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SHORT COMMUNICATION

The oldest synallactid sea cucumber (Echinodermata: Holothuroidea: Aspidochirotida)

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Abstract Aspidochirote holothurian ossicles were discovered in Upper Ordovician-aged Öjlemyr cherts from Gotland, Sweden. The well-preserved material allows definitive assignment to the family Synallactidae, a deep-sea sea cucumber group that is distributed worldwide today. The new taxon *Tribrachiodemas ordovicicus* gen. et sp. nov. is described, representing the oldest member of the Aspidochirotida. The further fossil record of Synallactidae and evolutionary implications are also discussed.

Keywords Echinodermata · Holothuroidea · Ordovician · Sweden · Baltic Sea

Kurzfassung Erstmals werden aspidochirotide Holothuriensklerite aus oberordovizischen Öjlemyrflinten Gotlands (Schweden) beschrieben. Das vorzüglich erhaltene Material erlaubt eine definitive Zuordnung zur Familie der Synallactidae, deren Vertreter heute kosmopolitisch verbreitet nur in der Tiefsee vorkommen. Das neue Taxon *Tribrachiodemas ordovicicus* gen. et sp. nov. wird beschrieben, welches den stratigraphisch ältesten Vertreter der Aspidochirotida repräsentiert. Der übrige Fossilbericht synallactider Holothurien und deren evolutionäre Auswirkungen werden ebenfalls diskutiert.

Schlüsselwörter Echinodermata · Holothuroidea · Ordovizium · Schweden · Ostsee

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Introduction

Sea cucumbers, or holothurians, are an abundant and diverse group of Echinodermata. The more than 1,420 described extant species (Smiley 1994; Kerr 2003) occur in all marine environments from the intertidal to the deepest oceanic trenches, where they may constitute >90 % of the biomass (Belyaev 1972). Among these are synallactid holothurians, a group of aspidochirote sea cucumbers that is restricted to the deep water of all oceans today (e.g., Théel 1886; Sluiter 1901; Mitsukuri 1912; Ohshima 1915; Pawson 1965; O'Loughlin and Ahearn 2005) and is characterised by a small to medium size, tube feet, shield-shaped tentacles, lack of tentacle ampullae and specific body-wall ossicles in the form of tables and rods. The family has a cosmopolitan distribution and comprises nearly 140 species in more than 15 genera (Pawson 1982; Solís-Marín 2005, Reich herein); members of the Synallactidae appear frequently as characteristic animals of the abyssal megafauna including tracks and fecal remains (Pawson 1978; Young et al. 1985; Bluhm and Gebruk 1999). The majority of synallactid species appear to spend their life on the sediment surface. Most modern species of Synallactidae (*Mesothuria, Synallactes*) traverse the seabed and feed on the uppermost layer of sediment. Other species (of this family) with more gelatinous body walls (within *Bathyplotes*, *Hansenothuria, Paelopatides* and *Scotothuria*) are capable of active swimming (cf. Billett et al. 1985; Miller and Pawson 1990).

Compared to their modern counterparts, the palaeobiology and early evolutionary history of fossil holothurians are poorly understood (Gilliland 1993; Reich 2010a). Within the meagre fossil record of Holothuroidea (914 nominally described species; Reich 2010b), there are only a handful of synallactid species (Gilliland 1993). Based on

