

# Shallow-water brittle-star (Echinodermata: Ophiuroidea) assemblages from the Aptian (Early Cretaceous) of the North Atlantic: first insights into bathymetric distribution patterns

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In spite of their excellent preservation potential and abundance, brittle-star microfossils are still an underexploited source of alpha-taxonomical data. Knowledge on the Lower Cretaceous fossil record of the ophiuroids is particularly patchy, hampering the use of the ophiuroids as a model organism to explore macroevolutionary, taphonomic and other further-reaching aspects. Here, we describe three ophiuroid assemblages mostly based on dissociated lateral arm plates from the early Aptian of Cuchía (Cantabria, northern Spain), and the latest Aptian of Wizard Way (Texas, USA). A total of eleven species were identified. Ten species are new to science, three of which (*Ophiolence sanmigueli* sp. nov., *Ophi-onella eloy* sp. nov. and *Ophiodoris holterhoffi* sp. nov.) are formally described as new. The two Spanish assemblages are dominated by an ophionereidid and an ophiolapidid, and the Texan one by an ophionereidid and, to a much lesser extent, an ophiacanthid assemblage. Our analysis reveals that the eastern (Cuchía) and western (Texas) North Atlantic faunal spectra were not fundamentally different from each other during the Aptian. We furthermore present the first clear bathymetric gradient in the ophiuroid fossil record, comparing the Texan assemblage with a recently discovered coeval fauna from middle bathyal palaeodepths of Blake Nose, western North Atlantic, and show that Aptian shallow-water (<200 m) and deep-sea ophiuroid communities were clearly distinct. Finally, we argue that the Aptian shallow-water assemblages, although dominated by families which typically occur in present-day mid- to low-latitude shallow seas, have no modern equivalents in terms of family-level composition.

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## Introduction

Echinoderms are among the most important invertebrate fossil groups. In fact, their skeletal plates quite conveniently combine a high fossilisation potential and sufficient morphological disparity for taxonomic identification (e.g., Donovan 1996, 2001; Gale 2011). As a result, echinoderms have been successfully used in the past as model organisms to explore large-scale palaeoecologic, palaeoclimatologic and macroevolutionary patterns (e.g., Aronson 1987; Baumiller & Gahn 2004; Kroh 2007; Hunter & Underwood 2009; Thuy & Meyer 2012). Recently, dissociated lateral arm plates of ophiuroids have been suggested as a particularly promising yet largely unexplored source of evidence in this respect, mostly because they abundantly occur as microfossils in most marine sediments and are determinable to genus and even species level (Thuy & Stöhr 2011). Indeed, ophiuroid lateral arm plates have provided key evidence to explore the geological history of the modern deep-sea fauna (Thuy et al. 2012) and the macroevolutionary patterns in the bathymetric distribution of a modern deep-sea ophiuroid family (Thuy 2013).

Yet, the fossil record of the ophiuroids, unlike that of other echinoderm groups (e.g., Hess 2011), is still only patchily known, in spite of fairly numerous taxonomic studies (e.g., Hess 1962, 1964, 1965a, 1965b, 1966, 1975a, 1975b; Kutscher & Hary 1991; Kutscher 1996; Kutscher & Jagt 2000; Kutscher & Villier 2003; Thuy 2005; Thuy 2011; Thuy & Kroh 2011; Thuy 2013). For some stratigraphic stages, fewer than 20 fossil ophiuroid species are known, which corresponds to less than 1 percent of the present-day diversity of the class, amounting to 2064 currently recognised species (Stöhr et al. 2012).

The Aptian is one of these blank areas with respect to ophiuroid palaeodiversity, with, until recently, only a single nominal ophiuroid species described (Taylor 1966). Smith & Rader (2009), Thuy et al. (2012) and Thuy (2013) added another five nominal ophiuroid species and eight unnamed species reports for the Aptian, resulting in as few as 14 species in total for the entire stage. Clearly, much more data are needed until even an approximate picture of Aptian ophiuroid diversity becomes discernible. This is all the more desirable considering that the Early Cretaceous was a crucial time in the evolution of the Ophiuroidea, witnessing the divergence of a number of important modern groups (Stöhr et al. 2012).

Here, we report on three ophiuroid assemblages mostly based on lateral arm plates from Aptian shallow-water deposits of the North Atlantic, two from Spain and one from Texas. The main purpose of this study is to contribute to a better understanding of ophiuroid diversity in the Aptian in particular and in the Early Cretaceous in general, and thus to expand the alpha-taxonomic basis for further-reaching studies. In addition, we compare the here described shallow-water assemblages with the near-coeval, middle bathyal North Atlantic ophiuroid assemblage described by Thuy et al. (2012) and Thuy (2013) presenting

first insights into the bathymetric distribution of Lower Cretaceous ophiuroids.



**Fig. 1:** Palaeogeographic reconstruction for the late Aptian (from Erbacher et al. 2001, modified) with the position of the studied assemblages (Cuchía, Spain, and Wizard Way, Texas) in the western North Atlantic. Thick lines denote palaeocoastlines and grey areas represent emerged land. The star indicates the position of the middle bathyal Blake Nose assemblage of Thuy et al. (2012).

## Geological context

The ophiuroid assemblages described herein were extracted from bulk sediment samples from two localities. One sample was retrieved from the Echinoid Marker Bed of Smith & Rader (2009), at the base of Unit 2 of the Lower Member of the Glen Rose Formation, Texas, United States of America, near Wizard Way, southwest of Austin, on the western side of the palaeo-North Atlantic. This site has been dated to a latest Aptian age (Stricklin et al. 1971; Smith & Rader 2009), thus postdating OAE (Oceanic Anoxic Event) 1a but predating OAE 1b. The Echinoid Marker Bed is an orbitoline-rich, marly wackestone that underlies rudist bioherm limestones. It was presumably deposited in a peri-reefal setting below normal wave base (Smith & Rader 2009).

Further samples were retrieved from the Cuchía section in Cantabria, Spain, ca. 5 km E of Suances at the Playa de los Caballos, on the eastern side of the palaeo-North Atlantic (Fig. 1). It exposes superbly a transgressive-regressive sequence of a Lower (–Middle?) Albian age. Dark transgressive/maximum flooding marls of ca. 55 m thickness are referred to as Marl Member of the Caranceja Formation *sensu* Garcia-Mondejar 1982 (see Wilmsen 2005), which is equivalent to the Patrocinio Formation of Najarro et al. (2011). The marls rest with a sharp contact on coarse-grained calcarenites (Calcarenite Member of the Caranceja Formation; Wilmsen 2005). They show frequent intercalations of blood-red to brown weathering clay-ironstone layers, in which ammonites occur frequently in two levels (Collignon 1979). The succession grades progressively *via* highly fossiliferous, massively bedded silty

marls into prodelta turbidites and fluvial sandstones with wood remains and abundant ichnofossils *Ophiomorpha nodosa* (Lundgren). A detailed description of the section is given by Wilmsen (2005).

Five samples from the Marl Member were processed. It turned out that the bathymetrically deepest part of the section yielded only scarce material. However, some 20 m above the base of the section (ca. 2 m above the second ammonite level), microfauna becomes abruptly abundant. Thus, we considered two samples from an interval above the second ammonite layer (Cuchía 1: 1.5 m above the second ammonite layer, and Cuchía 2: 10 m above the second ammonite layer). Biostratigraphically, the fauna derives from a critical interval close or within the OAE 1a. Collignon (1979) and Wilmsen (2005) regarded the second ammonite level to represent already the *Deshayesites deshayesi* Zone (late Early Aptian). This would then mean that the here described fauna from Cuchía postdates OAE 1a. Najarro et al. (2010), however, re-interpreted the fauna as *D. weissi* Zone (middle Lower Aptian), and  $\delta^{13}\text{C}$  correlations seem to confirm this assessment. Thus, our fauna appears to coincide stratigraphically with the OAE 1a (Selli Event).

