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RESEARCH PAPER

A new alcyonacean octocoral (Anthozoa) from the Late Silurian of Gotland, Sweden

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Abstract

A new species and genus of stem-group 'soft corals' (Anthozoa: Octocorallia: Alcyonacea) is described and illustrated in detail, as well as compared to other species of the sparse octocorallian fossil record. *Sueciatractos leipnitzae* gen. et sp. nov. has been collected from the Upper Silurian Hemse beds of the Isle of Gotland, Sweden. The new taxon differs from all other taxa by its unique form of sclerites which were fused at first glance, but stacked compactly, densely packed aggregates forming a nearly solid skeleton or former supporting layers in part. *Sueciatractos* is compared with other fossil octocoral species that were known by microscopic/mesoscopic sclerites.

Keywords Anthozoa · Octocorallia · Alcyonacea · Silurian · New taxa · Gotland · Sweden

Introduction

Silurian times witnessed one of the most concentrated intervals of reefal development in earth's history, based in large part on tabulate and rugose coral as well as stromatoporoid assemblages (Zapalski and Berkowski 2019). However, the Palaeozoic/Mesozoic fossil record of other anthozoan cnidarians, such as octocorals, is more than sparse (e.g. Reich 2007, 2009; Fernández-Martínez et al. 2018, 2019). In particular, pre-Ordovician octocorallian taxa are heavily debated (*Echmatocrinus*—Ausich and Babcock 1998; Reich 2007, 2009 versus Sprinkle and Collins 1998; *Pywackia*—Taylor et al. 2013 versus Landing et al. 2015), which is in contrast to the time-calibrated trees published recently by Quattrini et al. (2020) and McFadden et al. (2021), where the origin of octocorals was placed in the Ediacaran period. In addition, just recently also the group of Devonian/Carboniferous Heterocorallia has been discussed as putative Octocorallia (Berkowski et al. 2021).

The Silurian octocoral *Atractosella* (with three named species), although previously misidentified as sponge scleres (Hinde 1887, 1888; Bengtson 1979), echinoid spines (Regnéll 1956) and ostracoderm fish (Lamont 1978), is widespread and has been found in England (Hinde 1887, 1888), Scotland (Stewart et al. 2007; Candela and Crighton 2019), Sweden (Regnéll 1956; Bengtson 1979, 1981a, b; Brood 1981, 1982), Estonia (Hints et al. 2022) and the bottom of the Baltic Sea (Reich 2000, 2002).

Other Palaeozoic octocorallian anthozoans include *Nonnegorgonides ziegleri* (Dapingian and Sandbian; Lindström 1971) and *Petilavenula varifurcata* (Floian; Cope 2005) as well as the recently published *Catenatus argentinus* (Floian–Darriwilian; Carrera et al. 2021), *Termieralcyon copperi* (Silurian–Permian; Fernández-Martínez et al. 2019), and *Lafustalcyon vachardi* (Serpukhovian; Denayer et al. 2022).

The aim of this contribution is to report and describe new Silurian octocoral findings, which complement the previously patchy fossil record.

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Geological setting, material and methods

Gotland, situated in the Baltic Sea east of the Swedish coast, consists of Silurian rocks ranging from Telychian to Ludfordian strata (latest Llandovery to latest Ludlow) and are dominated by limestones and marls (e.g. Sandström 1998; Sandström et al. 2021; Fig. 1). Reefs and reefal structures on and around Gotland have been mapped and investigated by several researchers (e.g. Hadding 1941; Manten 1971; Eriksson and Laufeld 1978; Bjerkéus and Eriksson 2001; Flodén et al. 2001; Sandström et al. 2021).

The exact regional and stratigraphic reference data for the Tänglings locality (Fig. 1) can be found in the corresponding papers from Laufeld (1974), Larsson (1979), Stridsberg (1985), Bergman (1989), Copper (2004) and Jeppsson et al. (2006). Tänglings is part of the inland central Hemse reef complex which is unfortunately understudied. The Hemse Group is one of the least understood units of the Gotland Silurian sequence (Sandström et al. 2021). After a transgressive phase around the Wenlock–Ludlow boundary with deposition of marls and little or no reef development, a highstand which favoured extensive reef growth with fringing reefs and stromatoporoid biostromes followed (Sandström et al. 2021).

