in vertical to slightly oblique row from ventral to dorsal edge of lateral arm plate; spine articulations relatively close to distal edge of lateral arm plate; ventral edge of lateral arm plate convex, with protrusions of five ambulacral groove spine articulations. Inner side of lateral arm plate (Fig. 4B) with large, well-defined vertebral articulation in dorso-proximal corner, with clearly depressed center; inner distal edge of lateral arm plate very weakly elevated and separated from remaining outer surface by low, moderately well-defined vertical ridge; large, moderately-defined tubercle notch distally sharply bordered by ridge of elevated distal edge; ventral edge of lateral arm plate without incision for tentacle notch but with five small, poorly-defined, nearly equidistant and equal-sized ambulacral groove spine articulations.

Paratype (supplements)

NRM PAL Ec38328 (Fig. 4C–D) is a dissociated median to distal lateral arm plate approximately 1.4 times as long as high; outline, outer surface ornamentation and spine articulations as in holotype; ventral edge with only four protrusions of ambulacral groove spine articulations.

Remarks

The lateral arm plates of *Ophiolofsson immolation* gen. et sp. nov. can be distinguished from their congeners by the fine outer surface tuberculation combined with three small, inconspicuous lateral arm spine articulations in a vertical row along the entire distal plate edge.

Occurrence

Tjälderviken and Filehajdar.

Ophiolofsson archspire gen. et sp. nov.

urn:lsid:zoobank.org:act:6613A01F-46C2-4E99-A187-A34C2199E3C5

Figs 4E–J, 7

Diagnosis

Species of *Ophiolofsson* gen. nov. with lateral arm plates showing very coarse, widely spaced tubercles on the outer surface, arranged in loose vertical rows; four relatively small lateral spine articulations along the entire distal plate portion; ambulacral groove spine articulations absent or very small and almost indiscernible; very shallow tentacle notch incision in ventral edge of median and distal lateral arm plates.

Etymology

Species named after Canadian, technical death metal band, Archspire, in recognition of their transcendent form of this music style while simultaneously building on the tradition formed by the progenitor bands.

Type material

Holotype

SWEDEN • Gotland, Lau Backar; NRM PAL Ec38330.