## Material and methods

The ophiuroid remains described herein were retrieved from the sieving residues of bulk sediment samples. Micropalaeontological sample processing involved immersion in 10 percent hydrogen peroxide and soaking in an oversaturated, hot soda solution respectively for the two Spanish samples, and washing in a clay processing device (Ward 1981) for the Texan sample. The ophiuroid remains were picked from the  $>250\ \mu\text{m}$  residue fraction using a dissecting microscope. Selected specimens were cleaned using an ultrasonic tank. They were then mounted on aluminium stubs and coated with platinum or palladium for scanning electron microscopy. Lateral arm plates of modern ophiuroids, used for morphological comparison, were extracted from complete specimens using household bleach ( $\text{NaOCl}$ ), as described by Thuy & Stöhr (2011).

The material from the Texan sample includes both disarticulated skeletal plates and articulated arm fragments, mostly displaying pristine preservation of even the finest stereom structures. The specimens from the Spanish samples are all fully disarticulated and show signs of pre-burial abrasion and/or diagenetic alteration, blurring some of the finer structures of the stereom.

Identifications, ideally to species level, were almost exclusively based on the lateral arm plates (abbreviated in the descriptions as LAPs), following the terminology and guidelines of Thuy & Stöhr (2011). In the exceptional case of the Texan assemblage, it was possible to extract additional taxonomic evidence from vertebrae, oral plates and ventral and dorsal arm plates by combining these with a

particular type of lateral arm plates. This was possible on the one hand thanks to the co-occurrence of articulated arm fragments, and on the other hand because the lateral arm plates in question were by far the most abundant in the sample. Higher-level classification follows Smith et al. (1995) and the amendments by Martynov (2010) and Thuy et al. (2012).

A detrended correspondence analysis was computed using the PAST software (Hammer et al. 2001) in order to compare the studied ophiuroids assemblages quantitatively with a coeval middle bathyal assemblage from the western North Atlantic (Thuy et al. 2012) and with modern ophiuroid communities from various depths. This analysis was based on the dataset of Thuy et al. (2012) (minus the Cretaceous shallow-water assemblages) and the relative abundances on family level of the here described assemblages, deduced from lateral arm plate counts. As in the analysis of Thuy et al. (2012), the ubiquitous Ophiuridae were removed from the dataset in order to enhance bathymetric trends in family-level compositions.

All types, figured and additional specimens were deposited in the collection of the Geoscientific Museum at the University of Göttingen (GZG.INV.).

## Systematic palaeontology

Class **Ophiuroidea** Gray, 1840

Order **Ophiurida** Müller & Troschel, 1840

Family **Ophiacanthidae** Ljungman, 1867

Genus **Ophiacantha** Müller & Troschel, 1842

*Type species.* – *Ophiacantha spinulosa* Müller & Troschel, 1842 [junior synonym of *Ophiacantha bidentata* (Bruzelius, 1805)]

*Diagnosis for LAPs.* – Ophiacanthid with dorsal and ventral lobes of spine articulations fused into continuous volute; ventral part of LAPs not protruding ventro-proximalwards; generally no more than one spur on the outer proximal and inner distal edges; ridge on inner side composed of long, oblique, straight to slightly bent main part with a pointed dorsal tip and with ventralward pointing, vertical to slightly oblique or bent extension generally at least as long as half of the main part; in many cases, main part and ventralwards pointing extension fused into large, irregularly triangular knob; tentacle notch small.

**Ophiacantha** sp. nov.

Figs. 2.1–2

*Material examined.* – GZG.INV.78820 (figured dissociated LAP), GZG.INV.78821 (figured dissociated LAP) and GZG.INV.78822 (6 dissociated LAPs) from Cuchía 2,

and GZG.INV.78823 (2 dissociated LAPs from Cuchía 1).

**Description.** – Relatively small, dissociated LAPs of stout aspect, proximal ones slightly higher than wide, distal ones slightly wider than high; dorsal edge concave as a result of a moderately well developed constriction; distal edge evenly convex; proximal edge evenly concave, devoid of spurs, kinks or protrusions; ventral portion of LAP weakly protruding ventro-proximalwards; outer surface stereom coarsely meshed, with trabeculae thickened into small tubercles; narrow band of much more finely meshed stereom along proximal edge of LAP. Seven (proximal LAPs) to five (distal LAPs) large, ear-shaped spine articulations freestanding on elevated distal portion of LAP, bordered proximally by poorly defined, knobby and irregularly wavy, vertical ridge; dorsal and ventral lobes of spine articulations merged into continuous, coarsely meshed volute with well developed sigmoidal fold; dorsalward increase in size of spine articulations and of gaps separating them; gap between spine articulations and distal edge of LAP narrower than half a spine articulation. Ventral edge of LAP weakly concave; tentacle notch invisible in external view.

Inner side of LAP with large, wide, prominent but poorly defined ridge composed of a nearly straight, oblique central part with pointed dorsal tip and vertical, ventralwards pointing dorsal extension nearly parallel to the proximal edge of the LAP; central part of the ridge and ventralwards pointing dorsal extension merged into vertically elongate, nearly triangular knob with concave ventral edge; ventral portion of main ridge part with rounded kink and ventro-proximalwards pointing extension not merged with ventral portion of LAP; inner side of distal edge of LAP devoid of spurs; very poorly defined, almost indiscernible, shallow tentacle notch between ventro-distal tip of LAP and slightly thickened ventro-proximal portion of LAP; single, small, poorly defined perforation discernible near distal edge of kink of ridge, in wide, shallow, almost indiscernible vertical furrow.

**Remarks.** – The large, ear-shaped spine articulations with a well developed sigmoidal fold in combination with the absence of a single, conspicuous, large perforation on the inner side unequivocally place the above described LAPs in the family Ophiacanthidae. On genus level, closest affinities are shared with the LAPs of *Ophiacantha* in its proper sense as defined by Thuy (2013), mainly on account of the general shape of the LAPs devoid of a strongly ventro-proximalwards protruding ventral portion, the absence of spurs on the outer proximal and inner distal edges, the continuous lobe of the spine articulations and the shape of the ridge on the inner side. There are superficial similarities with the LAPs of the extinct genus *Ophiogaleus* Thuy, 2013, assumed to share very close phylogenetic ties with *Ophiacantha* (Thuy 2013), in particular concerning the knobby rather than vertically striated outer surface. The absence of spurs on the outer proximal and

inner distal edges of the above described LAPs as well as the absence of a kink between the straight, oblique part of the ridge on the inner side and its widened, nearly triangular dorsal portion, however, preclude assignment to *Ophiogaleus*.

Among the fossil LAP types currently assigned to *Ophiacantha* according to the revised ophiacanthid fossil record (Thuy 2013), closest similarities are shared with *Ophiacantha jaegeri* Thuy, 2013, from the Hauterivian of Germany, especially on account of the outer surface ornamentation and the shape and arrangement of the spine articulations. LAPs of the species in question, however, differ from the above described specimens in their more fragile general appearance, the slightly lower number of spine articulations and the spur on the outer proximal and inner distal edges. The above described LAPs almost certainly belong to a new species, which, however, we refrain from formally describing here on account of the limited and poorly preserved material available.

The genus *Ophiacantha*, even if restricted as by Thuy (2013), includes several types of LAP morphologies, many of which most likely represent yet undescribed genera in the *Ophiacantha* lineage. On the basis of the observation that LAP morphology reflects phylogenetic relationships in ophiuroids (Thuy & Stöhr 2011), it can be assumed that *Ophiacantha jaegeri* and the new Aptian species represent another one of these groups.

**Occurrence.** – Early Aptian of Cuchía, Spain.

#### Genus *Dermocoma* Hess, 1964

**Type species.** – *Dermocoma wrighti* Hess, 1964.

**Diagnosis for LAPs.** – Ophiacanthid with LAPs commonly displaying a fine vertical striation on their outer surface; well developed spurs on the inner distal and, in some cases to a lesser extent, outer proximal edge; ventral portion of LAP strongly protruding ventro-proximalwards; up to six moderately large, ear-shaped spine articulations with continuous volute in notches of elevated distal portion of LAP; ridge on inner side of LAPs simple, continuous, generally slender, devoid of sharp kinks or conspicuously thickened parts; tentacle notch small to moderately large.

