

The first Cretaceous ophiopluteus skeleton (Echinodermata: Ophiuroidea)

Mike Reich^{1,2,3} 

¹SNSB—Bavarian State Collection of Palaeontology and Geology, Richard-Wagner-Straße 10, 80333 Munich, Germany <reich@snsb.de>

²Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 Munich, Germany <mike.reich@lmu.de>

³GeoBio-Center, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 Munich, Germany

Abstract.—Larvae of sea urchins, brittle stars, and allies are common, ecologically important, and diverse members of marine ecosystems in all of the world's oceans today. In contrast to modern representatives, the fossil record of echinoderm larvae is poorly known. This study reports the first ophiopluteus skeleton from Cretaceous sediments worldwide, obtained from chalky sediment of the Isle of Wolin, NW Poland. The evidence presented here, that it is possible to isolate fossil echinoderm larval skeletons from rocks, indicates a hidden diversity of such fragile fossils and thus the possibility of direct geological recording.

Introduction

Marine invertebrate larvae have fascinated scientists for centuries, and their implications for animal evolution and ecology have been the object of study since Johannes Müller's initial work (Müller, 1853) on echinoderm larvae (e.g., Lacalli, 2000; Nielsen, 2018). It has been recognized that all modern echinoderm representatives, such as sea urchins, starfish, and sea cucumbers, with the exception of crinoids (Nakano et al., 2003), have feeding (planktotrophic) larvae composed of a distinctive body plan, whereas benthic, free-living feeding larvae are missing in echinoderms (McEdward and Miner, 2001). Lecithotrophic (non-feeding) larvae with benthic (or planktonic) habits have been reported in all modern echinoderm representatives (e.g., McEdward and Miner, 2001; Arnone et al., 2015). All of these types of echinoderm larvae have unique morphologies, and, with the exception of the asteroid bipinnaria (Fig. 1.1), a calcitic skeleton (e.g., Pennington and Strathmann, 1990; Smith, 1997; Raff and Byrne, 2006). The pluteus of ophiuroids and echinoids has long arms supported by skeletal rods (Fig. 1.3–1.5) that greatly extend the ciliary bands, while the shorter-armed bipinnaria and auricularia characterize asteroids and holothuroids, respectively. In addition, the auricularia of sea cucumbers (Fig. 1.2) is unique in possessing distinct wheel-shaped ossicles (Metschnikoff, 1869; Mortensen, 1898, 1913, 1920, 1921, 1931, 1937, 1938; Dan, 1968; Hendler, 1991; Holland, 1991; Smiley et al., 1991; Balser, 2002; Byrne and Selvakumaraswamy, 2002; Emler et al., 2002; McEdward et al., 2002; Sewell and McEuen, 2002).

Anyone working with Recent echinoderm larvae would probably consider preservation and fossilization to be unlikely, given their apparent fragility and size. Taphonomic studies, such as those on sea urchin embryos and larvae by Raff et al. (2006), showed that larval skeletal elements can be preserved under non-reduced and normal sea water conditions, giving

echinoderm larvae the potential to fossilize, for example, as proposed by Wray (1992).

Echinoderms have an excellent fossil record since the Cambrian (Lefebvre et al., 2013; Zamora et al., 2013; Reich et al., 2018), making them ideal subjects for investigating larval skeletons and patterns and processes of life history evolution. However, not much attention has been paid to fossil larvae or larval skeletons of Echinodermata (Williamson, 2013). Apart from some misinterpreted fossils from the Palaeozoic (e.g., Fritsch, 1908) and Mesozoic (e.g., Girard et al., 2008), some larval skeletons from ophioplutei and echinoplutei (Ophiuroidea, Echinoidea) were briefly described or figured from early (Rioul, 1959) and late (Deflandre-Rigaud, 1946; refigured and interpreted in Sieverts-Doreck, 1958; Kryuchkova and Solov'yev, 1975; Solovjev, 2014) Jurassic sediments of Normandy, France. In addition, a few larval ossicles of Holothuroidea were reported from European Triassic (Gilliland, 1993), Jurassic (Gilliland, 1992; Reich and Stegemann, 2012), and Cretaceous (Reich, 2003) strata (see Table 1 and Fig. 3).

Thus, the current available fossil record of echinoderm larvae is essentially nonexistent (Jablonski and Lutz, 1983) and biased due to missing studies or lack of awareness of such small and fragile microfossils. However, modified micropaleontological techniques and/or the detailed study of residues below 100 µm have the promise to provide a much better fossil record for skeletal elements of echinoderm larvae, and therefore yield insights into developmental modes during echinoderm evolution (Bottjer et al., 2006). Here, I explore this issue, presenting a promising first example for future focused studies.