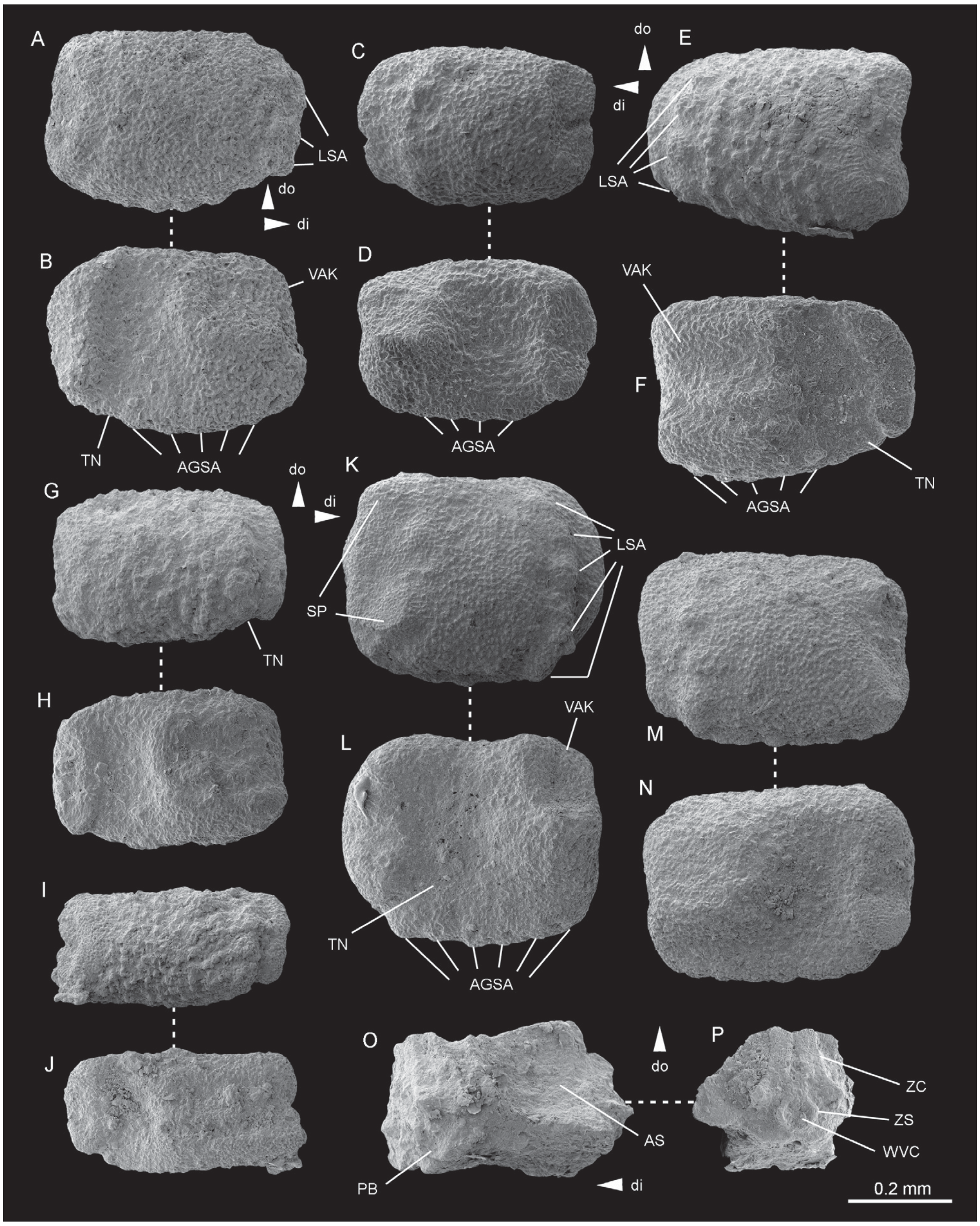

Fig. 4. Dissociated lateral arm plates and vertebra of ophiuroids from the Silurian of Gotland. **A–B**. *Ophiolofsson immolation* gen. et sp. nov., holotype, NRM PAL Ec38328, proximal lateral arm plate in external (A) and internal (B) views. **C–D**. *O. immolation*, paratype, NRM PAL Ec38329, median to distal lateral arm plate in external (C) and internal (D) views. **E–F**. *Ophiolofsson archspire* gen. et sp. nov., holotype, NRM PAL Ec38330, proximal lateral arm plate in external (E) and internal (F) views. **G–H**. *O. archspire*, paratype, NRM PAL Ec38331, median lateral arm plate in external (G) and internal (H) views. **I–J**. *O. archspire*, paratype, NRM PAL Ec38332, distal lateral arm plate in external (I) and internal (J) views. **K–L**. *Ophiolofsson hendersonorum* gen. et sp. nov., holotype, NRM PAL Ec38333, proximal lateral arm plate in external (K) and internal (L) views. **M–N**. *O. hendersonorum*, paratype, NRM PAL Ec38334, median to distal lateral arm plate in external (M) and internal (N) views. **O–P**. *O. hendersonorum*, paratype, NRM PAL Ec38335, vertebra in lateral (O) and distal (P) views. Abbreviations: AGSA = ambulacral groove spine articulations; AS = muscle attachment surface; di = distal; do = dorsal; LSA = lateral spine articulations; PB = podial basin; SP = spur; TN = tentacle notch; VAK = vertebral articular knob;WVC = water vessel canal; ZC = zygocondyle; ZS = zygosphene.

Paratypes

SWEDEN • 2 specs: same data as for holotype; NRM PAL Ec38331, NRM PAL Ec38332.

Type locality and stratum

Ludlow Series, Ludfordian Stage, uppermost part of the Lower Icriodontid conodont subzone sensu Jeppsson (2005), Eke Formation; Lau Backar, Gotland, Sweden.

Description

Holotype (Fig. 4E–F)

NRM PAL Ec38330 is a small dissociated proximal lateral arm plate approximately 1.2 times as long as high, of rounded general aspect, with weakly convex dorsal and ventral edges and strongly convex distal edge; proximal edge weakly concave, with rounded dorsal and ventral edges, and with poorly defined, central depression encompassed by broad band of more finely-meshed stereom along proximal plate edge; outer surface with very coarse, widely-spaced tuberculation composed of enlarged trabecular intersections, arranged in loose, vertical rows and covering entire outer surface except for band of more finely-meshed stereom at proximal edge; four relatively small lateral arm spine articulations in vertical row at some distance from distal edge, equidistant, two central spine articulations largest; spine articulations poorly defined, rugose but strongly prominent, with small, inconspicuous central opening; ventralmost spine articulation at ventral edge of lateral arm plate; dorsalmost spine articulation close to dorsal plate edge; ventral edge of lateral arm plate without protrusions for ambulacral groove spine articulations. Inner side of lateral arm plate (Fig. 4F) with large, well-defined, weakly prominent, laterally elongate vertebral articular knob with large, shallow central depression; inner side of distal edge with two large, weakly prominent and poorly defined spurs; relatively large, deep and well-defined tentacle notch; ventral edge of lateral arm plate without incision for tentacle notch but with five small and vaguely visible ambulacral groove spine articulations.

Paratype supplements and variation

NRM PAL Ec38331 (Fig. 4G–H) is a small dissociated median lateral arm plate approximately 1.3 times as long as high; in agreement with holotype but with less strongly concave proximal edge; lateral arm spine articulations as in holotype; ventral edge with very weak incision for tentacle notch. Inner side of lateral arm plate as in holotype but with larger central depression in vertebral articular knob.

NRM PAL Ec38332 (Fig. 4I–J) is a small dissociated distal lateral arm plate approximately 1.5 times as long as high; dorsal and ventral edges very weakly convex to almost straight; proximal edge almost straight; outer surface as in holotype; three lateral arm spine articulations as in holotype, nearly equal-sized; ventral edge with very small incision for tentacle notch. Inner side with large, laterally elongate vertebral articular knob with large central depression; tentacle notch relatively large; ambulacral groove spine articulations invisible.

Remarks

The lateral arm plates of *Ophiolofsson archspire* gen. et sp. nov. stand out in having very coarse, widely-spaced outer surface tubercles arranged in loose vertical rows. It furthermore differs from its congeners in lacking clearly discernible ambulacral groove spine articulations and in showing a very weak tentacle notch incision in median to distal lateral arm plates.

Occurrence

Lau Backar and Gannor.

Ophiolofsson hendersonorum gen. et sp. nov.

urn:lsid:zoobank.org:act:A24BEBB4-3C6C-4E9F-93F1-2340AE5B416D
Figs 4K–P, 7

Diagnosis

Species of *Ophiolofsson* gen. nov. with lateral arm plates of rounded rectangular outline; outer surface with a moderately coarse, dense tuberculation; outer proximal edge with two spurs, a ventral one with an even surface and a smaller dorsal one with a convex, knob-like surface; up to five relatively small but prominent lateral spine articulations arranged in a continuous row along the entire distal plate edge; up to six large, conspicuous, protruding ambulacral groove spine articulations along the ventral plate edge.

Etymology

Species named after the Canadian couple, Tim and Sephora Henderson, for their work with the influential and pioneering metal music outlet, BraveWords.

Type material

Holotype

SWEDEN • Gotland, Lau Backar; NRM PAL Ec38333.

Paratypes

SWEDEN • 2 specs; same data as for holotype; NRM PAL Ec38334, NRM PAL Ec38335.

Type locality and stratum

Ludlow Series, Ludfordian Stage, uppermost part of the Lower Icriodontid conodont subzone sensu Jeppsson (2005), Eke Formation; Lau Backar, Gotland, Sweden.