#### *Dermocoma* sp. nov.

Fig. 2.3

**Material examined.** – GZG.INV.78824 (figured dissociated LAP) and GZG.INV.78825 (6 dissociated LAPs) from Cuchía 2, and GZG.INV.78826 (one dissociated LAP) from Cuchía 1.

**Description.** – Relatively small dissociated LAPs, proximal one slightly more than 1.5 times higher than wide, median one slightly lower; ventral third to quarter of LAP strongly protruding ventro-proximalwards, with convex ventral edge; dorsal edge nearly straight; distal edge slightly wavy;

proximal edge concave, slightly wavy, with poorly defined, weakly prominent and protruding swollen central area, no clearly defined spurs discernible. Outer surface of LAPs with very finely meshed, seemingly smooth stereom, no vertical striation discernible. Five (proximal LAPs) to four (median ones) moderately large, ear-shaped spine articulations in notches of weakly elevated distal portion of LAP; spine articulations nearly equidistant and approximately of similar size except for slightly larger median ones; ventral lobes with weak connection with distalwards projecting tip of outer surface stereom separating notches, and merged with dorsal lobe into continuous volute; spine articulations proximally sharply bordered by edge of notches; gap between spine articulations and distal edge of LAP very narrow. Ventro-distal edge of LAP with large, rather shallow tentacle notch.

Inner side of LAPs with relatively thin, poorly defined and weakly prominent ridge devoid of conspicuously thickened parts or extensions, composed of oblique and slightly dorsalswards bent dorsal portion, and shorter ventral portion, connected with dorsal one by gentle kink and seemingly merged with ventral portion of LAP; inner side of distal edge devoid of spurs; no perforation or vertical furrow discernible. Inner side of tentacle notch concave, well defined.

**Remarks.** – The above described LAPs are clearly assignable to the Ophiacanthidae on account of the spine articulation structure and the absence of a single, large perforation on the inner side. Within this family, greatest affinities are shared with the LAPs of the extinct genus *Dermocoma* as suggested by the relatively small size, the continuous volute, the regular arrangement and the position within notches of the slightly elevated distal LAP edge of the spine articulations, the conspicuous ventro-proximalward pointing ventral portion of the LAPs as well as the shape of the ridge on the inner side (Thuy 2013). Among all the species and unnamed LAP types assigned to *Dermocoma*, none is compatible with the above described specimens. In fact, the lack of both a well developed vertical striation and spurs on the outer proximal and inner distal edges is a unique combination of characters in the genus *Dermocoma* (Thuy 2013). Thus, the above described material most probably belongs to a new species of *Dermocoma*. In the light of the limited amount and the poor preservation of the material available to date, however, we refrain from formally naming the new species.

The here described occurrence narrows down a lengthy stratigraphic gap in the fossil record of the genus between an unnamed new species of *Dermocoma* from the late Valanginian of Austria and another unnamed congener from the early Albian of the United Kingdom (Thuy 2013).

**Occurrence.** – Early Aptian of Cuchía, Spain.

### Genus *Ophiojagtus* Thuy, 2013

**Type species.** – *Ophiojagtus acklesi* Thuy, 2013

**Diagnosis for LAPs.** – Ophiacanthid with stout, thick, strongly curved LAPs generally with a high height/width ratio; outer surface devoid of ornamentation elements; no spurs on outer proximal and inner distal edges; ventral portion of LAPs long to extremely long, strongly protruding ventralwards and often with widened ventral tip; proximal edge commonly with proximalwards pointing protrusion; large, ear-shaped spine articulations composed of thick, continuous volute, freestanding on bulging distal portion of LAP and not bordered proximally by a ridge-like structure; broad, well defined ridge on the inner side of the LAPs, generally with dorso-proximalwards pointing dorsal part; tentacle notch large but poorly defined and generally shallow.

### *Ophiojagtus acklesi* Thuy, 2013

\*2013 *Ophiojagtus acklesi* Thuy, p. 219; figs. 38: 5-7.

**Diagnosis.** – Species of *Ophiojagtus* with relatively small LAPs displaying four to five spine articulations, a very long ventral portion and a very short ridge on the inner side not extending onto the ventral portion of the LAP but with a strongly widened dorsal tip projecting onto the inner side of the well developed protrusion of the proximal LAP edge.

**Remarks.** – This species was described and figured in detail by Thuy (2013) on the basis of specimens which are part of the assemblage described herein.

**Occurrence.** – Latest Aptian of Wizard Way, Texas, U.S.A.

### *Ophiojagtus* sp. nov.

Fig. 2.4

**Material examined.** – GZG.INV.78827 (figured dissociated LAP) and GZG.INV.78828 (one dissociated LAP) from Cuchía 1, and GZG.INV.78829 (three dissociated LAPs) from Cuchía 2.

**Description.** – Moderately large, dissociated LAPs, at most 1.5 times higher than wide; of stout and massive aspect; dorsal edge slightly concave, with conspicuously pointed dorso-proximal tip of LAP; distal edge evenly convex; proximal edge with large, rounded, non-prominent central protrusion; ventral portion of LAP very narrow, tongue shaped, devoid of thickened ventral tip, accounting for one quarter of the total LAP height. Outer surface with very finely meshed stereom, devoid of conspicuous ornamentation elements; slightly more coarsely meshed stereom on ventral portion of LAP; outer surface stereom arranged in fine, weakly developed horizontal stripes close to protrusion of proximal edge in some LAPs. Four large,

ear-shaped spine articulations freestanding on strongly bulging distal portion of LAP, and composed of a thick, continuous and slightly rugose volute; very weak dorsalward increase in size of gaps separating spine articulations; two median spine articulations larger than dorsal and ventral ones; gap between spine articulations and distal edge of LAP narrower than one spine articulation. Ventro-distal edge of LAP with very large but rather shallow tentacle notch.

Inner side of LAP with moderately wide, prominent, well defined ridge, composed of oblique, slightly proximalwards bent dorsal part with a rounded, tongue-shaped dorsal tip slightly extending onto the inner side of the protrusion of the proximal LAP edge, and a much narrower ventral part extending onto the inner side of the ventral portion of the LAP and almost reaching the ventral tip of the latter; no spurs on the inner side of the distal edge of the LAP; inner side of the tentacle notch very large but shallow and very poorly defined. No perforations discernible; very shallow, poorly defined vertical furrow distally lining ridge.

**Remarks.** – The above described LAPs display the highly distinctive combination of characters which is uniquely found in the extinct ophiacanthid genus *Ophiojagtus*, as described by Thuy (2013). Within this genus, no currently known species or unnamed LAP type displays a similarly narrow and short ventral portion devoid of widened ventral tip combined with a narrow ventral part of the ridge on the inner side extending well onto the inner side of the ventral LAP portion. The above described LAP type most probably belongs to a new species of *Ophiojagtus* but the limited amount and the poor preservation of the material at hand preclude a meaningful formal description.

**Occurrence.** – Early Aptian of Cuchía, Spain.

#### Family **Amphiuridae** Ljungman, 1867

##### Genus **Amphilimna** Verrill, 1899

**Type species.** – *Ophiocnida olivacea* Lyman, 1869

**Diagnosis for LAPs.** – Small to medium-sized, fragile, conspicuously triangular and strongly arched LAPs; outer surface with coarsely meshed stereom, devoid of tubercles or striation; diffuse, non-prominent and non-protruding area of more finely meshed stereom on outer proximal edge of LAP; highly distinctive, medium-sized spine articulations composed of two horizontally elongate, straight, parallel lobes separated proximally by a single lens-shaped knob extending beyond the two lobes proximally; inner side of LAP with a small, relatively short, strongly bent ridge with a ventro-distalwards pointing tip and a ventro-proximalwards pointing tip.