Materials and methods

This study is based on a single specimen from partly silicified limestones (cherty limestones, according to other authors)

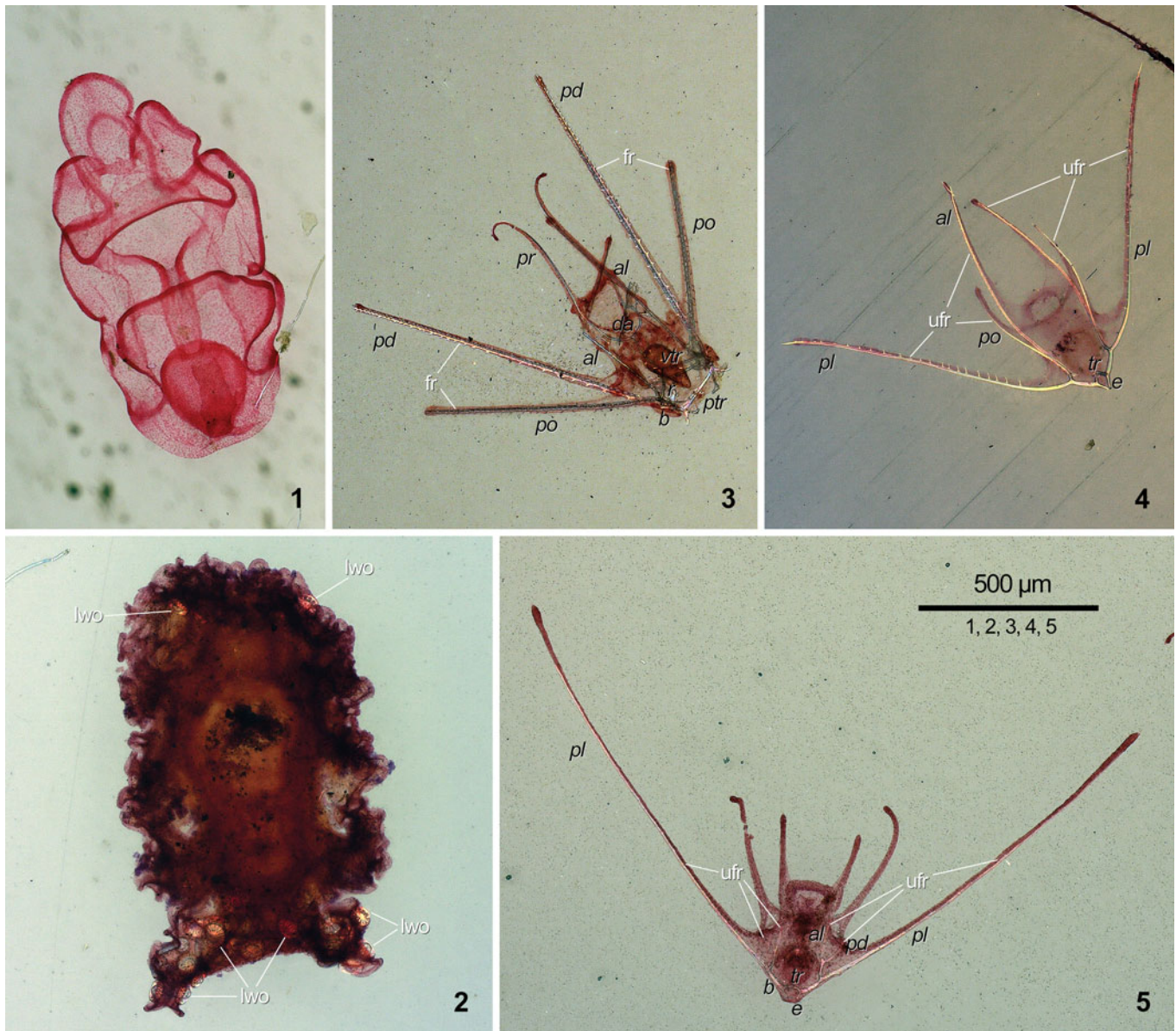


Figure 1. Modern echinoderm larvae. All polarized light micrographs (crossed nicols). (1) Bipinnaria (Asterozoa); larval stage of *Asterias rubens* (Linnaeus, 1758) (ZMUC TM-F/45)—Strib, Kattegat (collected in 1879). (2) Auricularia (Holothurozoa); giant larva 'Auricularia nudibranchiata Chun'; larval stage of *Protankyra brychia* (Verrill) (ZMUC TM-F/36)—Misaki, Sagami Bay (collected in 1899). (3) Fully formed echinopluteus (Echinozoa); larval stage of *Heterocentrotus mamillatus* (Linnaeus, 1758) (ZMUC TM-F/51)—Hurghada, Red Sea (collected in 1936). (4) Six-armed ophiopluteus (Ophiurozoa) [*Ophiopluteus mancus* Mortensen]; larval stage of *Amphiura filiformis* (O.F. Müller, 1776) (ZMUC TM-E/86)—Kristineberg, Gullmarfjord (collected in 1918). (5) Not fully formed ophiopluteus (Ophiurozoa); larval stage of *Macrophiolithrix propinqua* (Lyman, 1861) (ZMUC TM-E/100)—Hurghada, Red Sea (collected in 1936). Note wheel-shaped ossicles of holothuroid auricularia (2) and skeletal rods in plutei (3–5). All specimens from (permanent) microscopic slides mounted with Canada Balsam stored in T. Mortensen collection at ZMUC. Abbreviations in white letters: fr = fenestrated skeletal rods; ufr = unfenestrated skeletal rods; lwo = larval wheel ossicles. Abbreviations in black letters: al = anterolateral rod; b = body rod; da = dorsal arch; e = end rod; pd = posterodorsal rod; pl = posterolateral rod; po = postoral rod; pr = preoral arm; ptr = posterior transverse rod; r = recurrent rod; tr = transverse rod; vtr = ventral transverse rod. Scale bar = 500 µm.

embedded in Late Cretaceous chalk. The material is very well preserved due to the fact that the silicification process caused by weakly acidic environmental conditions started very early diagenetically before sediment compaction (Herrig, 1982, 1993). After processing these sediments with hydrofluoric acid (HF; e.g., Schallreuter, 1982), the (SiO₂-impregnated) sediment matrix was dissolved and all the calcareous material was (secondarily) changed into calcium fluoride (CaF₂). The method has been used to great effect in extracting calcareous

microfossils from otherwise unyielding rocks, such as Late Cretaceous cherty chalk or the Late Ordovician Backstein ('Brick') limestone and Öjlemyr flint (all in the Baltic Sea area). The treatment of these kinds of cherty limestones resulted in large amounts of excellent, well-preserved ostracode (e.g., Schallreuter, 1971; Herrig, 1994, 2004; Schallreuter and Hinz-Schallreuter, 2013; Horne and Siveter, 2016) and echinoderm (e.g., Schallreuter, 1975; Reich, 1995, 2002, 2010) material, among these numerous rarely found groups from the fossil

Table 1. Fossil larval skeletons of modern echinoderm representatives reported in the scientific literature (in stratigraphic order, revisions included).