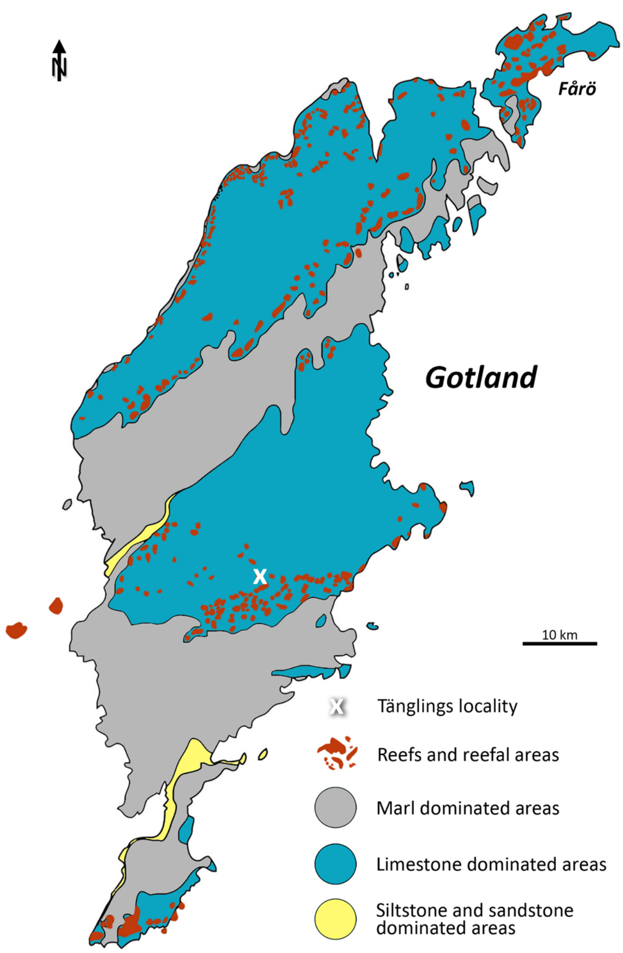

Fig. 1 Map of Gotland showing the major facies distribution of Silurian sediments, including reefs and reefal structures (after Hadding 1941, Manten 1971 etc.; modified from Sandström 1998, Sandström et al. 2021)

The Tänglings locality contains a rich associated fauna of tabulate and rugose corals, stromatoporoids, echinoids, cyclocystoids, brachiopods, trilobites, ostracods, polychaetes, nautiloids, bryozoans, and sponges (Rothpletz 1913; Regnéll 1956; Martinsson 1962; Ramsköld 1983; Bergman 1995; Stridsberg and Turek 1997; Rhebergen 2005; Young and Kershaw 2005; Kutscher 2008; Reich and Kutscher 2010; Holmer et al. 2013) as well as crinoids, paracrinoids, blastozoans, ophiuroids, asteroids, and gastropods (herein).

All studied octocoral specimens were isolated and picked from residues after washing and sieving unlithified reefal rock samples in hot water or tenside solution, using standard techniques (Wissing et al. 1999). The material is derived from samples collected by Manfred Kutscher (Sassnitz), Heilwig Leipnitz (Uelzen), and Mike Reich. The figured and type material is deposited in the State Natural History Museum, Brunswick (*Staatliches Naturhistorisches Museum, Braunschweig*), Germany. Additional material will be stored at the Swedish Museum of Natural History (*Naturhistoriska riksmuseet*), Stockholm, Sweden.

Selected specimens were documented by digital microscopy (Keyence VHX 7000) first, and later coated with gold and studied and photographed using a Phenom XL G2 (ThermoFisher Scientific) scanning electron microscope (SEM) at Brunswick and Munich. The energy-dispersive X-ray spectroscopy (EDS) was also done at the latter SEM.

Institutional abbreviations

SNHMB, Staatliches Naturhistorisches Museum, Braunschweig, Germany; NRM, Naturhistoriska riksmuseet, Stockholm, Sweden.

Systematic palaeontology

The current classification of octocorals is mainly based on the papers and monographs by Wilhelm G. Kükenthal, Sydney J. Hickson and Frederick M. Bayer (see Pérez et al. 2016). Not all of the groups included within the Octocorallia have well-defined synapomorphies, which is why the phylogenies available so far (e.g. Berntson et al. 2001; Won et al. 2001; Sánchez et al. 2003; Park et al. 2012; McFadden et al. 2006, 2021) are not always fully conclusive. However, McFadden et al. (2022) recently revised the higher-level systematics of octocorals, which we follow here.