Description

Holotype (Fig. 4K–L)
NRM PAL Ec38333 is a large dissociated proximal lateral arm plate, almost as high as long, with weakly concave dorsal edge, weakly convex ventral edge and strongly convex distal edge; proximal edge irregularly convex, with a central depression ventro-distally bordered by large, prominent and well-defined oval spur (SP) with even surface, and dorso-distally by smaller, prominent but poorly-defined spur with convex surface; outer surface with moderately coarse tuberculation except in depressed area of outer proximal edge; five relatively small, equidistant lateral spine articulations, extending from dorsal to ventral plate edge, with weak dorsal decrease in size; ventral edge devoid of incision but with six protrusions for ambulacral groove spines articulations. Inner side of lateral arm plate (Fig. 4L) with large, prominent, poorly defined vertebral articular knob in dorso-proximal corner of plate, with large, deep central depression; inner distal edge with rounded, bulging dorsal and ventral corners; tentacle notch large but relatively shallow and poorly defined; five large, conspicuous ambulacral groove spine articulations all along ventral plate edge.

Paratype (supplements)
NRM PAL Ec38334 (Fig. 4M–N) is a large dissociated median to distal lateral arm plate approximately 1.3 times as wide as high, well in agreement with holotype but with less strongly convex distal edge; proximal edge with two conspicuous knobs as in holotype; outer surface ornamentation as in holotype; spine articulations similar to those of holotype but only four instead of five; ventral edge with six small, inconspicuous protrusions of ambulacral groove spine articulations. Inner side with large vertebral articular structure; inner distal edge as in holotype but with even surface on ventro-distal edge; six small, poorly defined ambulacral groove spine articulations all along ventral edge; tentacle notch as in holotype.

NRM PAL Ec38335 (Fig. 4O–P) is a dissociated proximal to median vertebra, roughly cylindrical, approximately 1.3 times as long as high and slightly wider than high, with rounded triangular cross section and slightly constricted waist; large, articular surface on proximal part of lateral sides matching vertebral articular knob on inner side of lateral arm plates; water vessel canal entirely enclosed by vertebra; distal face with two large, comma-shaped, prominent, well-defined zygocondyles, dorsalwards converging and with more prominent ventral tip; opening of water vessel canal encompassed by zygosphene.

Remarks

The lateral arm plates of *Ophiolofsson hendersonorum* gen. et sp. nov. differ from those of their congeners in having two characteristic spurs on the outer proximal edge, the ventral one of which shows a conspicuous, even surface, and in having up to five relatively small lateral spine articulations arranged over the entire distal plate edge.

Occurrence

Lau Backar.

Genus ***Ophiopetagno*** Thuy, Eriksson & Numberger-Thuy, 2022

Type species

Ophiopetagno paicei Thuy, Eriksson & Numberger-Thuy, 2022, by original designation.

Diagnosis (modified from Thuy *et al.* 2022)

Ankhurid ophiuroid with relatively thin, slightly arched, elongate lateral arm plates; ventro-proximalwards protruding ventral portion; ventral plate edge with a clear tentacle notch incision and with well-developed ambulacral groove spine articulations; large, prominent lateral spine articulations consisting of a single round opening surrounded by an elevated ring; inner side of lateral arm plates with large, sub-triangular vertebral articular knob; vertebrae roughly cylindrical, with slightly concave waist; lateral sides with deep podial basin distally, and subtriangular articulation surface proximally, matching vertebral articular knob on inner side of lateral arm plates; distal side with large, dorsally converging zygocondyles; water vessel canal running entirely within vertebra, distally enclosed by large zygosphene.

Other species included

Ophiopetagno bonzo sp. nov., *Ophiopetagno kansas* sp. nov., *Ophiopetagno doro* sp. nov., *Ophiopetagno* sp. 1 and *Ophiopetagno* sp. 2.

Ophiopetagno bonzo sp. nov.

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Figs 5A–D, 7

Diagnosis

Species of *Ophiopetagno* with lateral arm plates showing a weakly convex dorsal edge, a conspicuous, coarse outer surface ornamentation, an oblique distal edge, three relatively small, inconspicuous lateral spine articulations, up to seven small ambulacral groove spine articulations along the entire ventral edge in proximal plates, indiscernible in median to distal plates.

Etymology

Species named after John H. Bonham (RIP), also known as ‘Bonzo’, former drummer of rock band Led Zeppelin, for raising drumming in rock music to a new level.

Type material

Holotype

SWEDEN • Gotland, Nyhamn; NRM PAL Ec38336.

Paratype

SWEDEN • 1 spec.; same data as for holotype; NRM PAL Ec38337.

Type locality and stratum

Llandovery Series, Telychian Stage, *Pterospathodus amorphognathoides* conodont Zone, Lower Visby Formation (units a and b); Nyhamn, Gotland, Sweden.

Description

Holotype (Fig. 5A–B)
NRM PAL Ec38336 is a dissociated proximal lateral arm plate nearly two times as long as high, relatively thin, with weakly concave dorsal edge, oblique, convex distal edge and irregularly concave proximal edge, pinnacled and lined by narrow band of more finely meshed stereom; ventral portion very long, weakly protruding ventro-proximalwards, with evenly convex ventral edge with seven weak protrusions for ambulacral groove spine articulations and small, shallow tentacle notch incision; outer surface with conspicuous, coarse tuberculation consisting of trabecular intersections transformed into irregularly-sized, prominent knobs, covering entire outer surface except for narrow band along proximal edge and stereom distally bordering spine articulations; four relatively small, inconspicuous lateral spine articulations composed of round opening surrounded by elevated, irregular ring, superficially similar to outer surface tubercles, equal-sized, arranged in continuous row along entire distal plate edge. Inner side of lateral arm plate (Fig. 5B) with large, oval to rounded triangular, well-defined but weakly prominent vertebral articular surface at some distance from inner dorso-proximal corner and separated from inwards protruding dorsal edge; tentacle notch small, deep, moderately well-defined, with shallow incision in ventral edge; seven small ambulacral groove spine articulations along entire ventral edge.

