Cambrian holothurians ? – The early fossil record and evolution of Holothuroidea

Mike REICH (Göttingen, Germany)

Introduction

The Holothuroidea, commonly known as sea cucumbers, are an extant class of echinoderms which comprise about 1800 living species (cf. Fig. 1). Holothurians can be considered as a successful group as they are found at all depths in the marine realm, from intertidal zone to the ocean trenches, where they may constitute a large portion of the total biomass, and are distributed over all latitudes from the polar regions to the tropics. Sea cucumbers may be ecologically significant species and at high densities represent potential major bioturbators.

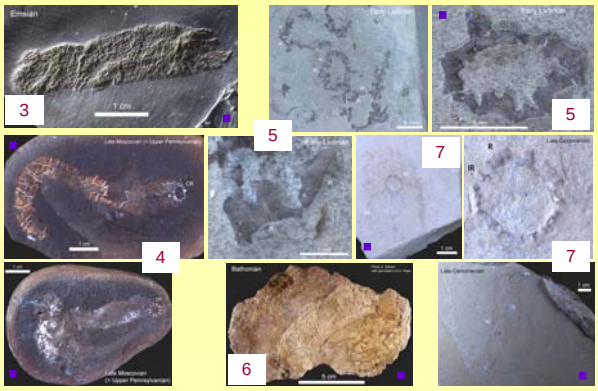
From palaeontological perspective the most important feature of sea cucumbers is their skeleton. The two main components of this are the circum-oesophageal, or calcareous, ring which comprises a variable number of calcitic plates or pieces (0.1–50.0 mm), and sclerites (0.01–10.0 mm), otherwise known as spicules, ossicles or deposits, embedded in the soft tissue matrix of the body wall, tube feet, tentacles and occasionally other tissues. Sclerites exhibit a wide variety of shapes, termed morphotypes, which are identified by common names such as anchor, plate or wheel (Fig. 2).

Holothurians (sea cucumbers) have an extremely sparse fossil record, and are known globally from just 800 paraspecies (form species based on isolated sclerites) as well as nearly 30 species (body fossils and sclerite associations) based on a few hundreds of complete specimens from less than 15 localities (Reich 2002, 2004c).

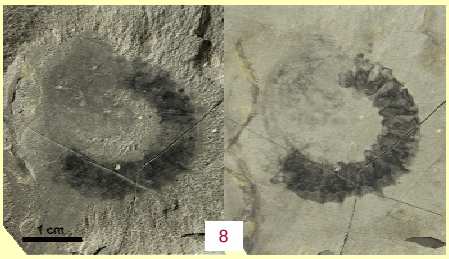
Compared to their modern counterparts, the palaeobiology and evolutionary history of holothurians are poorly understood. In part this is due to their disjunct skeletal remains, and almost entirely sclerites and calcareous ring elements, which are released following decomposition of the surrounding tissue. However, under favourable conditions, holothurians may be preserved complete in Fossil Lagerstätten, e. g. the Early Devonian Hunsrück Slate, the Late Carboniferous Mazon Creek Formation, the Triassic Muschelkalk, the Lebanon Fish shale, and others (e. g. Smith & Gallemí 1991, Reich 2004a, 2004b; Figs. 3-7).

Fig. 1: The six higher groups of Recent Holothuroidea.

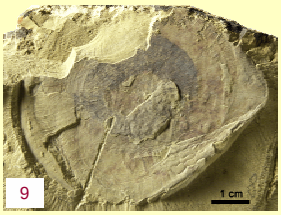
Fig. 2: Several Recent holothurians with *in situ* calcareous ossicles. [coll. Reich, GZG]



Figs. 3-7: Several holothurian body fossils from various Fossil-Lagerstätten; showing clearly the typical calcareous ring structure.
(3) Early Devonian Hunsrück Slate, Germany [*Palaeocucumaria hunsrueckiana* Lehmann, 1958 (Arthrochirotida); SMNS]; (4) Late Carboniferous Mazon Creek Formation, Illinois, U.S.A. [gen. et sp. nov., with sclerites of *Achistrum* morphotype (Apodida); coll. Reich GZG]; (5) Middle Triassic Muschelkalk, southern Germany [gen. et sp. nov. (Aspidochirotida); MHI]; (6) Middle Jurassic, Switzerland [*Holothuriopsis pawsoni* Hess, 1973 (?Apodida); MHI]; (7) early Upper Cretaceous Fish shale, Lebanon [gen. et sp. nov. (Aspidochirotida); coll. Reich GZG].