| Reference(s) | Locality/Localities | Age | Original assignment [translations in brackets] | Revised assignment |
|-------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------|----------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|
| • Fritsch, 1908, p. 797–798, fig. 1 | Czech Republic: Bohemia | Ordovician: Sandbian | • ‘... ein Pluteus eines Crinoiden’ [a pluteus of a crinoid] (<i>Furca bohémica</i> Fritsch, 1908) | Cephalic shield—Arthropoda: Marrellomorpha: Mimatasteridae (cf., Rak et al., 2013) |
| • Gilliland, 1993, p. 116–117 | Slovakia: Ružomberok district | Triassic: early Carnian | • ‘Synaptid wheel: <i>T. liptovskaensis</i> Gazdzicki et al., 1978’ | Auricularia (wheel ossicles)—Synaptidae or stem group Synaptidae (<i>‘Theelia’ liptovskaensis</i> Kozur and Mock in Gazdzicki et al., 1978) |
| • Gilliland, 1992, p. 192–193, pl. 3, figs. 7–15 | UK, Warwickshire, Gloucestershire, and Devon | Jurassic: mid Hettangian + late Hettangian + early Sinemurian | • ‘Larvae of Synaptidae: <i>T. synapta</i> ’ Gilliland, 1992 | Auricularia (wheel ossicles)—Synaptidae or stem group Synaptidae |
| • Rioult, 1959, fig. 6 | France, Normandy, Tilly-sur-Seulles | Jurassic: late Pliensbachian | • ‘Spicule de stade larvaire d’Echinide’ [Spicule of echinoid larval stadium] | Echinopluteus (fenestrated rod)—Echinoidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 1; • Kryuchkova and Solov’yev, 1975, fig. 9a; • Solovjev, 2014, fig. 14a | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Squelettes incomplets de pluteus’ [Incomplete skeletons of pluteus]; • ‘Skeletal elements of larval sea urchins ... Incomplete skeletons of plutei’; • ‘Skeletal elements of larval echinoids ... Incomplete skeletons of pluteuses’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 2; • Kryuchkova and Solov’yev, 1975, fig. 9b; • Solovjev, 2014, fig. 14b | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Fragments de baguettes brachiales de pluteus’ [Fragments of brachial spines of pluteus]; • ‘Skeletal elements of larval sea urchins ... Fragments of perforated spicules of plutei’; • ‘Skeletal elements of larval echinoids ... Fragments of perforated spines of pluteuses’ | Echinopluteus (incomplete body skeleton)—Echinoidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 3; • Kryuchkova and Solov’yev, 1975, fig. 9c; • Solovjev, 2014, fig. 14c | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Squelettes incomplets de pluteus’ [Incomplete skeletons of pluteus]; • ‘Skeletal elements of larval sea urchins ... Incomplete skeletons of plutei’; • ‘Skeletal elements of larval echinoids ... Incomplete skeletons of pluteuses’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 4; • Sieverts-Doreck, 1958, pl. V, fig. 1; • Kryuchkova and Solov’yev, 1975, fig. 9d; • Solovjev, 2014, fig. 14d | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Squelettes incomplets de pluteus’ [Incomplete skeletons of pluteus]; • ‘Unvollkommenes Skelett einer Echinidenlarve’ [Incomplete skeleton of an echinoid larva]; • ‘Skeletal elements of larval sea urchins ... Incomplete skeletons of plutei’; • ‘Skeletal elements of larval echinoids ... Incomplete skeletons of pluteuses’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 5; • Kryuchkova and Solov’yev, 1975, fig. 9e; • Solovjev, 2014, fig. 14e | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Squelettes incomplets de pluteus’ [Incomplete skeletons of pluteus]; • ‘Skeletal elements of larval sea urchins ... Incomplete skeletons of plutei’; • ‘Skeletal elements of larval echinoids ... Incomplete skeletons of pluteuses’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 6; • Kryuchkova and Solov’yev, 1975, fig. 9e; • Solovjev, 2014, fig. 14f | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Fragments de baguettes brachiales de pluteus’ [Fragments of brachial spines of pluteus]; • ‘Skeletal elements of larval sea urchins ... Fragments of perforated spicules of plutei’; • ‘Skeletal elements of larval echinoids ... Fragments of perforated spines of pluteuses’ | Echinopluteus (skeletal rod)—Echinoidea, uncertain family/order |