Paratype (supplements)
NRM PAL Ec38337 (Fig. 5C–D) is a dissociated median to distal lateral arm plate approximately 2.2 times as long as high, well in agreement with holotype except for straight to very weakly convex dorsal edge and ventral edge devoid of discernible ambulacral groove spine protrusions; three lateral spine articulations similar to those of holotype. Vertebral articular ridge on inner side longer and better defined than that of holotype; ambulacral groove spine articulations not clearly discernible; tentacle notch incision better defined than in holotype.

Remarks

The lateral arm plates of *Ophiopetagno bonzo* sp. nov. differ from those of all other species in having a conspicuous, coarse outer surface tuberculation. Similarities are most notable with the single unnamed lateral arm plate of *Ophiopetagno* sp. 2 from Hoburgen (see below), especially because of the outer surface ornamentation in *O. bonzo*. However, the dorsal edge is weakly convex rather than concave, the distal edge is oblique, the lateral spine articulations are smaller and almost indiscernible, and there are up to seven ambulacral groove spine articulations only in proximal lateral arm plates.

Occurrence

Nyhamn.

Ophiopetagno kansas sp. nov.

urn:lsid:zoobank.org:act:50FC1EAE-EDFA-4383-B0CF-40A185EA421F

Figs 5E–J, 7

Diagnosis

Species of *Ophiopetagno* with lateral arm plates of oval general outline, with a clearly convex dorsal edge, a fine outer surface tuberculation, and three small, weakly prominent lateral spine articulations in a continuous row.

Etymology

Species named after American rock band Kansas, for producing some of the most inspiring songs in the history of rock music, including 'Carry On Wayward Son' and 'Dust in the Wind'.

Type material

Holotype

SWEDEN • Gotland, Tjälderviken; NRM PAL Ec38338.

Paratypes

SWEDEN • 2 specs; same data as for holotype; NRM PAL Ec38339, NRM PAL Ec38340.

Type locality and stratum

Wenlock Series, Whitwell Stage, *Ozarkodina sagitta sagitta* conodont Zone, Slite Group (upper part – "*Pentamerus gothlandicus* beds" or equivalents); Tjälderviken, Gotland, Sweden.

Description

Holotype (Fig. 5E–F)

NRM PAL Ec38338 is a dissociated proximal lateral arm plate nearly two times as long as high, relatively thin, with weakly convex dorsal edge, strongly convex distal edge and angular concave proximal edge, lined by pinnacled band of more finely-meshed stereom followed by elevated band of more coarsely-meshed stereom showing weak horizontal striation; ventral portion long, weakly protruding ventro-proximalwards, with evenly convex ventral edge with five weak protrusions for ambulacral groove spine articulations and small, moderately deep tentacle notch incision; outer surface with fine tuberculation covering entire outer surface except for double band along proximal edge; three relatively small, prominent, freestanding lateral spine articulations composed of round opening surrounded by elevated, irregular ring, roughly equal-sized, arranged in continuous row along entire distal plate edge, distally bordered by very broad, low and relatively thin shelf. Inner side of lateral arm plate (Fig. 5F) with large, rounded triangular, well-defined and prominent vertebral articular surface at some distance from inner dorso-proximal corner and separated from inwards-protruding dorsal edge; tentacle notch relatively wide, deep, moderately well-defined, with incision in ventral edge; five to six small ambulacral groove spine articulations along entire ventral edge.

Paratype (supplements)

NRM PAL Ec38339 (Fig. 5G–H) is a dissociated median lateral arm plate approximately 2.1 times as long as high, similar to holotype but devoid of clearly discernible ambulacral groove spine protrusions along ventral edge; three lateral spine articulations similar to those of holotype but smaller. Vertebral articular ridge on inner side longer and in more ventral position than that of holotype; ambulacral groove spine articulations not clearly discernible.

NRM PAL Ec38340 (Fig. 5I–J) is a dissociated distal lateral arm plate almost three times as long as high, with straight dorsal and ventral edges; no ambulacral groove spine articulations discernible along ventral edge; three spine articulations as in holotype. Vertebral articular ridge on inner side longer and more prominent than that of holotype; tentacle notch deeper and more sharply defined.