For terminology of octocoral skeletons and gross morphology used in this study, see Bayer (1956), Bayer et al. (1983), Williams (1993) and Fabricius and Alderslade (2001).

Sub-Phylum **Anthozoa** Ehrenberg, 1834
Class **Octocorallia** Haeckel, 1866
Order **Malacalcyonacea** McFadden, van Ofwegen and Quattrini, 2022
Stem-group **'Alcyoniina'** Lamouroux, 1812

Genus ***Sueciatractos*** nov.

ZooBank LSID. zoobank.org:act:FE717877-0696-4503-A22D-6685D4DE606D.

Type species. Sueciatractos leipnitzae gen. et sp. nov.

Etymology. The generic name is a combination of Latin *Suecia* (Sweden) and Greek *άτρακτος* (spindle), referring to the morphology and the origin of the material.

Diagnosis. Colony growth form and shape of polyps unknown. Taxon probably without skeletal axis. Distinct sclerites of coenenchyme are uniform pointed spindles, somewhat angular (Figs. 2C, 4A–G) and regular stacked (Figs. 2C, 5A–D). These densely packed sclerite aggregates may therefore be part of the former supporting layer.

Remarks and discussion. These specimens show a number of distinctive features, which support the erection of a new genus. *Sueciatractos* gen. nov. differs from all other Palaeozoic alcyonacean (sclerite-bearing) genera (*Atractosella*, Figs. 2A, B, 3A–K; *Catenatus*; *Lafustalcyon*) by the stacked arrangement of sclerites (Fig. 5A–D) as well as by the form and shape of these sclerites (Fig. 4A–G). Only the sclerites of *Termieralcyon* are comparably densely packed as aggregates. However, the *Termieralcyon* sclerite morphotypes described by Fernández-Martínez et al. (2019: fig. 5) are quite distinct in morphology and size from the *Sueciatractos* sclerites described here.

Range. Silurian: Ludlow; Gotland, Sweden.

Sueciatractos leipnitzae sp. nov.
Figures 2C, 4A–G, 5A–D

ZooBank LSID. zoobank.org:act:A25FD6FC-7BB8-4AFA-8B10-0AD86AEFB821.

Material. 102 single sclerites and 71 stacks of sclerites (SNHMB-G.5511–5672), including the holotype (SNHMB-G.5500, Fig. 4A) and paratypes (SNHMB-G.5501, 5502, 5505–5509, Figs. 4B, C, F, G, 5A–C) as well as further figured material (SNHMB-G.5503, 5504, 5510, Figs. 4D, E, 5D).

Locality and horizon. Tänglings, Gotland, Sweden (see Laufeld 1974: 133; Larsson 1979: 179; Stridsberg 1985: 63; Bergman 1989: 127; Copper 2004: 156 and Jeppsson et al. 2006: fig. 1). From the lower part of the Late Silurian Hemse Group; Ludlow: latest Gorstian (or the middle part = 'Etelhem Fm.'; Ludlow: earliest Ludfordian).

Etymology. The species epithet honours Heilwig Leipnitz (*1928; Uelzen, Germany) for her generous palaeontological donations to public museums (and in honour of her 95th birthday this year).

Diagnosis. As for the genus.

Description. Morphology of soft parts like colony shape, branching patterns, polyps, etc., unknown. Coenenchyme sclerites are simple, straight, uniform, spindle-shaped on both sides, and somewhat angular in longitudinal direction (length 1.0–4.0 mm). The sclerites are thickest in the middle, with a diameter of about 0.45–1.0 mm. No obvious, or only slight/smooth surface ornamentation of sclerites (due to the diagenetic overprint; cf. also Majoran 1987), visible (Fig. 4A–G). Sclerites are densely packed aggregates (Figs. 2C, 5A–D) probably of the former inner or outer supporting layer.

All collected sclerites and stacks of sclerites are preserved in the form of low-magnesium calcite (chemical composition identified by EDS analysis). In contrast, modern alcyoniid sclerites are composed of high-magnesium calcite (cf. Conci et al. 2021). However, the preservation of our fossil material as low-magnesium calcite is typical and not surprising due to diagenetic overprinting.