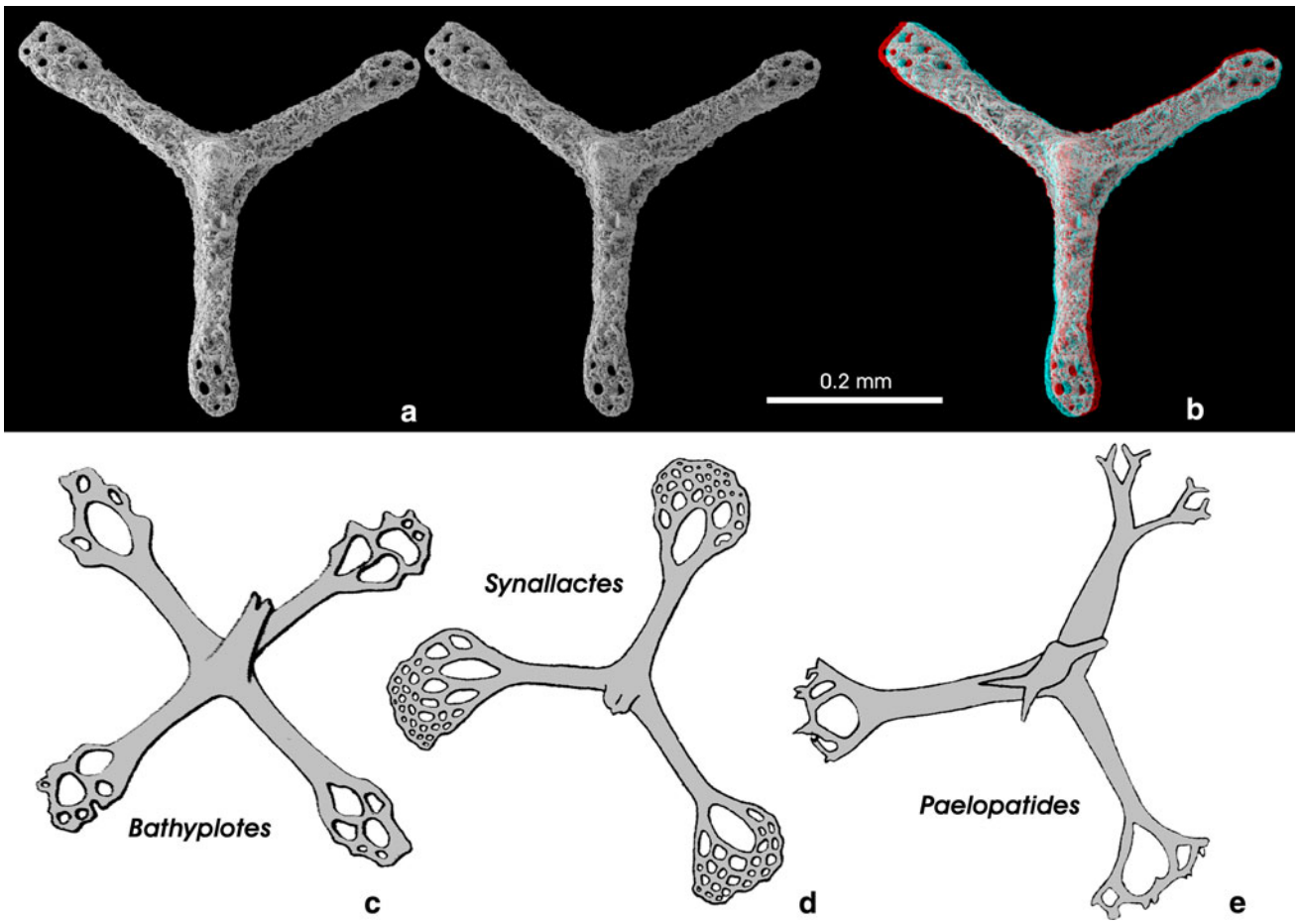

Fig. 1 **a–b** *Tribrachiodemas ordovicicus* gen. et sp. nov., holotype GZG.INV.20072, body wall ossicles, probably from the dorsal side. Upper Ordovician Öjlemyr chert (Late Katian or earliest Hirnantian) from Valle, Isle of Gotland, Sweden. **a** Stereoscopic images, **b** anaglyph image to provide a stereoscopic 3D effect. **c–e** Recent synallactid body wall sclerites for comparison (not to scale). **c** *Bathyplotes moseleyi* (Théel 1886) [from Théel 1886: pl. X, fig. 21 (pars), designated there as *Stichopus moseleyi* n. sp., modified]; **d** *Synallactes triradiata* Mitsukuri 1912 [from Mitsukuri 1912: text-fig. 2c, modified]; **e** *Paelopatides ovalis* (Walsh 1891) [from Koehler and Vaney 1905: pl. XI, fig. 1b, designated there as *Pelopatides ovalis* (Walsh), modified]

isolated body-wall ossicles (e.g., Mostler 1968, 1969, 1972) as well as one body fossil (Cherbonnier 1978) from Triassic sediments of Europe, it was believed for a long time that the earliest Synallactidae originated during the Mesozoic marine revolution (Gilliland 1993). Recently, another synallactid ossicle species was described by Boczarowski (2001) from the Middle Devonian of Poland.

The purpose of this paper is to describe the stratigraphically oldest member of the Synallactidae (Aspidochirotida) and to discuss the synallactid fossil record.

Materials and methods

The material for this study comes from Upper Ordovician Öjlemyr cherts ('Gotland type'; Eiserhardt 1992), distributed as glacial erratic boulders on the western part of Gotland, Sweden (Wiman 1901; Schallreuter 1984). These grey-coloured chert nodules were built up by secondary matrix silicification within Upper Ordovician limestones.