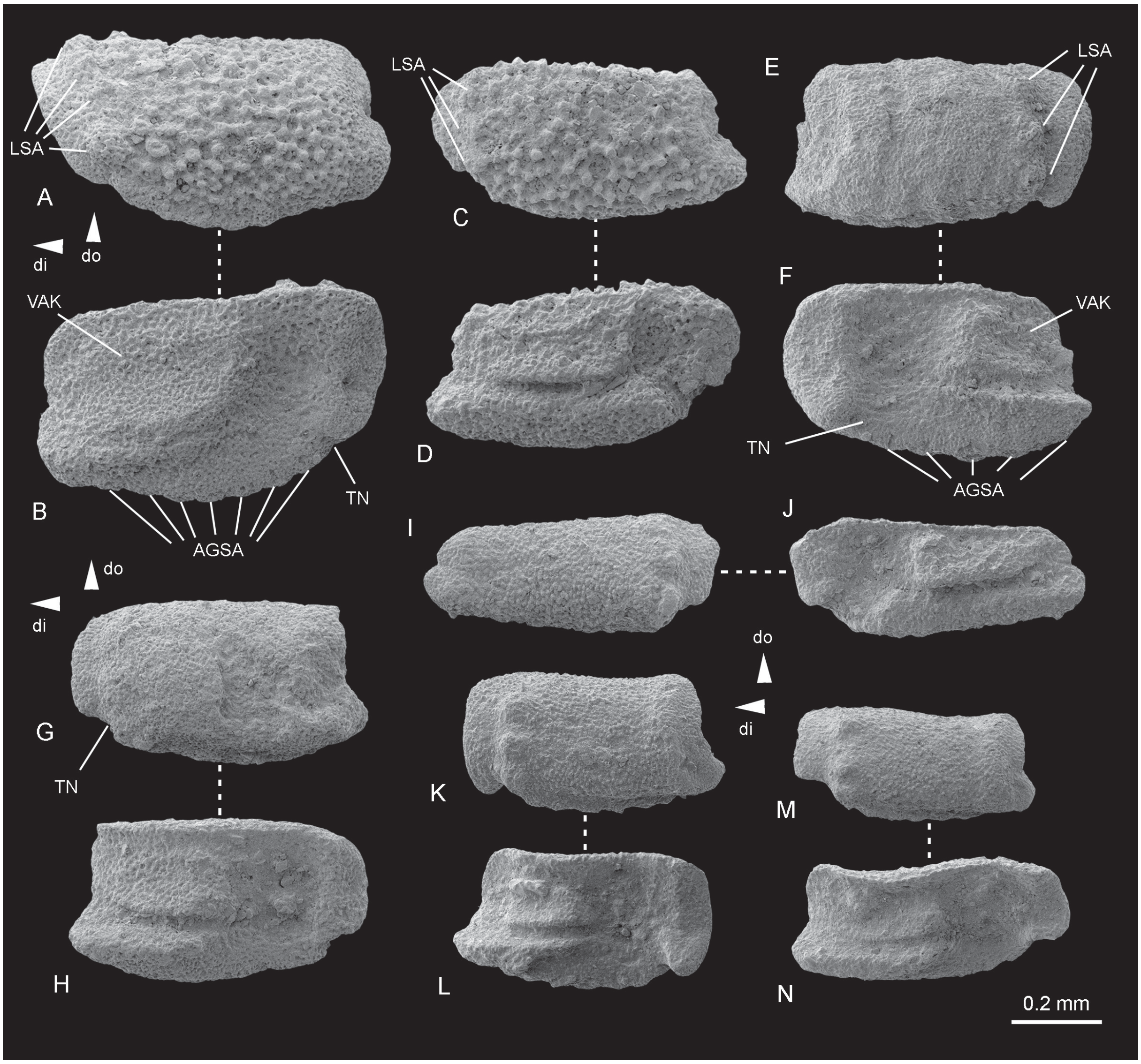

Fig. 5. Dissociated lateral arm plates of ophiuroids from the Silurian of Gotland. **A–B**. *Ophiopetagno bonzo* sp. nov, holotype, NRM PAL Ec38336, proximal lateral arm plate in external (A) and internal (B) views. **C–D**. *O. bonzo*, paratype, NRM PAL Ec38337, median to distal lateral arm plate in external (C) and internal (D) views. **E–F**. *Ophiopetagno kansas* sp. nov, holotype, NRM PAL Ec38338, proximal lateral arm plate in external (E) and internal (F) views. **G–H**. *O. kansas*, paratype, NRM PAL Ec38339, median lateral arm plate in external (G) and internal (H) views. **I–J**. *O. kansas*, paratype, NRM PAL Ec38340, distal lateral arm plate in external (I) and internal (J) views. **K–L**. *Ophiopetagno paicei* Thuy, Eriksson & Numberger-Thuy, 2022, from Thuy *et al*. (2022), proximal lateral arm plate in external (K) and internal (L) views. **M–N**. *O. paicei*, from Thuy *et al*. (2022), distal lateral arm plate in external (M) and internal (N) views. Abbreviations: AGSA = ambulacral groove spine articulations; di = distal; do = dorsal; LSA = lateral spine articulations; TN = tentacle notch; VAK = vertebral articular knob.

Remarks

Among the species of *Ophiopetagno* that have a fine outer surface tuberculation of the lateral arm plates, *Ophiopetagno kansas* sp. nov. stands out in having lateral arm plates with an overall oval outline with a clearly convex dorsal edge, and much smaller and less conspicuous lateral spine articulations.

Occurrence

Tjälderviken.

Ophiopetagno paicei Thuy, Eriksson & Numberger-Thuy, 2022

Figs 5K–N, 7

Diagnosis (emended from Thuy *et al.* 2022)

Species of *Ophiopetagno* with lateral arm plates showing a concave dorsal edge, fine outer surface tuberculation, a deep tentacle notch incision, three relatively large, prominent lateral spine articulations in a continuous row, and ambulacral groove spine articulations in a continuous row along the entire ventral edge with a weak offset from the latter.

Remarks

Ophiopetagno paicei was described by Thuy *et al.* (2022) as part of the species pair shown to be at the origin of the modern ophiuroid clade. The lateral arm plates of *O. paicei* differ from those of its congeners described herein in having a concave dorsal edge and three relatively large spine articulations in a continuous row along the distal plate edge.

Ophiopetagno doro sp. nov.

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Figs 6A–F, 7

Diagnosis

Species of *Ophiopetagno* with lateral arm plates showing a weakly convex dorsal edge, a conspicuously oblique proximal edge with a proximalwards pointing ventro-proximal tip, a moderately coarse outer surface ornamentation, three large, prominent lateral spine articulations showing a gap between the dorsal and the median articulation, and a row of ambulacral groove spine articulations with a sharp offset with respect to the ventral edge.

Etymology

Species named after heavy metal singer Dorothee Pesch, also known as 'Doro', to honor her commitment, musical career and role as a pioneer and gate opener for female vocalists in metal music.

Type material

Holotype

SWEDEN • Gotland, Petsarve; NRM PAL Ec38341.

Paratypes

SWEDEN • 2 specs; same data as for holotype; NRM PAL Ec38342, NRM PAL Ec38343.

Type locality and stratum

Ludlow Series, Ludfordian Stage, Upper Icriodontid conodont subzone sensu Jeppsson (2005), Eke Formation, upper part; Petsarve, Gotland, Sweden.

Description

Holotype (Fig. 6A–B)
NRM PAL Ec38341 is a dissociated proximal lateral arm plate approximately 1.7 times as long as high, relatively thin, with weakly concave dorsal edge, convex distal edge and oblique proximal edge showing proximalwards protruding ventro-proximal tip and lined by shallow groove followed by slightly raised band of more finely-meshed stereom; ventral portion long, weakly protruding ventro-proximalwards, with weakly convex ventral edge with four slightly protruding protrusions for ambulacral groove spine articulations lined by sharp offset along ventral edge, and small, deep tentacle notch incision; outer surface with moderately fine tuberculation covering entire outer surface except for groove and raised band along proximal edge and shelf distally bordering spine articulations; three large, conspicuous and prominent lateral spine articulations composed of round opening surrounded by elevated, relatively regular ring, with dorsalward increase in size and with larger gap between dorsal and middle articulations, separated from distal plate edge by very large shelf. Inner side of lateral arm plate (Fig. 6B) with large, rounded triangular, well-defined and prominent vertebral articular surface in centre of proximal plate portion at some distance from inner dorso-proximal corner and separated from inwards protruding dorsal edge; tentacle notch very large, deep, well-defined, with small but deep incision in ventral edge, proximally bordered by thickened ventro-proximal plate portion; four relatively large but inconspicuous ambulacral groove spine articulations along entire ventral edge.