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|-------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------|---------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|
| • Deflandre-Rigaud, 1946, fig. 7; • Sieverts-Doreck, 1958, pl. V, fig. 2; • Kryuchkova and Solov'yev, 1975, fig. 9ж; • Solovjev, 2014, fig. 14g | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Fragments de baguettes brachiales de pluteus’ [Fragments of brachial spines of pluteus]; • ‘Bruchstück eines Brachial-Stabes einer Echinidenlarve’ [Fragment of the brachial spine of echinoid larva]; • ‘Skeletal elements of larval sea urchins ... Fragments of perforated spicules of plutei’; • ‘Skeletal elements of larval echinoids ... Fragments of perforated spines of pluteuses’ | Echinopluteus (skeletal rod)—Echinoidea, uncertain family/order |
| • Deflandre-Rigaud, 1946, fig. 8; • Kryuchkova and Solov'yev, 1975, fig. 9з; • Solovjev, 2014, fig. 14h | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Fragments de baguettes brachiales de pluteus’ [Fragments of brachial spines of pluteus]; • ‘Skeletal elements of larval sea urchins ... Fragments of perforated spicules of plutei’; • ‘Skeletal elements of larval echinoids ... Fragments of perforated spines of pluteuses’ | Echinopluteus (skeletal rod)—Echinoidea, uncertain family/order |
| • Deflandre-Rigaud, 1950, p. 42–43, figs. 107–108; • Gilliland, 1993, p. 116–117 | France, Normandy, Villers-sur-Mer | Jurassic: early Oxfordian | • ‘Scélrites rotiformes ... stades larvaires des Synaptidés [Wheel-like sclerites ... larval stages of synaptids]: <i>Auricularites parviradiatus</i> cent. nov. + <i>Auricularites arcuatus</i> cent. nov.’; • ‘Synaptid wheels: <i>A. arcuatus</i> and <i>A. parviradiatus</i> ’ | Auricularia —(?)Synaptidae (<i>‘Auricularites arcuatus</i> Deflandre-Rigaud, 1950 + <i>‘A.’ parviradiatus</i> Deflandre-Rigaud, 1950) |
| • Girard et al., 2008, fig. 3C | France, Nouvelle-Aquitaine | Cretaceous: late Albian / early Cenomanian | • ‘Spine of an echinopluteus / larval spine of a sea urchin’ | Juvenile spine—Echinoidea |
| • Reich, 2003, fig. 2A–C | Germany, Western Pomerania, Isle of Rügen | Cretaceous: early Maastrichtian | • ‘?larval wheels: <i>Theelia</i> ? parasp. (Apodida: Synaptidae) | Auricularia (wheel ossicles)—Synaptidae |
| • Rögl and Bolli, 1973, pl. 18, fig. 2 | Cariaco Basin, Caribbean Sea | Quaternary: late Pleistocene | • ‘Internal skeletons of Echinopluteus’ | Echinopluteus (incomplete body skeleton)—Echinoidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 3 | Cariaco Basin, Caribbean Sea | Quaternary: late Pleistocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 4 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 5 | Cariaco Basin, Caribbean Sea | Quaternary: late Pleistocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 6 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (complete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 7 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 8 | Cariaco Basin, Caribbean Sea | Quaternary: late Pleistocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (incomplete body skeleton)—Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 9 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • ‘Internal skeletons of Echinopluteus’ | Ophiopluteus (complete body skeleton)—Ophiuroidea, uncertain family/order |