##### **Amphilimna** sp. nov.

Fig. 2.5

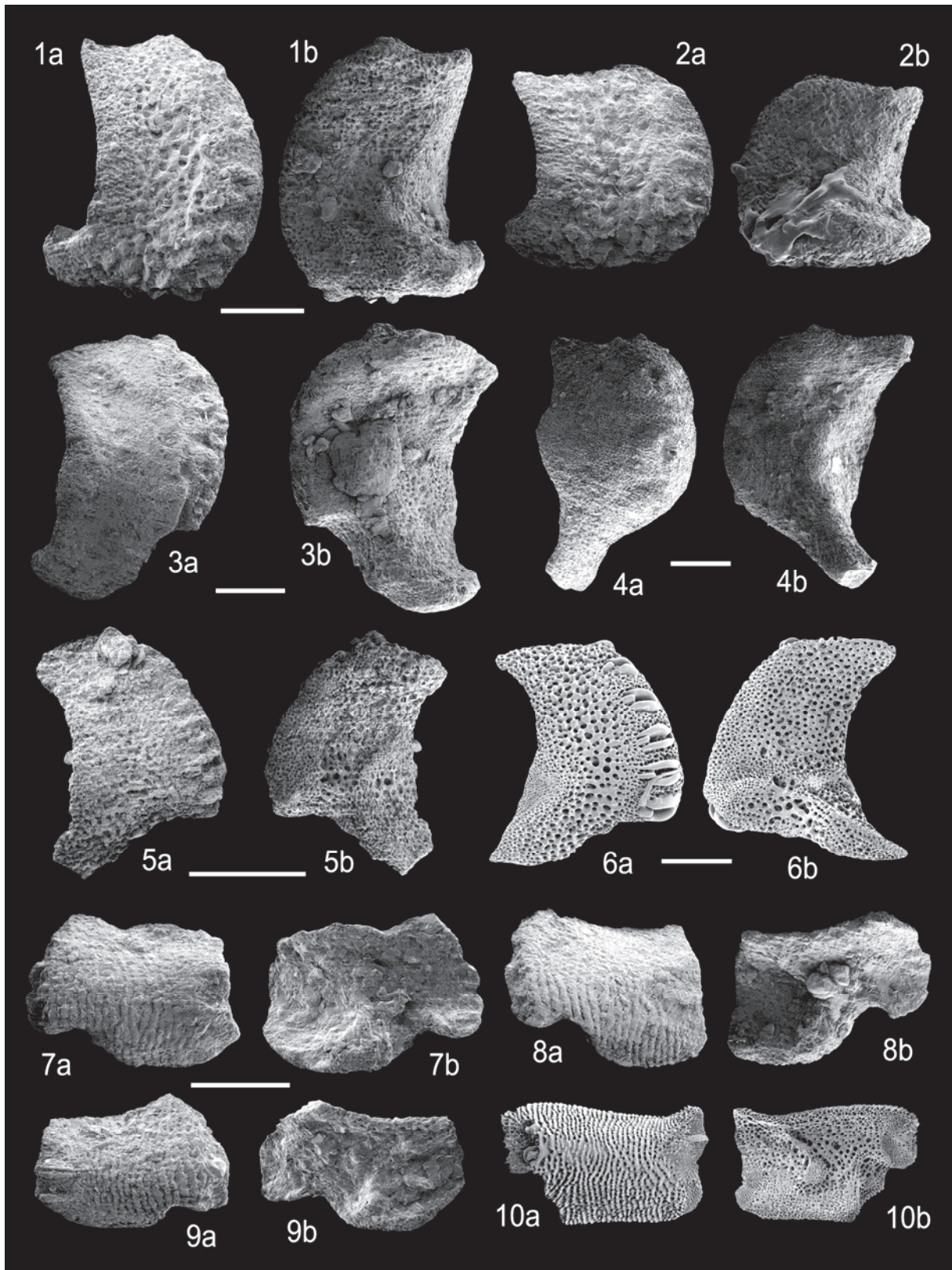
**Material examined.** – GZG.INV.78830 (figured dissociated LAP) and GZG.INV.78831 (8 dissociated LAPs) from Cuchía 2, and GZG.INV.78832 (3 dissociated LAPs) from Cuchía 1.

**Description.** – Very small, dissociated LAPs, proximal ones slightly higher than wide, distal ones nearly as high as wide; LAP outline triangular and strongly arched; dorsal edge straight to weakly convex; distal edge strongly convex; proximal edge strongly concave; ventral quarter of LAP conspicuously ventro-proximalwards protruding; outer surface with coarsely meshed stereom, becoming finer towards spine articulations; diffuse are of more finely meshed stereom in the centre of the proximal edge, non-prominent and non-protruding. Five equal-sized, nearly equidistant spine articulations integrated into outer surface stereom of distal LAP edge; spine articulations composed of two straight, parallel horizontally elongate equal-sized lobes separated proximally by a single, lens-shaped knob extending beyond lobes proximally; ventralmost spine articulation on ventro-distal tip of LAP; gap between spine articulations and distal edge of LAP very narrow.

Inner side of LAP with moderately well defined, short, strongly bent ridge with ventro-distalwards pointing tip and higher, slightly less well defined ventro-proximalwards pointing tip; no spurs on inner side of distal edge; no clearly defined perforation but very weakly defined, shallow, vertical furrow between distal tip of ridge and distal edge of LAP; inner side of tentacle notch moderately well defined, deep.

**Remarks.** – The above described LAPs display the highly distinctive, triangular, strongly bent outline combined with coarsely meshed outer surface stereom, spine articulations composed of two parallel lobes separated proximally by a single lens-shaped knob extending beyond the lobes proximally, and a strongly bent ridge, which unequivocally places them in the extant amphiurid genus *Amphilimna* (Fig. 2.6). Although the material available is sparse and rather poorly preserved, precluding a formal description, the find is remarkable. In fact, it represents the first fossil record of the genus, and one of the very few Lower Cretaceous occurrences of the Amphiuridae. It even marks the second oldest amphiurid record, after *Xanthamphiura hanteriviensis* Hess, 1970 from the Hauterivian of Switzerland, thus endorsing the assumption that much of the early divergence of the family took place in the Early Cretaceous (Stöhr et al. 2012).

**Occurrence.** – Early Aptian of Cuchía, Spain.



**Fig. 2:** (1–2) *Ophiacantha* sp. nov., dissociated LAPs in external (a) and internal (b) views from the early Aptian of Cuchía, Spain; (1) proximal LAP (GZG.INV.78820), (2) distal LAP (GZG.INV.78821) (both Cuchía 2 sample). (3) *Dermocoma* sp. nov., dissociated proximal LAP (GZG.INV.78824) in external (a) and internal (b) views from the early Aptian of Cuchía, Spain (Cuchía 2 sample). (4) *Ophiojagtus* sp. nov., dissociated proximal LAP (GZG.INV.78827) in external (a) and internal (b) views from the early Aptian of Cuchía, Spain (Cuchía 2 sample). (5) *Amphylimna* sp. nov., dissociated proximal LAP (GZG.INV.78830) in external (a) and internal (b) views from the early Aptian of Cuchía, Spain (Cuchía 2 sample). (6) *Amphylimna olivacea*, recent, proximal LAP in external (a) and internal (b) views. (7–9) *Ophioleuce sanmigueli* sp. nov., dissociated LAPs in external (a) and internal (b) views; (7) proximal LAP (holotype, GZG.INV.78833) (Cuchía 1 sample), (8) median LAP (paratype, GZG.INV.78835) (Cuchía 2 sample), (9) distal LAP (paratype, GZG.INV.78834) (Cuchía 1 sample). (10) *Ophioleuce brevispinum*, Recent, median LAP in external (a) and internal (b) views. All scale bars equal 250  $\mu$ m.

Family **Ophiuridae** Müller & Troschel, 1840  
 Subfamily **Ophioleucinae** Matsumoto, 1915

Genus **Ophioleuce** Koehler, 1904

*Type species.* – *Ophioleuce seminudum* Koehler, 1904

*Diagnosis for LAPs.* – Small, fragile LAPs generally with a low height/width ratio; outer surface ornamentation commonly consisting in a vertical striation composed of overlapping lamellae; commonly well developed, horizontally elongate spurs on the outer proximal and inner distal edges; tentacle notch moderately deep, with ventro-distal tip of LAP weakly projecting ventralwards; inner side of LAP generally with a simple, narrow ridge, in some cases continuous, in some cases divided in two parts.

***Ophioleuce sanmigueli* sp. nov.**

Figs. 2.7–9

*Etymology.* – The species is dedicated to the family of Basilio Coz San Miguel in Boo de Pielagos (Cantabria, northern Spain) for the friendship and support throughout the years to one of us (FW).