Paratype (supplements)
NRM PAL Ec38342 (Fig. 6C–D) is a dissociated median lateral arm plate approximately 1.9 times as long as high, similar to holotype but with sharper and more conspicuous offset between row of ambulacral groove spine articulations and ventral plate edge; distalward increase in size of ambulacral groove spine articulations; three lateral spine articulations as in holotype but with larger gap between dorsal and middle spine articulations. Inner side as in holotype.

NRM PAL Ec38343 (Fig. 6E–F) is a dissociated distal lateral arm plate two times as long as high, similar to holotype but with slightly concave dorsal edge, with sharper offset between row of six ambulacral groove spine articulations. Inner side as in holotype.

Remarks

Ophiopetagno doro sp. nov. is characterized by having lateral arm plates with large, conspicuous lateral spine articulations with a marked gap between the dorsal and median ones. It furthermore differs from its congeners in having a strongly oblique proximal edge with a proximalwards pointing ventro-proximal tip.

Occurrence

Petsarve.

Ophiopetagno sp. 1

Figs 6G–H, 7

Material studied

NRM PAL Ec38344.

Description

NRM PAL Ec38344 (Fig. 6G–H) is a dissociated proximal or median lateral arm plate approximately 1.8 times as long as high, with weakly concave dorsal edge, convex distal edge and oblique proximal edge lined by shallow groove; ventral portion long, weakly protruding ventro-proximalwards, with weakly convex ventral edge with central protrusion caused by three ambulacral groove spine articulations; outer surface with very fine tuberculation covering entire outer surface except for groove along proximal edge and shelf distally bordering spine articulations; large, dorsally rounded, moderately well-defined elevation in middle of outer surface; three small, inconspicuous lateral spine articulations directly at