Remarks and discussion. The Telychian/Sheinwoodian/Homerian *Atractosella cataractaca* Bengtson, which is stratigraphically and regionally close, has only loosely embedded sclerites (Fig. 2A, B) that show a typical surface granulation (Figs. 2B, 3A–K) and appear not to be irregularly cemented (like in Pleistocene/Holocene "*Sinularia* spiculites" or "Alcyonarian limestones"; cf. Konishi 1981; Accordi et al. 1989; Schuhmacher 1997; Jeng et al. 2011; Fig. 2F). The morphological variability of the sclerites (bent and branched/multiaxial spindles; Figs. 2B, 3F, K) is also clearly greater in *Atractosella* than in *Sueciatractos* gen. nov. Modern revisions are lacking for the other two *Atractosella* species—the Telychian *A. andreae* (Lamont) and the Homerian *A. siluriensis* Hinde. However, these seem very similar to *A. cataractaca* described from Gotland, Sweden (Bengtson 1981b), the Baltic Sea bedrock (Reich 2002) and


A
10.0 mm
D
B
1.0 mm
E
C
1.0 mm
5.0 mm
F

◀**Fig. 2** **A**, **B** Disintegrated *Atractosella cataractaca* Bengtson, 1981b on a limestone slab (**A**) [SNHMB-G.5673], as well as isolated sclerites (**B**) [SNHMB-G]—Blåhäll/Gotland, Sweden; Mulde Brick-clay Member, Halla Formation; Silurian: Wenlock: Homerian. **C** *Sueciatractos leipnitzae* gen. et sp. nov., isolated sclerites and stacks of densely packed sclerites [SNHMB-G]—Tänglings/Gotland, Sweden; lower part of the Hemse Group; Silurian: Ludlow: latest Gorstian (or the middle part of the Hemse Group = Etelhem Formation; Ludlow: earliest Ludfordian). **D** Modern *Dendronephthya* species normally form upright, branched colonies with a distinct stalk, and showing the only loosely embedded calcareous sclerites—Blue Hole near Dahab/Sinai, Egypt. **E** Modern *Sinularia* colonies are often low, lobed and encrusting, and with cemented internal sclerites at the base—Blue Hole near Dahab/Sinai, Egypt. **F** Partially cemented *Sinularia* sclerites forming an "Alcyonarian limestone"/"*Sinularia* spiculite" [SNHMB-G.5499]—north of Dahab/Sinai, Egypt; Quaternary: Pleistocene

Estonia (Hints et al. 2022). The Serpukhovian *Lafustalcyon vachardi* Denayer et al. and the Silurian–Permian *Termieralcyon copperi* Fernández-Martínez et al. clearly show a different morphology and ornamentation of sclerites, which are not fused, but densely packed (Fernández-Martínez et al. 2019; Denayer et al. 2022).

Modern octocoral species with densely packed sclerite aggregates are known from various clades of the Scleralcyonacea and Malacalcyonacea (see McFadden et al. 2022), whereas species with fused sclerites are known from members of the Clavulariidae, Alcyoniidae and Xeniidae (all Malacalcyonacea), among others (e.g. Bayer 1981, 1995; van Ofwegen and Haddad 2011; Halász et al. 2014).

Discussion

Interpretation of octocoral fossils is often challenging, due to differences in the range of characters (sclerites, axes, etc.) available for study. Nearly all octocorals possess microscopic sclerites, which are found in varying concentrations embedded in the coenenchyme. These calcitic bodies, providing support and protection, around 5.0–0.02 mm in size, are the most important feature used in the identification of octocorals (e.g. Bayer 1956; Bayer et al. 1983; Fabricius and Alderslade 2001). Also, the microstructure as well as the arrangement of the sclerites in the octocoral colonies can be an important taxonomic feature (Aharonovich and Benayahu 2012; Fabricius and Alderslade 2001; McFadden et al. 2022). In addition, there is a co-occurrence of different sclerite types within one species and colony (e.g. Tentori and van Ofwegen 2011). Therefore, it is often difficult to assign isolated fossil sclerites to specific higher-level groups within the Alcyonacea, and other Octocorallia. Our new genus and species described here (*Sueciatractos leipnitzae*) can undoubtedly be assigned to the 'Alcyoniina' (or stem-group 'Alcyoniina'), since the absence of an axis and simple spindle-shaped sclerites are synapomorphies of these.