*Diagnosis.* – Species of *Ophioleuce* with very small, fragile LAPs; proximal LAPs 1.5 times wider than high; weakly developed constriction; two well defined, horizontally elongate spurs on the outer proximal and inner distal edges; outer surface almost completely covered by fine, regular vertical striation composed of overlapping lamellae with smooth distal edge proximally, and coarsely denticulate distal edge distally; three small spine articulations with dorsalward decrease in size; tentacle notch moderately deep, with ventro-distal tip of LAP weakly projecting ventralwards; inner side of LAP with simple, continuous, narrow ridge devoid of widened parts.

*Type locality and horizon.* – Cuchía 1 sample, Marl Member of the Caranceja Formation, *Deshayesites weissi* Zone, middle early Aptian of Cuchía, Cantabria, Spain.

*Type material.* – GZG.INV.78833 (holotype); GZG.INV.78834 (paratype) from Cuchía 1 and GZG.INV.78835 (paratype) from Cuchía 2.

*Additional material.* – GZG.INV.78836 (8 dissociated LAPs) from Cuchía 2, and GZG.INV.78837 (5 dissociated LAPs) from Cuchía 1.

*Description of holotype.* – GZG.INV.78833 is a very small, dissociated proximal LAP of very fragile aspect; approximately 1.5 times wider than high; dorsal edge slightly fragmented, originally concave as a result of a weak constriction; ventral quarter of LAP protruding ventralwards, with slightly angular, convex ventral edge; distal edge irregularly convex; proximal edge nearly straight, with two sharply defined, lens-shaped, horizontally elongate, prominent but only very weakly protruding spurs; dorsal spur

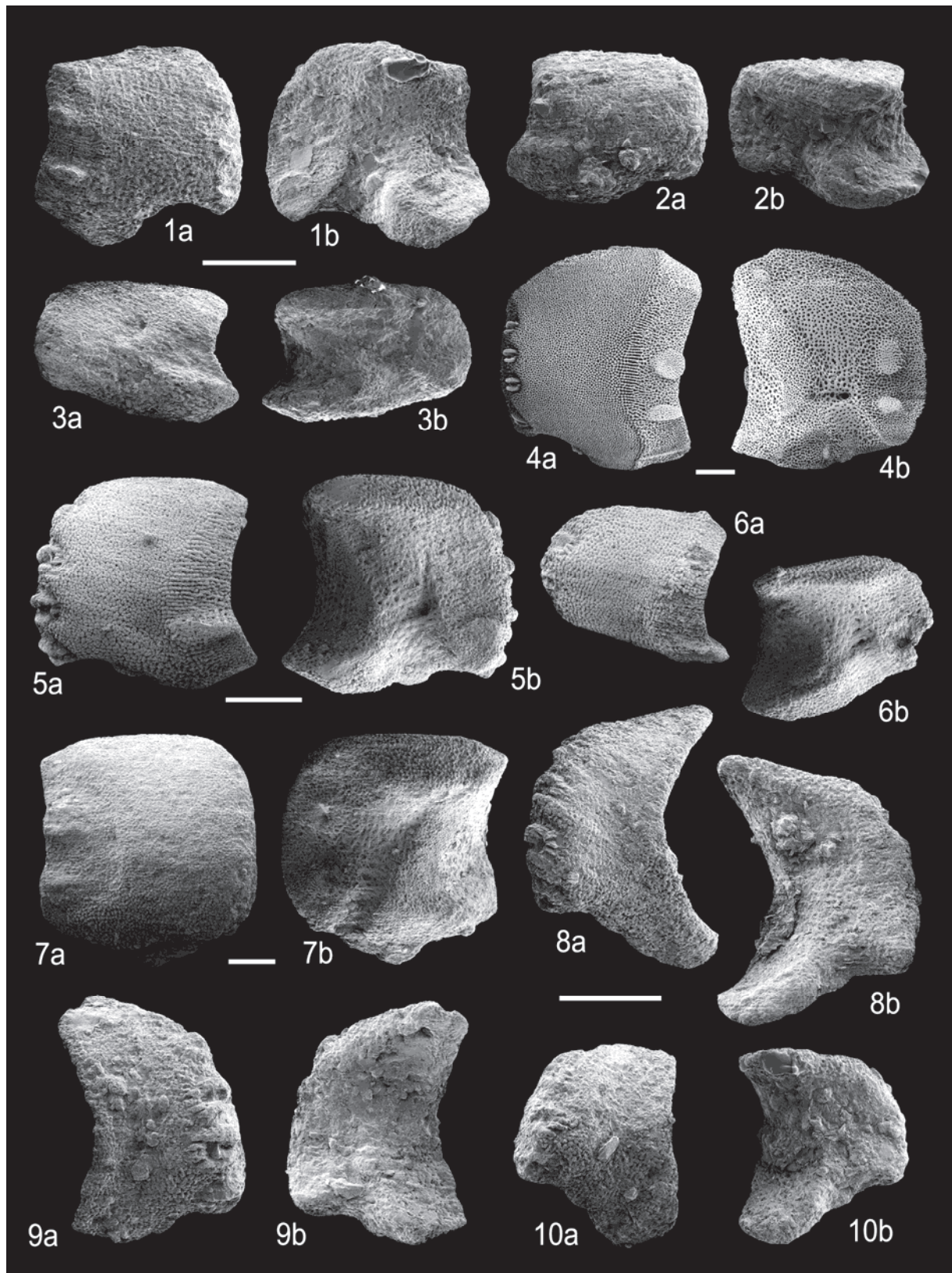
slightly larger than ventral one; slightly depressed area between spurs; outer surface predominantly covered by fine, regular vertical striation composed of distalwards overlapping, thin lamellae; distal edge of lamellae smooth in proximal lamellae, and coarsely denticulate in distal ones; lamellae replaced by finely meshed stereom in dorso-proximal area of outer surface; ventral portion of LAP entirely covered by striation. Three small, inconspicuous spine articulations inserted in deep notches of the distal LAP edge; weak dorsalward decrease in size of spine articulations and of gaps separating them; spine articulations composed of a small, thin, vertically elongate and nearly straight proximal lobe overlapped by distalmost lamella of outer surface striation, and slightly larger, higher, vertically elongate but bent distal lobe; gap between spine articulations and distal edge of LAP composed of very thin stereom, narrower than one spine articulation, widest ventrally and rapidly decreasing in width dorsalwards. Tentacle notch large, comparatively deep and well defined, with ventro-distal tip of LAP slightly projecting ventralwards.

Inner side of LAP with sharply defined, narrow simple ridge devoid of thickened parts and composed of a nearly straight, oblique dorsal portion; ventral portion of the ridge half as long as the dorsal one, connected with the latter by a gentle kink and with ventral tip sharply separated from inner side of ventral LAP portion; inner side of distal edge with two well defined, horizontally elongate, prominent but not protruding spurs; ventral spur larger than dorsal one; inner side of tentacle notch sharply defined, distally and proximally bordered by slightly thickened edge. No perforations or vertical furrow discernible.

*Paratype supplements and variation.* – GZG.INV.78835 is a very small, dissociated proximal to median LAP, approximately 1.5 times wider than high; dorsal edge evenly concave; ventral portion amounting for almost one third of the total LAP height; spurs on proximal edge of LAP similar to those of holotype but dorsal spur slightly smaller than ventral one; outer surface ornamentation as in holotype. Three spine articulations similar in shape, size, position and arrangement to those of holotype. Tentacle notch slightly deeper than in holotype, with ventro-distal tip of LAP slightly more strongly projecting ventralwards. Inner side well in agreement with that of holotype. Ridges on inner distal edge slightly smaller and less well defined than in holotype.

GZG.INV.78834 is a very small, dissociated distal LAP, almost two times wider than high; dorsal edge evenly concave; ventral portion accounting for one fifth of the total LAP height; spurs on outer proximal edge as in holotype but dorsal one much larger than ventral one; outer surface ornamentation as in holotype, with slightly better developed coarsely denticulate distal edge of the distal lamellae. Three spine articulations similar in size, shape, position and arrangement to those of holotype. Inner side partly obscured by sediment but well in agreement with holotype as far as discernible.