Öjlemyr cherts contain a rich and diverse assemblage of invertebrate fossils. This includes brachiopods, bryozoans, trilobites, poriferans, polychaetes, graptolites, ostracods (e.g., Schallreuter 1967, 1975a, 1983, 1984, 1985, 1987; Hillmer and Schallreuter 1987), chitinozoans (e.g., Eisenack 1968; Grahn 1982), acritarchs, algae (e.g., Eiserhardt 1991a, b, 1992) and melanosclerites (Trampisch 2007). Different members of echinoderms are also present, e.g., echinoids (Nestler 1968; Schallreuter 1989), holothuroids (Schallreuter 1975b), (?)ophiocistioids (Reich 2001a), crinoids, cystoids, asteroids and ophiuroids.

The age of Öjlemyr cherts was dated as earliest Hirnantian (F_{II} = Porkuni stage = Borkholm stage; Wiman

1901; Oraspõld 1975) or latest Katian ($F_{1}c$ = Pirgu stage = Lyckholm stage; Thorslund and Westergård 1938; Schallreuter 1981; Grahn 1982). The source area of the Öjlemyr cherts is presumed to be the region of the Hall Banks (algal reefs after Winterhalter et al. 1981) in the Baltic Sea off the northeast coast of Gotland (Martinsson 1958) or still further north to the Gulf of Bothnia (Spjeldnæs 1985).

The samples of cleaned and crushed rocks were processed following standard methods, including 35–40% hydrofluoric acid (HF) treatment, separation and sieving with a 63-µm nylon mesh (cf. Schallreuter 1982, 1983; Wissing and Herrig 1999).

Systematic palaeontology

Class **Holothuroidea** de Blainville, 1834
Order **Aspidochirotida** Grube, 1840
Family **Synallactidae** Ludwig, 1894
Genus ***Tribrachiodemas*** gen. nov.

Type species: *Tribrachiodemas ordovicicus* gen. et sp. nov.

Derivation of name: After the Greek τρί (tri), βραχιως (brachios), δέμας (demas) = three-armed body (masculine).

Diagnosis: Tri-radiate table-like ossicles, with terminally perforated flat tips. The solid spire in the centre consists of three terminally fused pillars. The angle between all table arms is always same.

Tribrachiodemas ordovicicus gen. et sp. nov.
Fig. 1a, b

Etymology: *ordovicicus*, in reference to the Ordovician age of the fossil.

Holotype: One body wall ossicle, GZG.INV.20072 (Fig. 1), deposited in the type collection of the Geoscientific Museum, Göttingen University (GZG), Germany.

Paratype: One body wall ossicle, GZG.INV.20073 (not figured), deposited in the type collection of the Geoscientific Museum, Göttingen University, Germany.

Type locality: Valle, Isle of Gotland, Sweden.

Type strata: Upper Ordovician, Late Katian ($F_{1}c$ = Pirgu stage) or earliest Hirnantian (F_{II} = Porkuni stage).

Specific diagnosis: See diagnosis of the genus.

Description: Simple tri-radiate table-like ossicles with a maximum diameter of 346 µm. The terminally sub-oval tips (maximum width 67 µm) are flat and perforated with four to five pores (diameter 8–13 µm). The solid pointed cone-shaped spire in the centre (maximum diameter 58–59 µm) consists of three centrically and terminally fused pillars. The angle between all table arms is always the same (120°).

Distribution: Known only from type locality and type stratum.