However, the octocorallian fossil record known so far is very patchy (Reich 2007, 2009). In addition to the Palaeozoic taxa already discussed, there is also Mesozoic

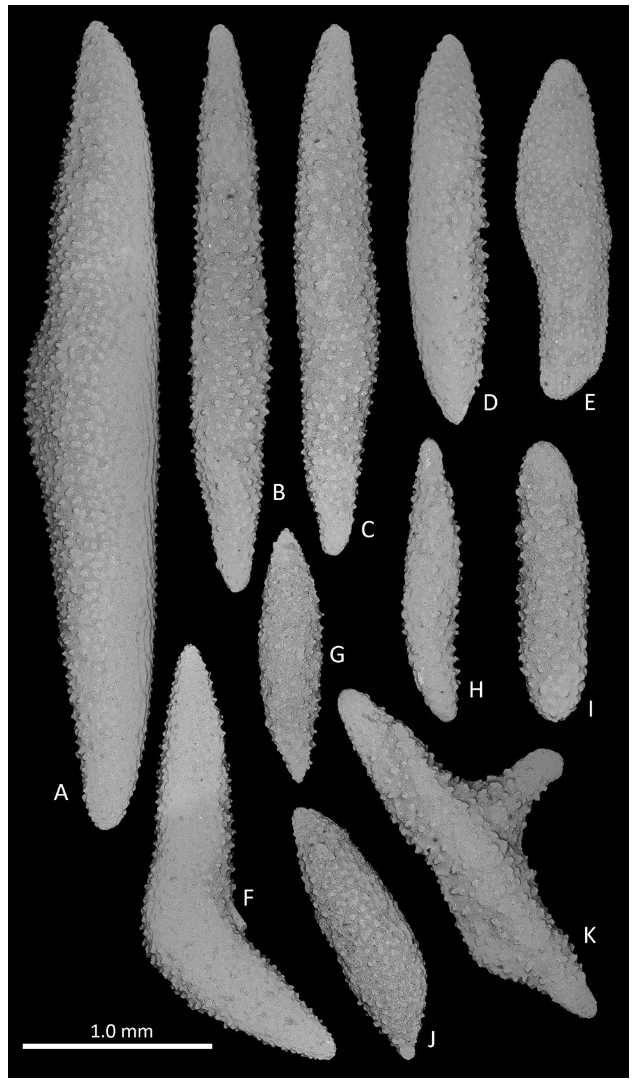

Fig. 3 **A**–**K** Isolated sclerites of *Atractosella cataractaca* Bengtson, 1981b—Blåhäll/Gotland, Sweden; Mulde Brick-clay Member, Halla Formation; Silurian: Wenlock: Homerian. **A**–**E**, **G**–**J** normal sclerites (spindles) of different sizes [SNHMB-G.5674–5678, 5680–5683]; **F** bent spindle [SNHMB-G.5679]; **K** multiaxial sclerite [SNHMB-G.5684]. All SEM images