**Fig. 3:** (1–3) *Ophiozonella eloy* sp. nov., dissociated LAPs in external (a) and internal (b) views, from the early Aptian of Cuchía, Spain; (1) proximal LAP (holotype, GZG.INV.78838), (2) median LAP (paratype, GZG.INV.78839) (both Cuchía 1 sample), (3) distal LAP (paratype, GZG.INV.78840) (Cuchía 2 sample). (4) *Ophiozonella nivea*, recent, proximal LAP in external (a) and internal (b) views. (5–6) *Ophiozonella thomasi* sp. nov., dissociated LAPs from the latest Aptian of Wizard Way, Texas; (5) proximal LAP (holotype, GZG.INV.78843), (6) distal LAP (paratype, GZG.INV.78844). (7) *Ophiotitanos?* sp., dissociated median(?) LAP (GZG.INV.78845) in external (a) and internal (b) views, from the early Aptian of Cuchía, Spain (Cuchía 2 sample). (8–10) *Ophiodoris?* sp. nov., dissociated LAPs in external (a) and internal (b) views, from the early Aptian of Cuchía, Spain; (8) proximal LAP (GZG.INV.78848), (9) proximal LAP (GZG.INV.78849) (both Cuchía 2 sample), (10) median to distal LAP (GZG.INV.78851) (Cuchía 1 sample). All scale bars equal 250  $\mu$ m.

**Remarks.** – The very fragile nature of the above described LAPs, the fine vertical striation, the comparatively deep tentacle notches as well as the spine articulations composed of a straight vertical proximal lobe and a slightly larger, bent vertical distal lobe, defined by Martynov (2010) as irregular rhombic spine articulation, strongly favours an assignment to the ophiurid subfamily Ophioleucinae (Fig. 2.10). Knowledge on the fossil record of this group has been rather sparse so far. Hess (1964) introduced the new genus *Sinosura* for fossil ophiuroid remains from the Pliensbachian of the United Kingdom and discussed possible ophioleucinid affinities of the new genus.

Smith et al. (1995) tentatively placed *Sinosura* in the Ophioleucinae, a view later challenged by Hess & Meyer (2008) but then again explicitly endorsed by Thuy et al. (2011) on the basis of new observations on pristinely preserved material. *Ophiopinna* Hess, 1960 from the Callovian of France is another fossil ophiuroid for which ophioleucinid affinities have been suggested (Hendler & Miller 1991). A third fossil ophiuroid with supposed ophioleucinid affinities was described by Thuy (2011) as *Eirenura papillata* Thuy, 2011, from the Pliensbachian of France. Recently, ophiuroid material from Aptian deep-sea sediment cores were assigned to the extant genus *Ophiolence* on the basis of striking similarities in LAP morphology with recent *Ophiolence brevispinum* (H. L. Clark, 1911) (Thuy et al. 2012).

The above described ophioleucinid occurrence thus significantly adds to the rather fragmentary knowledge of the fossil record of a seemingly ancient but poorly documented ophiuroid group. On genus level, the LAPs in question are incompatible with any of the currently known fossil genera with supposed ophioleucinid affinities. LAPs of *Sinosura* generally have significantly more spine articulations, deeper tentacle notches and differently shaped ridges on the inner side. In *Ophiopinna*, some of the LAPs display highly distinctive articulations for the feather-shaped arm spines, and *Eirenura* has relatively high, rectangular LAPs with numerous spine articulations and a very weak vertical outer surface striation composed of small scales arranged in vertical rows. Among the extant representatives of the Ophioleucinae, however, striking similarities in LAP morphology are shared with *Ophiolence*. The above described LAPs are thus assigned to this genus. Confusion with the probable congener from the Aptian deep-sea sediments of the North Atlantic (Thuy et al. 2012) is precluded on account of the discontinuous ridge on the inner side of the latter.

Recent representatives of the Ophioleucinae are restricted to deep-sea settings (Thuy et al. 2012). The here described material from shallow marine deposits represents the youngest record of the family at shelf depths.

**Occurrence.** – Early Aptian of Cuchía, Spain.

## Family **Ophiolepididae** Ljungman, 1867

### Genus **Ophiozonella** Matsumoto, 1915

**Type species.** – *Ophiozonella longispina* H. L. Clark, 1908

**Diagnosis for LAPs:** Ophiolepidid with rather stout, compact LAPs with straight to evenly convex rather than pointed dorsal edge; relatively small ventral portion protruding ventro-proximalwards; outer proximal and inner distal edges generally with one or two well developed, horizontally elongate spurs composed of densely meshed but not massive stereom; relatively small spine articulations composed of nearly parallel dorsal and ventral lobes connected proximally by one to three minute knobs; large and deep tentacle notch; inner side of LAPs with poorly defined and weakly prominent, vertical, slightly proximalwards bent ridge.

### **Ophiozonella eloy** sp. nov.

Figs. 3.1–3

**Etymology.** – Species named after the Family Eloy in Lenceres (Cantabria). The Bar Eloy and the Autoservicio Eloy have been important alimentation, information and social centres for one of the authors (F.W.) during his large number of field campaigns to the area since 1990.

**Diagnosis.** – Species of *Ophiozonella* with relatively small LAPs, two spurs on the outer proximal and inner distal edges; ventral spurs larger than the dorsal one; fine horizontal striation between the spurs, at least in proximal LAPs; up to four small, nearly equal-sized spine articulations integrated into the outer surface stereom of the distal LAP edge; relatively deep tentacle notch; ridge on inner side poorly defined, weakly prominent, proximalwards bent; inner side of tentacle notch encompassed distally and proximally by thickened edges.

**Type locality and horizon.** – Cuchía 1 sample, Marl Member of the Caranceja Formation, *Deshayesites weissi* Zone, middle early Aptian of Cuchía, Cantabria, Spain.

**Type material.** – GZG.INV.78838 (holotype); GZG.INV.78839 (paratype) from Cuchía 1 and GZG.INV.78840 (paratype) from Cuchía 2.

**Additional material.** – GZG.INV.78841 (43 dissociated LAPs) from Cuchía 1, and GZG.INV.78842 (141 dissociated LAPs) from Cuchía 2.

**Description of holotype.** – GZG.INV.78838 is a small, dissociated proximal LAP, nearly as high as wide; dorsal edge straight; distal edge evenly convex; ventral fifth of LAP protruding ventro-proximalwards; proximal edge concave with two well defined, oval, horizontally elongate, prominent but only weakly protruding spurs, ventral one larger than dorsal one; proximal edge of LAP lined by an area of finely meshed stereom, encompassing spurs, and with fine

horizontal striation between the spurs; remaining outer surface of LAP with moderately coarsely meshed stereom. Four small spine articulations integrated into outer surface stereom near distal edge of LAP; spine articulations nearly equidistant and of similar size except for slightly smaller dorsalmost one; small, short, horizontally elongate dorsal and ventral lobes of spine articulation proximally connected by two to three small, round knobs; gap between spine articulations and distal edge of LAP slightly narrower than one spine articulation. Tentacle notch large, well defined and relatively deep, with ventro-distal tip of LAP projecting ventralwards.

Inner side of LAP with poorly defined, weakly prominent, slightly proximalwards bent vertical ridge; ventral part of ridge not merged with thickened ventral edge of LAP, better defined and more strongly prominent than dorsal part of ridge; inner side of distal edge with two well defined, oval, horizontally elongate spurs, ventral one of which clearly larger than dorsal one; inner side of tentacle notch conspicuously well defined, large, deep, distally and proximally encompassed by thickened edges. No perforations or vertical furrow discernible.

**Paratype supplements and variation.** – GZG.INV.78839 is a small, dissociated median LAP, slightly wider than high; generally well in agreement with holotype; dorsal edge weakly convex; two spurs on proximal edge, slightly larger but less well defined than in holotype; fine horizontal striation between spurs not discernible. Three small, poorly preserved spine articulations seemingly similar to those of holotype; dorsal gap between spine articulations slightly larger than ventral one. Tentacle notch shallower than in holotype. Ridge on inner side of LAP very poorly defined, slightly shorter and more strongly bent than in holotype; spurs on inner side of distal edge hardly discernible; inner side of dorsal thickened.