Table 1. Continued.

| Reference(s) | Locality/Localities | Age | Original assignment [translations in brackets] | Revised assignment |
|-----------------------------------------|------------------------------|-------------------------------------|---------------------------------------------------|---------------------------------------------------------------------------------------|
| • Rögl and Bolli, 1973, pl. 18, fig. 10 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • 'Internal skeletons of Echinopluteus' | Ophiopluteus (detail of body skeleton)— Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 11 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • 'Internal skeletons of Echinopluteus' | Ophiopluteus (detail of body skeleton)— Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 12 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • 'Internal skeletons of Echinopluteus' | Ophiopluteus (detail of body skeleton)— Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 13 | Cariaco Basin, Caribbean Sea | Quaternary: Holocene | • 'Internal skeletons of Echinopluteus' | Ophiopluteus (detail of body skeleton)— Ophiuroidea, uncertain family/order |
| • Rögl and Bolli, 1973, pl. 18, fig. 14 | Cariaco Basin, Caribbean Sea | Quaternary: late Pleistocene | • 'Internal skeletons of Echinopluteus' | Echinopluteus (fenestrated rod)— Echinoidea, uncertain family/order |

record, making this 'preservational window' unique to science. The fluoridization process mentioned above normally results in replication of even the finest details of the former calcium carbonate shell or ossicle, such as fine pores or fragile spines (Reich, 2014, p. 9–11). The focus of this method is different from the simple fluoridization process used (e.g., Sohn, 1956; Lane and Sevastopulo, 1981) to get translucent or clean microfossils.

To date, this special extraction method used here was largely neglected and often misunderstood with regard to detailed disaggregation of the cherty limestones, as well as the transformation and preservation of calcareous fossils after treatment (e.g., Melnikova et al., 2010). The method used in the present study should not be mistaken for another hydrofluoric acid treatment (Pessagno and Newport, 1972) used to extract siliceous microfossils such as radiolarians from compact cherts or flints. The main difference consists in the host rock: partly silicified limestone or chalk versus pure chert or radiolarite.

Locality and stratigraphic information.—The partly silicified limestone was collected in 1994 at a small, abandoned chalk quarry near Keça (Kamp; 53°52'44.93"N, 14°27'21.13"E), ~1.0 km northeast of the classic outcrop of the 'Wolin Chalk' between Lubin (Lebbin) and Wapnica (Kalkofen) (e.g., von Hagenow and Borchardt, 1850; Behrens, 1878; Deecke, 1907; Böhm, 1920; Alexandrowicz, 1966). The island of Wolin (Wollin) is located in the Odra River mouth, north of Szczecin (Stettin), NW Poland. The age of the chalk, based on its macro- and microfossil content, is late Turonian—*Subprionocyclus neptuni* ammonite zone, ca. 90 Ma (stratigraphic overview in Reich and Wiese, 2010).