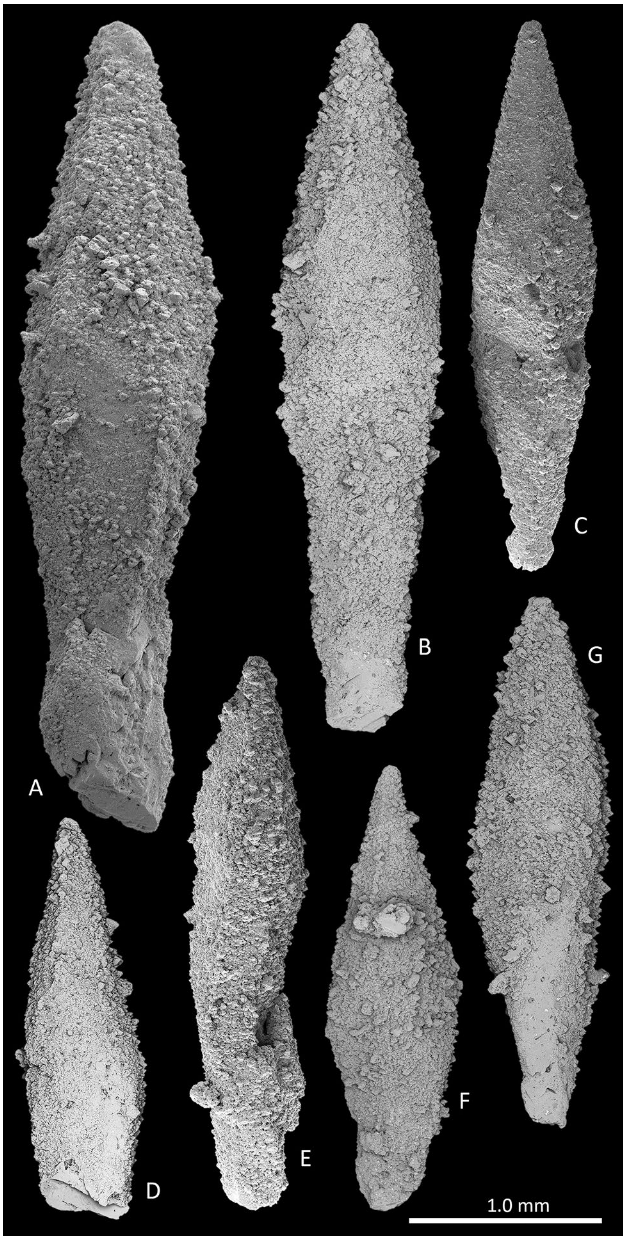

Fig. 4 **A**–**G** Isolated sclerites of *Sueciatractos leipnitzae* gen. et sp. nov. [SNHMB-G.5500–5506]—Tänglings/Gotland, Sweden; lower part of the Hemse Group; Silurian: Ludlow: latest Gorstian (or the middle part of the Hemse Group = Etelhem Formation; Ludlow: earliest Ludfordian). **A** holotype [SNHMB-G.5500]; **B**, **C**, **F**, **G** paratypes [SNHMB-G.5501, 5502, 5505, 5506]; **D**, **E** further specimens [SNHMB-G.5503, 5504]. All SEM images

and Cenozoic evidence. Isolated alcyonacean sclerites (formerly of the Alcyoniina, Holaxonia, Stolonifera, Scleraxonia, Calcaxonia; now Malacalcyonacea and Scleralcyonacea) were mostly recorded from Cretaceous (Počta 1886; Papp 1972; Alexandrowicz 1977; Moosleitner 1990; Herrig et al. 1996; Reich and Frenzel 2002; Reich et al. 2005; Schlagintweit and Gawlick 2009; Frenzel et al. 2014), Paleogene (Hickson 1938; Deflandre-Rigaud 1955, 1956, 1957; Kocurko 1988; Kocurko and Kocurko 1992) and Neogene (Deflandre-Rigaud 1955, 1956, 1957; Kristan-Tollmann 1966; Langer 1989) sediments. Jurassic reports (Hasse 1890; Cayeux 1921) are, unfortunately, still questionable, even if partially articulated octocorals are known from similar strata (Barthel 1978; Heyng and Viohl 2015). Only a few partially articulated finds or larger parts (e.g. holdfasts, axes) of octocorals are also known from later geological periods (e.g. Voigt 1958; Giammona and Stanton jr. 1980; Kocurko 1988; Kocurko and Kocurko 1992; Bayer 1992; Helm and Schülke 2003; Lozouet and Molodtsova 2008; Zuschin and Gebhardt 2009; Löser 2000, 2016).

However, the Permo–Triassic gap of this record is certainly striking. To what extent this is related to the different seawater chemistry (calcite versus aragonite seas) in earth's history remains to be clarified in the future.

Conclusions

This study increases our knowledge on the early evolutionary history and diversification of soft corals and their relatives. Our results show that the Alcyoniina (or stem-group Alcyoniina) was already present with various soft coral skeletal structures in Silurian times, regardless of the large gaps of articulated/isolated alcyonacean sclerite material in the later fossil record.

This group of octocorals complements and increases the biodiversity of stromatoporoid–tabulate/rugose coral associations (and the Anthozoa in general) within the Silurian ecosystems of Gotland, Sweden.

In addition, we continue to believe that the incomplete alcyonacean fossil record is primarily related to examination gaps and the limited number of octocoral palaeontologists, rather than preservational gaps. However, as the primary biomineralization of octocorals is also an important factor of their diversity, more basic and advanced studies on the octocorallian fossil record are urgently needed.