GZG.INV.78840 is a small, dissociated distal LAP, approximately 1.5 times wider than high; dorsal edge weakly convex; two spurs on outer proximal edge, much larger than in holotype but less sharply defined; ventral spurs conspicuously larger than dorsal one; no fine horizontal striation discernible between spurs; Three small, nearly equidistant spine articulations similar to those of holotype. Tentacle notch much shallower than in holotype. Ridge on inner side as in holotype but more strongly oblique; two spurs on inner distal edge large but very weakly defined; inner side of dorsal edge thickened.

**Remarks.** – The above described LAPs show striking similarities with those of extant ophiolpidid *Ophiozonella*, in particular *O. nivea* (Lyman, 1875) (Fig. 3.4) on account of the shape, number and size of the spine articulations, the two spurs on the outer proximal and inner distal edges, the presence of a fine horizontal striation associated the spurs, and the shape of the ridge on the inner side. The material in question is thus assigned to the extant genus *Ophiozonella*. Very similar LAPs were described as *Ophiozonella stoebræ* Thuy & Kroh, 2011 from the Barremian of

France. These differ, however, in displaying much larger spine articulations, a single spur on the outer proximal and inner distal edges and a much more sharply defined ridge on the inner side. The same holds true for the LAPs of the slightly younger *Ophiozonella thomasi* sp. nov. (see below).

The here described Aptian specimens share similarities with some of the dissociated LAPs assigned to the extinct genus *Ophiopetra* Enay & Hess, 1962, in particular *Ophiopetra batbonica* Hess, 1964 and some of the LAP types described as *Ophiopetra?* *oertlii* Hess, 1965 (Hess 1965a; Kutscher 1996). The type species *Ophiopetra lithographica* Enay & Hess, 1962, in contrast, most probably belongs to the Ophiacanthidae, as a recent re-examination of the type material surprisingly revealed (previously unpublished). Disentangling the *Ophiopetra*-complex and correctly re-assigning the different species and LAP types exceeds the scope of the present study. The relevant point here is that assignment of the above described LAPs to *Ophiopetra* can be excluded on account of the probably ophiacanthid affinities of the type species.

**Occurrence.** – Early Aptian of Cuchía, Spain.

### *Ophiozonella thomasi* sp. nov.

Figs. 3.5–6

**Etymology.** – Species named in honour of Thomas Daniel, for his friendship and his inestimable support to one of the authors (BT) of this study during the years in Göttingen.

**Diagnosis.** – Species of *Ophiozonella* with medium-sized LAPs of rounded squarish outline; ventral sixth of LAP protruding ventro-proximalwards; single well defined spur on the outer proximal and inner distal edges; outer surface with finely meshed stereom, with trabecular intersections transformed into tiny, polygonal tubercles; up to four relatively large spine articulations; inner side with moderately well defined, weakly prominent ridge with slightly widened dorsal tip.

**Type locality and horizon.** – Wizard Way, Texas, USA; Echinoid Marker Bed of Smith & Rader (2009), base of Unit 2 of the Lower Member of the Glen Rose Formation, latest Aptian.

**Type material.** – GZG.INV.78843 (holotype); GZG.INV.78844 (paratype).

**Description of holotype.** – GZG.INV.78843 is a medium-sized, dissociated proximal LAP, nearly as high as wide and of rounded squarish aspect; dorsal edge weakly convex; distal edge evenly convex; proximal edge evenly concave, with a single, large, well defined, prominent but not protruding, horizontally elongate spur composed of slightly more densely meshed stereom than remaining proximal edge and positioned in the middle of the ventral half of the edge; band of conspicuous, fine horizontal striation lining

proximal edge, widest in the middle of the proximal edge, more quickly narrowing dorsalwards than ventralwards; ventral sixth protruding ventro-proximalwards; outer surface with finely meshed stereom, with trabecular intersections developed into small polygonal tubercles. Four relatively large, nearly equal-sized spine articulations in shallow notches of distal edge of LAP, composed of parallel, horizontal dorsal and ventral lobes connected proximally by one to three small knobs; weak dorsalward increase in size of gaps separating spine articulations; gap between spine articulations and distal edge extremely narrow. Large, well defined but relatively shallow tentacle notch, with conspicuous, convex, ventralwards pointing protrusion in the proximal half of the notch.

Inner side of LAP with narrow, moderately well defined, weakly prominent, slightly oblique ridge with weakly widened dorsal tip; ventral tip of ridge not merged with thickened ventral edge of LAP; dorsal and ventral parts of the ridge connected by a very gently kink; inner side of distal edge with relatively small, poorly defined, slightly horizontally elongate, oval, weakly prominent knob; large, slightly irregular perforation between the kink of the ridge and the distal edge of the LAP, with well defined, short, dorsalwards projecting vertical furrow; inner side of tentacle notch large, well defined, distally and proximally bordered by thickened edges.

**Paratype supplements.** – GZG.INV.78844 is a medium-sized, dissociated distal LAP, approximately 1.5 times wider than high; generally well in agreement with holotype; spur on proximal edge less well defined and very close to the ventro-proximal tip of the LAP; band of fine horizontal striation lining proximal edge less well developed than in holotype; three spine articulations similar in shape, size, position and arrangement to those of holotype; ventralmost spine articulation largely lost due to fragmentation of the plate; tentacle notch very shallow.

Ridge on inner side of LAP similar to that of holotype but shorter and slightly more strongly bent; ventro-distal edge of LAP broken, no spur discernible; perforation between kink of ridge and distal edge of LAP slightly smaller than in holotype and dorsally bordered by two smaller perforations rather than furrow; tentacle notch as in holotype.

**Remarks.** – Assignment of the above described LAPs to *Ophiozonella* is based on the striking similarities with the LAPs of modern representatives of the genus, in particular with respect to the shape of the LAPs, the size, position and shape of the spine articulations, the ornamentation of the outer proximal edge, the shape of the ridge on the inner side and the development of the tentacle notch. LAPs of the slightly older congener *Ophiozonella eloy* sp. nov. from Spain (see above) can be easily distinguished since they display two spurs on the outer proximal and inner distal edges, much smaller spine articulations, deeper tentacle notches and a less well defined ridge on the inner side. Greatest similarities are shared with the LAPs of

*Ophiozonella stoebræ* from the Barremian of France (Thuy & Kroh 2011). These differ in the larger ventro-proximalwards projecting ventral portion, the irregular vertical striation on the outer surface, the absence of the band of fine horizontal striation lining the outer proximal edge, and the more strongly prominent ridge on the inner side.

Although the amount of material is very limited, the LAPs at hand are so clearly distinctive, also thanks to the excellent preservation, that they are taken here as a basis for the description of a new species.

**Occurrence.** – Latest Aptian of Wizard Way, Texa, U.S.A.

#### Family **Ophiidermatidae** Ljungman, 1867

##### Genus **Ophiotitanos** Spencer, 1907

**Type species.** – *Ophiotitanos tennis* Spencer, 1907

**Diagnosis for LAPs.** – Ophiidermatid with large LAPs of stout, massive aspect; two well defined, prominent and protruding spurs on outer proximal edge, paralleled by two well defined, weakly prominent spurs on inner distal edge; no fine horizontal striation on outer proximal edge; numerous (generally more than six) small spine articulations sunken in shallow notches of distal edge; inner side ventral tip of LAP devoid of strongly prominent knobs; tentacle notch commonly developed as within-plate perforation in distal and, in some cases, even median LAPs.

##### **Ophiotitanos?** sp.

Fig. 3.7

**Material examined.** – GZG.INV.78845 (figured LAP) and GZG.INV.78846 (8 dissociated LAPs) from Cuchía 2, and GZG.INV.78847 (one dissociated LAP) from Cuchía 1.