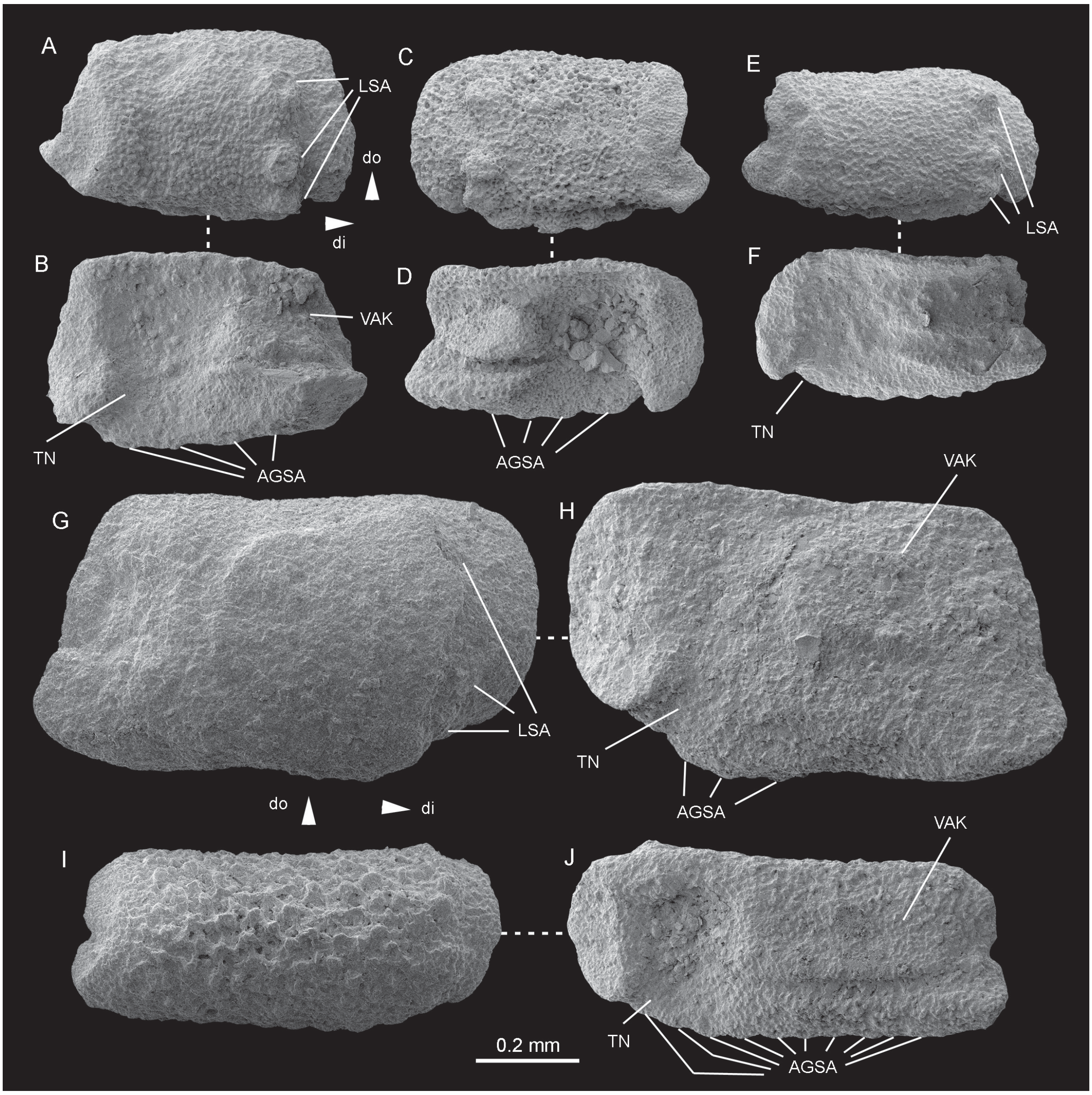

Fig. 6. Dissociated lateral arm plates of ophiuroids from the Silurian of Gotland. **A–B**. *Ophiopetagno doro* sp. nov, holotype, NRM PAL Ec38341, proximal lateral arm plate in external (A) and internal (B) views. **C–D**. *O. doro*, paratype, NRM PAL Ec38342, median lateral arm plate in external (C) and internal (D) views. **E–F**. *O. doro*, paratype, NRM PAL Ec38343, distal lateral arm plate in external (E) and internal (F) views. **G–H**. *Ophiopetagno* sp. 1, NRM PAL Ec38344, proximal to median lateral arm plate in external (G) and internal (H) views. **I–J**. *Ophiopetagno* sp. 2, NRM PAL Ec38345, median to distal lateral arm plate in external (I) and internal (J) views. Abbreviations: AGSA = ambulacral groove spine articulations; di = distal; do = dorsal; LSA = lateral spine articulations; TN = tentacle notch; VAK = vertebral articular knob.

distal edge of central elevation on outer surface, with larger gap between dorsal and middle articulations, separated from distal plate edge by very large shelf. Inner side of lateral arm plate (Fig. 6H) with large, oval to rounded triangular vertebral articular surface in center of proximal plate portion at some distance from inner dorso-proximal corner and separated from slightly inwards protruding dorsal edge; tentacle notch small, shallow but well-defined, with small but deep incision in ventral edge; three small, inconspicuous ambulacral groove spine articulations grouped in protruding part of ventral plate edge proximally bordering tentacle notch.

Remarks

The single lateral arm plate described herein as *Ophiopetagno* sp. 1 differs from those of its congeners in being much larger, having a very fine outer surface ornamentation and a central elevation, very small, inconspicuous lateral spine articulations, and ambulacral groove spine articulations reduced to a group on a protrusion of the ventral edge. The lateral arm plate in question clearly belongs to a new species but in the absence of more material allowing for assessment of the intraspecific variability, we refrain from formally naming it.

Occurrence

Hoburgen.

Ophiopetagno sp. 2
Figs 6I–J, 7

Material studied

NRM PAL Ec38345.

Description

NRM PAL Ec38345 (Fig. 6I–J) is a dissociated median or distal lateral arm plate approximately 2.5 times as long as high, with weakly concave dorsal edge, convex distal edge and oblique proximal edge lined by shallow groove followed by very narrow band of more finely-meshed stereom; ventral portion long, weakly protruding ventro-proximalwards, with very weakly convex ventral edge lined by at least ten ambulacral groove spine articulations; outer surface with conspicuously coarse tuberculation covering entire outer surface except for groove along proximal edge and shelf distally bordering spine articulations, and consisting of trabecular intersections transformed into irregular, widely spaced tubercles; three moderately large lateral spine articulations, nearly equal-sized and equidistant along entire distal plate edge, separated from latter by relatively short shelf. Inner side of lateral arm plate (Fig. 6J) with very large, well-defined, prominent, rounded triangular vertebral articular surface in center of proximal plate portion at some distance from inner dorso-proximal corner and separated from slightly inwards protruding dorsal edge; tentacle notch large, shallow but well-defined, with large, shallow incision in ventral edge; at least ten small but well-developed ambulacral groove spine articulations along entire ventral plate edge.

Remarks

The single lateral arm plate described as *Ophiopetagno* sp. 2 stands out in having a very coarse outer surface ornamentation. In this respect, it bears a superficial similarity to the lateral arm plates of *O. bonzo* sp. nov. The latter, however, show a conspicuously oblique distal edge, smaller lateral spine articulations and fewer ambulacral groove spine articulations. In the absence of more specimens, we cannot assess the morphological variability of *Ophiopetagno* sp. 2 and therefore refrain from describing it formally as a new species.

Occurrence

Hoburgen.

Clade **Ophiovalida** clade nov.

Diagnosis

Ankhurid ophiuroids with the water vessel canal at least partially open and with lateral arm plates devoid of ambulacral groove spines.

Etymology

From 'validus', Latin for 'valid, strong', because the node in question represents the origin of the modern ophiuroid bauplan.

Taxa included

Muldaster haakei, *Ophiurina lymani* Stürtz, 1890 and all members of the clade Myophiuroidea.

Remarks

We introduce the new clade name Ophiovalida clade nov. to designate the key node in the evolution of ophiuroids marked by two major skeletal innovations, 1) partial opening of the water vessel canal and 2) the loss of ambulacral groove spines. The node in question is exceptionally well-studied in terms of stratigraphic dating, phylogenetic signal and paleoenvironmental context (Thuy *et al.* 2022). Specifically, it marks the transition between two temporally consecutive species, *Ophiopetagno paicei* and *Muldaster haakei*. Given its significance as the 'moment of birth' of the modern ophiuroids, we decided to name the clade bound to this specific node.

Genus ***Muldaster*** Thuy, Eriksson & Numberger-Thuy, 2022

Type and only known species

Muldaster haakei Thuy, Eriksson & Numberger-Thuy, 2022, by original designation.

Diagnosis (modified from Thuy *et al.* 2022)

Ophiovalid (see above) ophiuroid with very small, strongly elongate and weakly constricted lateral arm plates, with protruding ventral portion distally incised by tentacle notch; two closely spaced lateral arm spine articulations each composed of single opening surrounded by elevated ridge; inner side of lateral arm plates with lacking bulges, perforations and other traces of groove spine articulations; vertebrae bone shaped, with strongly concave waist. Large, coarsely tuberculated zygocondyles on distal side of vertebrae merged into hourglass-shaped knob; water vessel canal enclosed by distal third and proximal quarter of vertebra, exposed at waist of vertebral body running in shallow furrow. Articulated arm segments with lateral arm plates meeting along ventral midline, exposing podial basins ventrally and vertebrae dorsally; arm spines short, conical, pointed; dorsal and ventral arm plates absent.