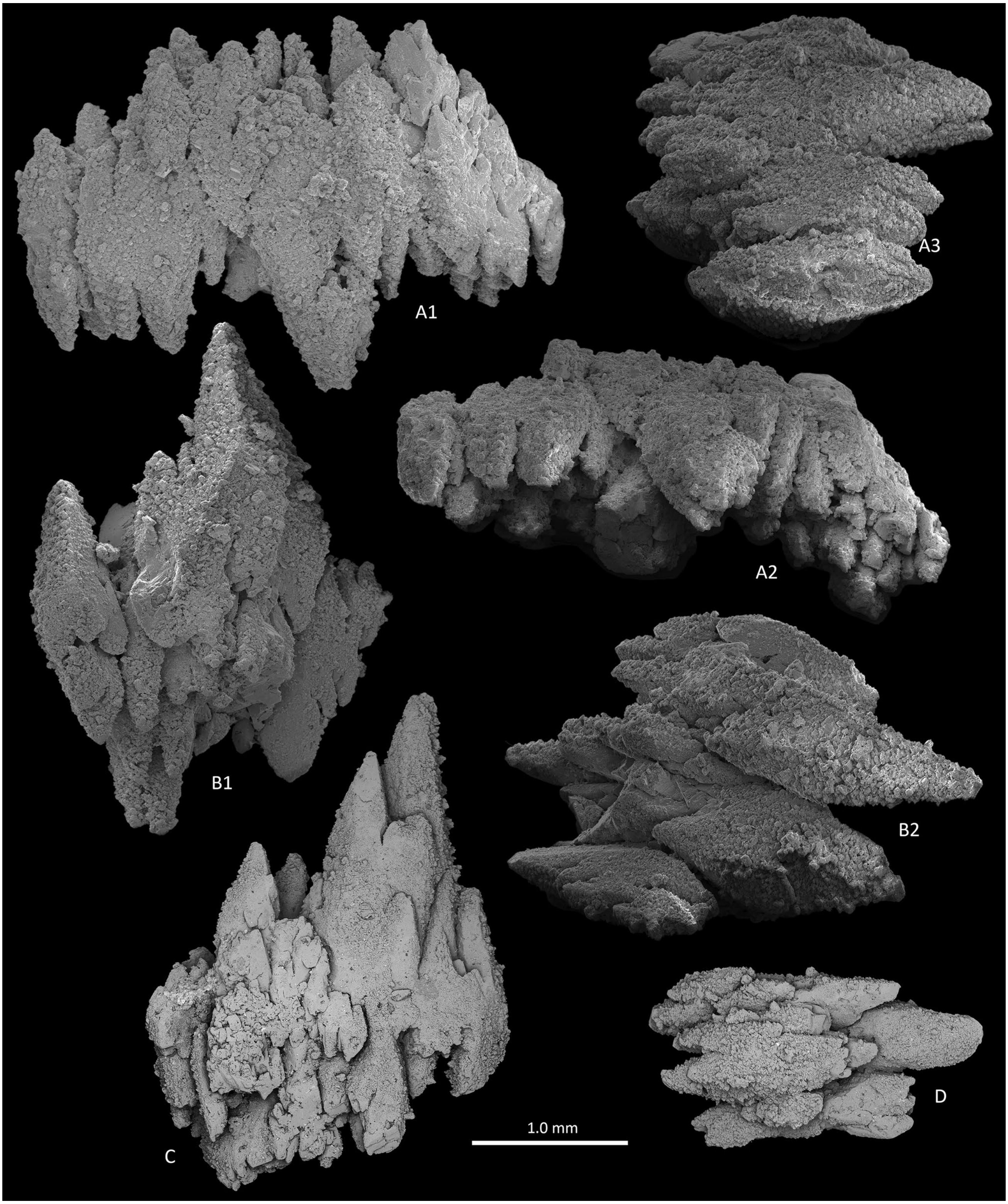

Fig. 5 **A**–**G** Stacks of sclerites of *Sueciatractos leipnitzae* gen. et sp. nov. [SNHMB-G.5507–5510]—Tänglings/Gotland, Sweden; lower part of the Hemse Group; Silurian: Ludlow: latest Gorstian (or the middle part of the Hemse Group = Etelhem Formation; Ludlow: earliest Ludfordian). **A1**–**A3**, **B1**–**B2**, **C** paratypes [SNHMB-G.5507–5509]; **D** additional specimen [SNHMB-G.5510]. All SEM images

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Availability of data and material All data are provided in the text and the figures.

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