Figs. 8-10: *Eldonia* from Early and Middle Cambrian Fossil-Lagerstätten.
(8) *Eldonia ludwigi* Walcott, 1911 – Burgess Shale, Canada [SMF]; (9) *Eldonia eumorpha* (Sun & Hou, 1987) – Chengjiang biota, P.R.C. [GZG]; (10) Life reconstruction of *Eldonia* [from Chen et al. 1996]



Cambrian holothurians ?

The records of Cambrian holothurians (*Eldonia*), e. g. from the Middle Cambrian Burgess Shale (Fig. 8) are very doubtfully at the present time. The systematic position of *Eldonia* has yielded much controversy since it original description as a sea cucumber from the Middle Cambrian Burgess Shale (Walcott 1911). Some researcher considered it a pelagic holothurian (A. H. Clark 1912, 1913, Croneis & McCormack 1932, Durham 1972, 1974, Friend in Gee 1992, Friend in Chen et al. 1995), and others proposed *Eldonia* is a coelenterate (H. L. Clark 1913), e. g. a hydrozoan siphonophore (Madsen 1956, 1957, 1962, Seilacher 1961) or a scyphozoan (Lemche 1960, Chen & Erdtmann 1989) as well as related to the Lophophorata (Dzik 1989, Chen et al. 1995).

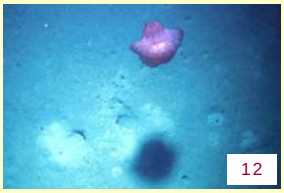
Presently the few species of *Eldonia* are known from Lower and Middle Cambrian as well as Ordovician strata (e. g. Walcott 1911; Chen et al. 1989, 1995; Friend et al. 2002; Alessandrello & Bracchi 2003; Fig. 9-10).

Further research is needed for new specimens of questionable holothurians from the Burgess Shale (coll. Royal Ontario Museum, Toronto) to discern between authentic holothurians and only morphological distantly similar organisms.

Eldonia versus Recent pelagic holothurians

In comparison to Recent pelagic sea cucumbers (Pelagothuriidae), *Eldonia* is, in my opinion, definitively not a holothurian. Within the Recent Holothu-roidea (> 1,800 species) the Pelagothuriidae (Elasipoda) are present with few representatives (*Enypniastes* and *Pelagothuria*; Fig. 11-12) in bathyal, abyssal and hadal areas (max. 7060 m water depth) of the Pacific, Indian, and Atlantic Ocean (Gebruk 1989). In all pelagic holothurians the body is gelatinous with rudimentary small feet as well as enlarged and fused papillae into a brim or velum, which is used for swimming. Typical is also the absence of the endo-skeleton, e. g. calcareous body ossicles and the calcareous ring; furthermore an external opening of the water vascular system (Heding 1950, Gebruk 1989). After investigations of nearly 100 *Eldonia* specimens, presently there is no evidence of these even mentioned well structures (e. g. rudimentary feet, hydropore etc.) in the known fossil species of *Eldonia*.

The Recent Pelagothuriidae is the highest evolved and very specialized family of the Elasipoda (Gebruk 1990), and phylogenetically closest to the stratigraphically older Psychropotidae.



Figs. 11-12: Recent pelagic / swimming sea cucumbers of the deep-sea (Pacific).
(11) *Peniagone* sp. [Elasipoda: Elpidiidae].
(12) *Enypniastes eximia* Théel, 1882 [Elasipoda: Pelagothuriidae]. [AWI]

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Abbreviations:
AWI = Alfred-Wegener-Institut, Bremerhaven, Germany; GZG = Geowissenschaftliches Zentrum, Universität Göttingen, Germany; NHMB = Naturhistorisches Museum Basel, Switzerland; MHI = Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany

■ = body fossils; ■ = calcareous ring elements; ■ = sclerites / ossicles of the body wall