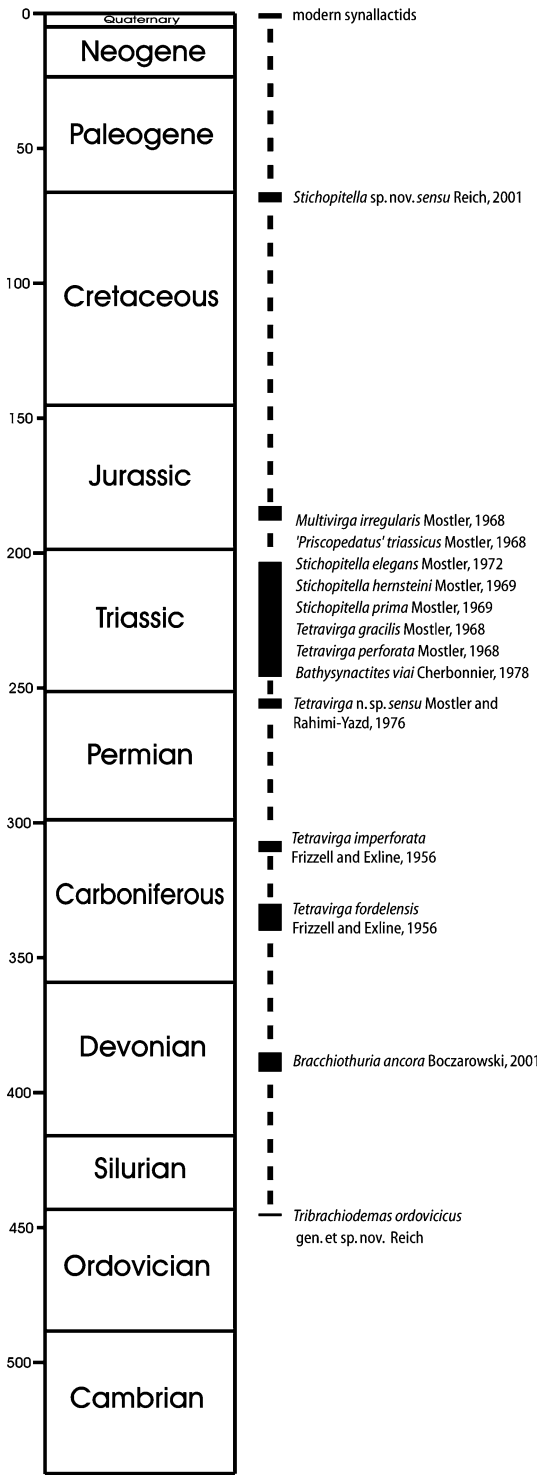

Fig. 2 General stratigraphical range chart for fossil synallactid holothurian species/groups (Holothuroidea: Aspidochirotida: Synallactidae)

Associated echinoderms: Holothurians, echinoids (*Bothriocidaris*), ?ophiocistioids (*Rogeriserra*), asterozoans, blastozoans and crinoids.

Fossil record of Synallactidae and phylogenetic implications

Besides one unique synallactid body fossil (*Bathysynactites viai*) from the Triassic (Late Ladinian) of the Tarragona area, Spain (Cherbonnier 1978), the remaining fossil record is based on body wall ossicles only (Fig. 2). A few fossil synallactid ossicle species are known from the Mesozoic, especially the Triassic (*Stichopitella* spp., *'Priscopedatus' triassicus*; Anisian to Norian sediments; e.g., Mostler 1969, 1972, 1977; Pawson 1980). Only single records were published from the Early Jurassic (*Stichopitella* sp. sensu Krainer and Mostler 1997) and the Late Cretaceous (Early Maastrichtian; *Stichopitella* sp. nov. sensu Reich 2001b; cf. Herrig et al. 1996, Reich et al. 2004). Up to now, no synallactid records from Paleogene and/or Neogene sediments are known. *Tetravirga* n. sp., described by Mostler and Rahimi-Yazd (1976) from the Late Permian (Wuchiapingian) of northern Iran, is probably also a member of the Synallactidae. In addition, other sclerite species (in part) of *Tetravirga* and *Multivirga*, recorded from the Carboniferous and Triassic (e.g., Frizzell and Exline 1956; Mostler 1968, 1971; Fig. 2), show synallactid affinities, but most of them were formerly assigned to the Elasipodida (partial discussion in Hansen 1975; Gilliland 1993). This needs to be clarified during a systematic revision of the original material. Recently, Boczarowski (2001) described another unequivocal Palaeozoic synallactid ossicle species (*Bracchiothuria ancora*) from the Middle Devonian (Givetian) of the Holy Cross Mountains (Poland), morphologically closely related to the modern *Paelopatides*.

The new synallactid species *Tribrachiodemas ordovicicus* gen. et sp. nov. from the Late Ordovician is the oldest representative of the Aspidochirotida and morphologically resembles modern species of *Synallactes* and *Bathyplotes*. The morphologically diverse group of Synallactidae (cf. Östergren 1896, 1907; Ekman 1927) is probably paraphyletic to polyphyletic (Kerr and Kim 2001), which has to be proved by detailed morphological and molecular biological investigations. The new Late Ordovician find strongly suggests a long evolutionary history of the Synallactidae and a very early diversification of Holothuroidea (cf. also Reich 2010a). Also, the first appearance of holothurian crown-group members (very early) in the Palaeozoic can be verified, as suggested recently by Smith et al. (2004); secondly, the divergence of the first three holothurian orders (Apodida, Elasipodida, Aspidochirotida) occurred during a relatively short time interval, from cs. 460–400 Ma (Upper Ordovician–Lower Devonian).

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