Discussion

The assessment of the ophiuroid fossil record is still heavily biased towards exceptional finds of intact skeletons. Since the latter are restricted to highly specific taphonomic conditions (Donovan 1991), a vast array of ophiuroid taxa remain overlooked or inaccessible (e.g., Thuy *et al.* 2022, 2023). The present study corroborates previous evidence that this bias can be overcome by considering dissociated skeletal plates that are much more common and widespread in the fossil record than intact skeletons.

The microfossils we describe herein not only revealed dwarfing in ophiuroids from the Silurian of Gotland, Sweden, in correlation with three successive extinction events, with the strongest body size decrease entailing skeletal modifications typical of modern ophiuroids, as shown in a previous study (Thuy *et al.* 2022). They furthermore added an entire new lineage to the ophiuroid fossil record,

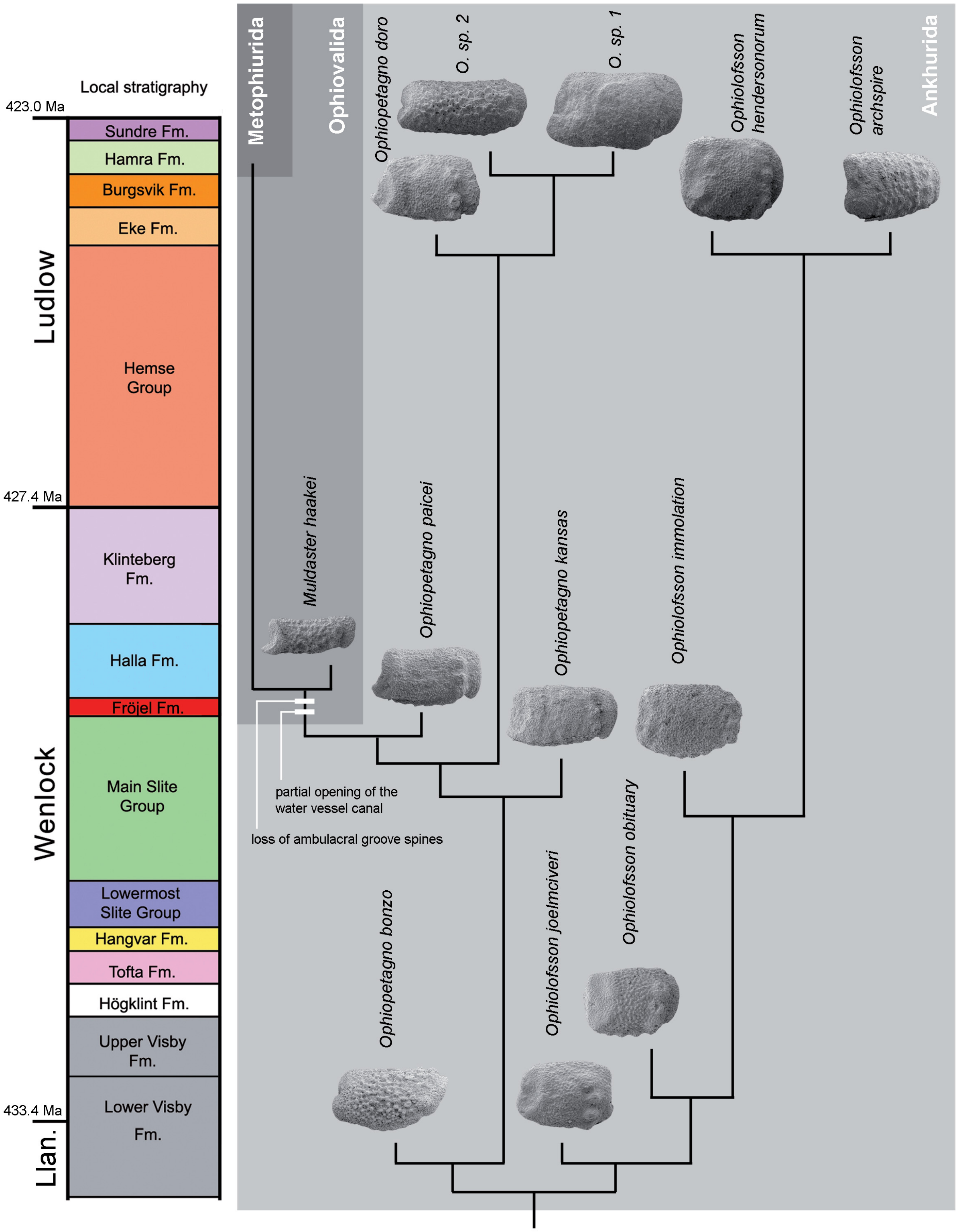

Fig. 7. Stratigraphic position of the taxa described in the present paper with their assumed evolutionary relationships and the nesting of the clades Ankhurida clade nov., Ophiovalida clade nov. and Metophiurida Matsumoto, 1913. Note that some lateral arm plates are mirrored to allow comparison in similar orientation.

representing the stem members of the extant clade and including three new genera and 12 new species in total, thus increasing the number of ophiuroid taxa known from the Silurian significantly.

While the key taxa that allowed constraining the origin of the extant ophiuroid clade, i.e., *Ophiopetagno paicei* and *Muldaster haakei*, were described previously (Thuy *et al.* 2022). Here, we describe the remaining taxa belonging to that same lineage. The evidence presented herein suggests that the stem of the extant ophiuroid clade was formed by two genera, *Ophiopetagno* and *Ophiolofsson* gen. nov., including six and five species, respectively, and spanning at least the upper Llandovery through the upper Ludlow (Fig. 7). The two genera are morphologically similar, suggesting close phylogenetic ties. We assess that *Ophiopetagno* and *Ophiolofsson* represent sister genera that coexisted through most of the Silurian in the shallow tropical seas of Gotland and underwent repeated body size reductions in correlation with environmental perturbations. Previously published phylogenetic evidence shows that during one of these perturbations, the *Ophiopetagno* lineage gave rise to *Muldaster haakei*, the oldest known member of the extant ophiuroid clade (Thuy *et al.* 2022).

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