Micropaleontological preparation techniques and documentation.—Echinoderm ossicles from partly silicified limestones were isolated by a special micropaleontological method (see above), using 30–35% HF (see details in Wissing et al., 1999, p. 42–44). After sufficient washing and careful sieving (sieve sizes: 0.03, 0.063, 0.1, and 1.0 mm), the residues were dehydrated at a temperature of ~70°C. All specimens were first picked and studied under a binocular microscope, and later mounted on stubs and gold-coated for investigation and imaging using a desktop scanning electron microscope (Phenom XL G2; Thermo Fisher Scientific).

The modern larval specimens for comparison were documented photographically using a digital microscope and camera equipment (Keyence VHX-7000); image stacks were prepared from up to five focal planes.

Repositories and institutional abbreviations.—The figured fossil specimen is deposited at the Bavarian State Collection of Palaeontology and Geology (SNSB-BSPG), Munich, Germany. Deflandre-Rigaud's fossil echinoderm material is part of the micropaleontological collection at the Muséum National d'Histoire Naturelle in Paris (MNHN). Additional modern larval material figured is part of the Theodor Mortensen collection at the Natural History Museum of Denmark, University of Copenhagen (ZMUC).

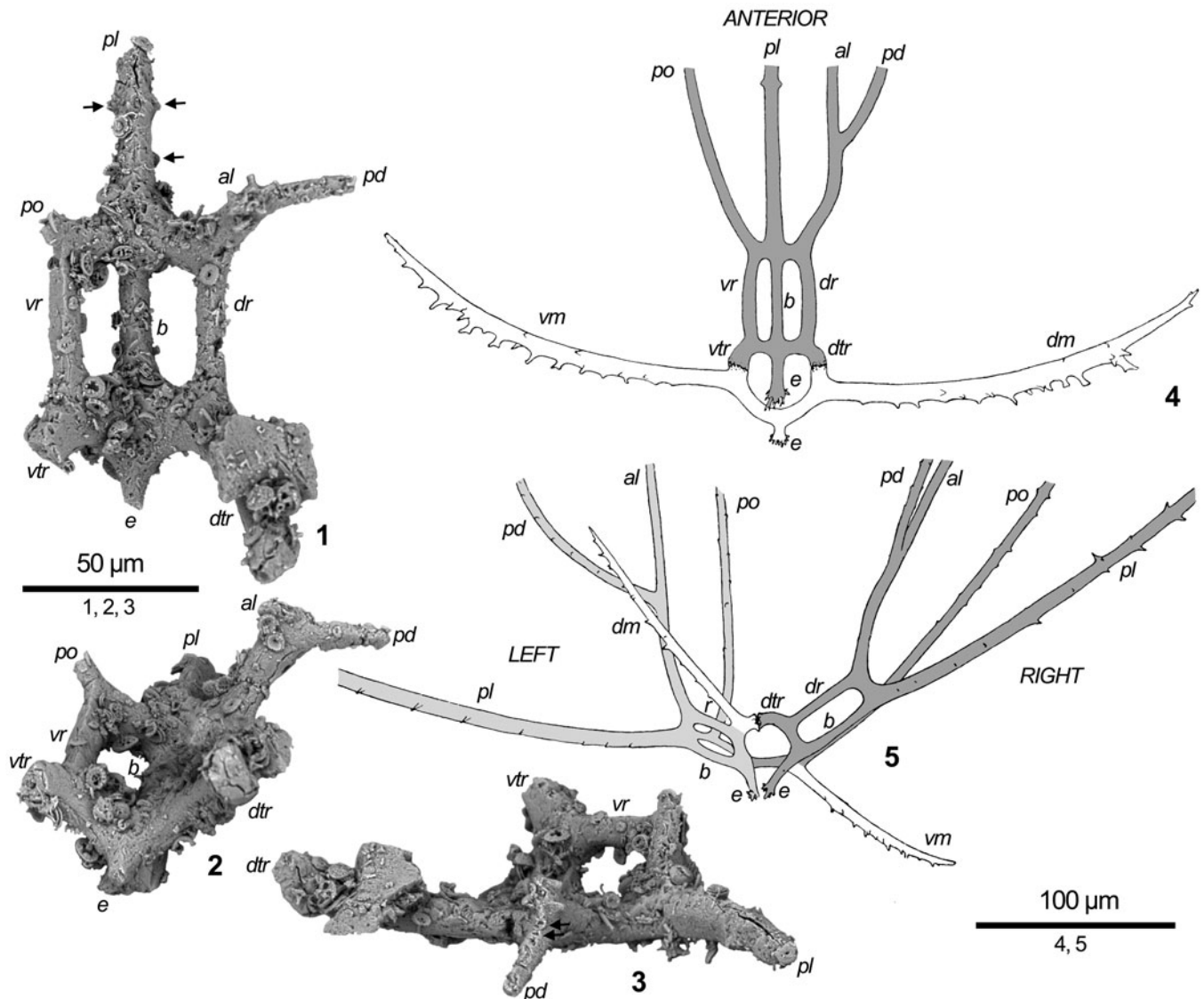


Figure 2. Late Cretaceous ophiopluteus in comparison with modern body skeletons. (1–3) Ophiopluteus, gen. and sp. A, right part of body skeleton (SNSB-BSPG 2020 XXXIX 5) from late Turonian chalk of Keapa, Isle of Wolin, NW Poland: (1) inner view; (2) inner oblique view; (3) lateral oblique view. Note small thorns at rods (black arrows). All scanning electron micrographs (specimen covered with coccoliths in part). (4, 5) ‘Ophiopluteus arcifer’ Mortensen, 1921, Recent (linked adult species unknown), compound body skeleton (left part = light gray; right part = dark gray; median processes = white) reported from Gulf of Siam, Strait of Malacca, and off Jolo, Philippines (modified from Mortensen, 1921). Abbreviations: *al* = anterolateral rod; *b* = body rod; *dm* = dorsal median process; *dr* = dorsal recurrent rod; *dtr* = dorsal transverse rod; *e* = end rod; *pd* = posterodorsal rod; *pl* = posterolateral rod; *po* = postoral rod; *vm* = ventral median process; *vr* = ventral recurrent rod; *vtr* = ventral transverse rod. Scale bars = 50 μm (1–3), and 100 μm (4, 5).

Systematic paleontology

Abbreviations as in Figure 1 (nomenclature modified from Mortensen, 1921).

Class Ophiuroidea Gray, 1840
 incerti ordinis
 incertae familiae

Ophiopluteus, gen. and sp. A
 Figure 2.1–2.3

Description.—The partially preserved body skeleton (*bs*) is fairly robust and of compound type. Only the right part of the body skeleton is present (Fig. 2.1–2.3). Dorsal and ventral median

processes are missing. The anteriorly directed, unfenestrated posterolateral (*pl*), anterolateral (*al*), posterodorsal (*pd*), and postoral (*po*) rods are partly broken off (Fig. 2.1), but with recurrent (*r*) and body (*b*) rods, as well as the other respective rod onsets, the main part of the body skeleton is still preserved. The incomplete posterolateral rod is set with bilaterally arranged small thorns (Fig. 2.1) and is circular in cross section (Fig. 2.3); the posterodorsal rod also has small thorns along the inner side (Fig. 2.3). The anterolateral and posterodorsal rods are somewhat erect, projecting to the center of the whole complex skeleton (Fig. 2.2). The short end rod (*e*), both transverse rods (*tr*), and the postoral rod are broken off. The body rod forms an angle of ~90° in cross section together with the dorsal and ventral recurrent rods. This structure is much longer than wide.

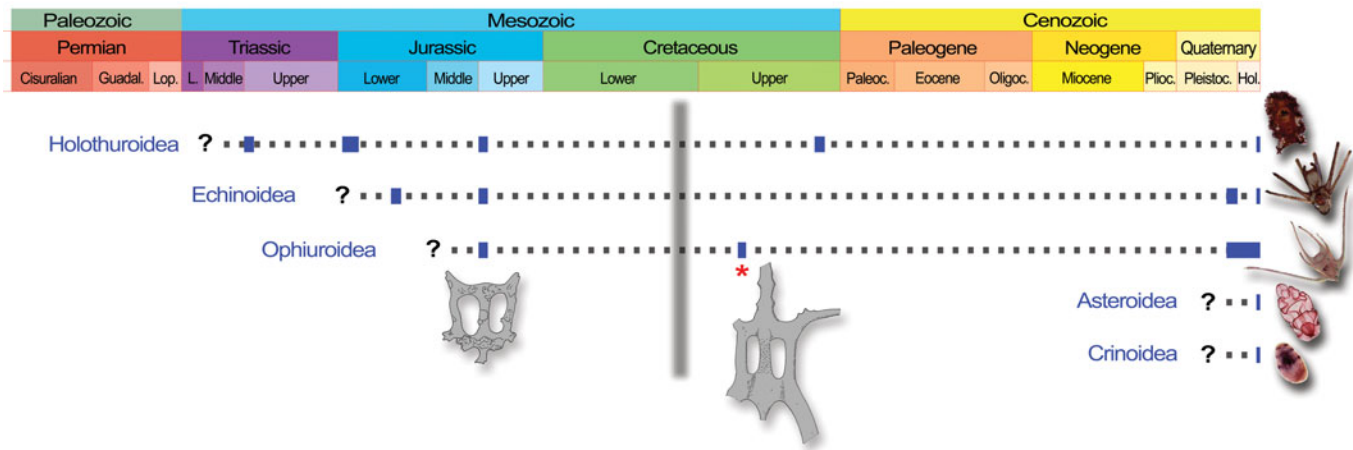


Figure 3. Summary of fossil record of modern echinoderm larvae (Crinoidea, Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea), based on data presented in Table 1. Gray vertical bar in Lower Cretaceous (ca. 110 Ma) highlights first appearance of representatives of Ophiuridae (Ophiurida), Ophiocomidae (Ophiacanthida), Amphiuridae, Ophiactidae, and Ophiotrichidae (latter all Amphilepidida; systematics after O'Hara et al., 2017)—modern ophiuroid families in which ophioplutei occur. Stratigraphic position of first Cretaceous ophiopluteus described herein indicated by (red) asterisk.

Material.—SNSB-BSPG 2020 XXXIX 5, only known specimen from the late Turonian chalk of Kępa, Isle of Wolin, NW Poland.

Remarks.—The assumed body length of this larva type is at least 0.17 mm. The incompleteness of the ophiopluteus skeleton described here with some processes broken off probably arose from handling during micropaleontological sieving and apparently does not have any taphonomic or diagenetic causes.

Modern ophioplutei occur only in the Ophiurida (Ophiuridae), Ophiacanthida (Ophiocomidae), and Amphilepidida (Amphiuridae, Ophiactidae, Ophiotrichidae) (McEdward and Miner, 2001; systematics after O'Hara et al., 2017). The following two main types can be distinguished within modern forms (Mortensen, 1921): (1) simple body skeleton, having single body rods (*b*) only; and (2) compound body skeleton, a ventral (*vr*) and a dorsal (*dr*) recurrent rod forming together with the body rods (*b*) two coarse meshes in each side (left and right) of the body (Fig. 2.5).

The size and general shape of the above-described fossil ophiopluteus body skeleton most resemble the Recent 'Ophiopluteus arcifer' Mortensen, 1921, reported from the Caribbean Sea, the Gulf of Panama, the Gulf of Siam, and the Strait of Malacca (Mortensen, 1921, p. 158). Unfortunately, since the adult of this type of ophiopluteus is not yet documented (M. Byrne, written communication, 2020), an assignment of the Turonian ophiopluteus body skeleton to an ophiuroid order or family is not possible. Similar unidentified modern ophioplutei that have been sampled in the mid-ocean may be teleplanic (Hendler, 1991). Because ophioplutei in littoral waters normally reflect the benthic adult population (e.g., Rees, 1954), these unidentified open sea ophioplutei are probably related to a deep-sea ophiuroid with essentially cosmopolitan distribution (Pacific and Atlantic Ocean), as similarly reported for bathyal/abyssal sea cucumbers (e.g., *Protankyra brychia* [Verrill, 1885] versus 'Auricularia nudibranchiata'; Pawson et al., 2003).

The mentioned type of modern ophiopluteus ('Ophiopluteus arcifer' Mortensen, 1921) is somewhat narrower than the

fossil one described herein, and the anterolateral and posterodorsal rods project in an anterior direction as do the posterolateral and postoral rods. The Cretaceous ophiopluteus skeleton is comparable to Upper Jurassic (lower Oxfordian) material described by Deflandre-Rigaud (1946; deposited at the MNHN). However, the structure formed by the body and recurrent rods is quadrangular, not rectangular, in shape (Fig. 3). Other published material from Pleistocene and Holocene sediments (Deep Sea Drilling Project) of the Cariaco Trench off Venezuela (Rögl and Bolli, 1973; misinterpreted as echinoplutei) shows that this ophiopluteus type in general apparently had a much greater diversity in Mesozoic and Cenozoic times than previously known. By reshaping the main skeletal structure from quadrangular to rectangular with different angles, it seems there have been evolutionary changes in which the body length of larvae is extended and the body flattened.

Conclusions

The late Turonian ophiopluteus body skeleton from NW Poland described herein originated from a larva of unknown ophiuroid species with a (?near-surface) planktotrophic larval stage. The fossil specimen is morphologically similar to a type of modern ophioplutei described by Mortensen (1921) that can probably be linked to deep-sea ophiuroid species. The new finding represents the first report of a Cretaceous ophiopluteus, which provides a window into the poorly known fossil record of echinoderm larvae.

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