**Description.** – Large, dissociated median to distal LAPs of very stout and massive aspect, rounded squarish in outline; nearly as high as wide to slightly wider than high; dorsal, ventral and distal edges evenly convex; proximal edge concave with two large, nearly equal-sized, moderately well defined, prominent but weakly protruding, horizontally elongate spurs in slightly sunken, semicircular depression of proximal edge; outer surface with very finely meshed stereom with trabecular intersections transformed into tiny tubercles in some plates merged into short vertical rows near ventral edge of LAP; up to five very small, nearly equal-sized and equidistant spine articulations sunken into shallow notches of distal edge of LAP; spine articulations composed of two oblique lobes, a slightly curved dorsal one and a smaller, straight ventral one; gap between spine articulations and distal edge of LAP narrower than one spine articulation. Tentacle notch invisible in external view.

Inner side of LAPs with relatively large, moderately well defined, prominent, tongue-shaped, vertical ridge, with rounded proximalwards bent dorsal tip and slightly widened, ventralwards pointing ventral tip not merged with ventral edge of LAP; inner side of distal edge of LAP with two large, nearly equal-sized, poorly defined and weakly prominent spurs composed of slightly more finely meshed stereom; dorsal and ventral edges of LAP thickened; tentacle notch developed as narrow, sharply defined, oblique furrow. No perforations discernible.

**Remarks.** – The above described LAPs share greatest similarities with the LAPs figured by Thuy & Kroh (2011: pl. 4, figs. 2-3) as *Ophiotitanos* sp., with respect to the stout and massive general aspect, the rounded squarish outline, the shape, size and position of the spine articulations, the two spurs on the outer proximal and inner distal edges, the shape of the ridge on the inner side and the development of the tentacle notch. Assuming that the here described LAPs are, indeed, median to distal ones, they are best assigned to the extinct genus *Ophiotitanos*. Given the sparse nature of the material available, however, it cannot be ruled out that the LAPs in question are, in fact, proximal ones of a yet unknown genus. In the light of these uncertainties, the LAPs at hand are best treated as an unnamed record tentatively assigned to *Ophiotitanos*.

In any case, spine articulation morphology in combination with the two spurs on the outer proximal and inner distal edges and the tongue-shaped ridge on the inner side strongly suggest ophiidermatid affinities. Thuy & Kroh (2011) transferred *Ophiotitanos* to the Ophiuridae, arguing that the distal tentacle openings developed as within LAP perforations challenge assignment to the Ophiidermatidae. New investigations on distalmost LAPs of recent ophiidermatids, however, revealed that within-plate perforations are not uncommon in a number of genera, among others *Ophiarachnella* Ljungman, 1872. We thus re-transfer *Ophiotitanos* to the Ophiidermatidae, in agreement with Kutscher & Jagt (2000), stressing, however, that the general skeletal morphology of *Ophiotitanos* is in need of reappraisal in order to definitely clarify its higher taxonomic position.

**Occurrence.** – Early Aptian of Cuchía, Spain.

Family **Ophionereididae** Ljungman, 1867

Genus ***Ophiodoris*** Koehler, 1904

**Type species.** – *Ophiodoris malignus* Koehler, 1904

**Diagnosis for LAPs.** – Ophionereidid with relatively small, fragile LAPs displaying a large, ventro-proximalwards protruding ventral portion; outer surface covered by small to medium-sized tubercles; large spine articulations in shallow notches of weakly bulging distal portion of LAP; spine articulations composed of a large, horizontally elongate,

slightly bent dorsal lobe and a smaller, horizontally elongate, straight ventral lobe; both lobes proximally separated by one to three slightly horizontally elongate knobs; inner side of LAPs with well defined ridge composed of a nearly vertical dorsal part with a ventralwards pointing extension on its ventral tip, a strongly oblique median part and a less well defined ventro-proximalwards pointing ventral part; single, large perforation near kink between median and ventral ridge parts.

***Ophiodoris?* sp. nov.**

Figs. 3.8–10

**Material examined.** – GZG.INV.78848 (figured LAP), GZG.INV.78849 (figured LAP) and GZG.INV.78850 (148 dissociated LAPs) from Cuchía 2, and GZG.INV.78851 (figured LAP) and GZG.INV.78852 (91 dissociated LAPs) from Cuchía 1.

**Description.** – Very small, dissociated LAPs, proximal ones slightly higher than wide, sickle-shaped; median and distal ones as wide as long to slightly wider than long, not sickle-shaped; dorsal edge oblique, straight in proximal LAPs, weakly convex in median to distal ones; dorso-proximal tip conspicuously pointed in proximal LAPs; distal edge evenly convex; proximal edge evenly concave, with poorly defined, almost indiscernible and very weakly protruding thickened central part; ventral third protruding ventro-proximalwards, conspicuously narrow in proximal LAPs; outer surface covered by very small tubercles, merged into very weak, irregular vertical rows near spine articulations. Four (proximal LAPs) to three (distal LAPs) large spine articulations in very shallow notches of slightly bulging distal portion of LAPs; spine articulations composed of a large, horizontally elongate, slightly bent dorsal lobe and a smaller, horizontally elongate, straight ventral lobe; both lobes proximally separated by two to three small, elongate knobs; spine articulations nearly equidistant, separated by tubercles of outer surface stereom; median spine articulations slightly larger than dorsalmost and ventralmost ones. Tentacle notch very large, relatively shallow.

Inner side of LAPs with moderately well defined, narrow ridge composed in proximal LAPs of a nearly vertical, straight dorsal part, a more strongly oblique, poorly defined median part and a similarly poorly defined ventro-proximalwards pointing ventral part not merged with ventral edge of LAP; ventral tip of dorsal part with poorly defined ventralwards pointing extension; all parts connected with rounded kinks; inner side of distal LAPs too poorly preserved to allow for distinction of ridge morphology; single, relatively large perforation near kink between median and ventral parts of ridge, with weakly defined, shallow vertical furrow projecting dorsalwards from perforation; inner side of tentacle notch large, well defined, distally and proximally encompassed by thickened edges.

**Remarks.** – The above described LAPs display a highly distinctive spine articulation morphology exclusively found in the LAPs of extant Ophionereididae and in some representatives of the Ophiochitonidae (Martynov 2010). The shape of the ridge on the inner side in combination with a single large perforation further endorses these affinities. The sickle-shaped outline of the LAPs, the outer surface ornamentation and the rather shallow tentacle notch not encompassed distally by a ventralwards protruding ventro-distal tip of the LAP favour assignment to the Ophionereididae. Within this family, similarities are greatest with *Ophiodoris* on account of the more fragile aspect of the LAPs but assignment to any of the other four ophionereidid genera cannot be satisfyingly ruled out as long as the respective LAPs have not been examined in detail. On account of this preliminary observation as well as the striking similarities with the LAPs of slightly younger *Ophiodoris holterhoffi* sp. nov. (see below), known from more conclusive material, we tentatively refer the above described LAPs to *Ophiodoris*. They can be easily told apart from the LAPs of *Ophiodoris holterhoffi* sp. nov. due to the pointed dorso-proximal tip, the two to three knobs separating the dorsal and ventral lobes of the spine articulations, and the outer surface ornamentation.

**Occurrence.** – Early Aptian of Cuchía, Spain.

***Ophiodoris holterhoffi* sp. nov.**

Figs. 4.1–8

**Etymology.** – Species named in honour of Frank Holterhoff, who kindly assisted one of the authors (A.S.G.) during fieldwork in Texas.

**Diagnosis.** – Species of *Ophiodoris* with very small, fragile LAPs; dorso-proximal tip of LAP truncated; outer surface with coarse tuberculation; up to four large spine articulations on slightly bulging distal edge of LAP, with dorsal and ventral lobes proximally separated by up to two medium-sized to large knobs.

**Type locality and horizon.** – Wizard Way, Texas, USA; Echinoid Marker Bed of Smith & Rader (2009), base of Unit 2 of the Lower Member of the Glen Rose Formation, latest Aptian.

**Type material.** – GZG.INV.78853 (holotype); GZG.INV.78854, GZG.INV.78855, GZG.INV.78856, GZG.INV.78857, GZG.INV.78858, GZG.INV.78859 and GZG.INV.78860 (paratypes).

**Additional material.** – GZG.INV.78861 (374 dissociated LAPs), GZG.INV.78862 (23 dissociated vertebrae) and GZG.INV.78863 (5 dissociated oral plates).

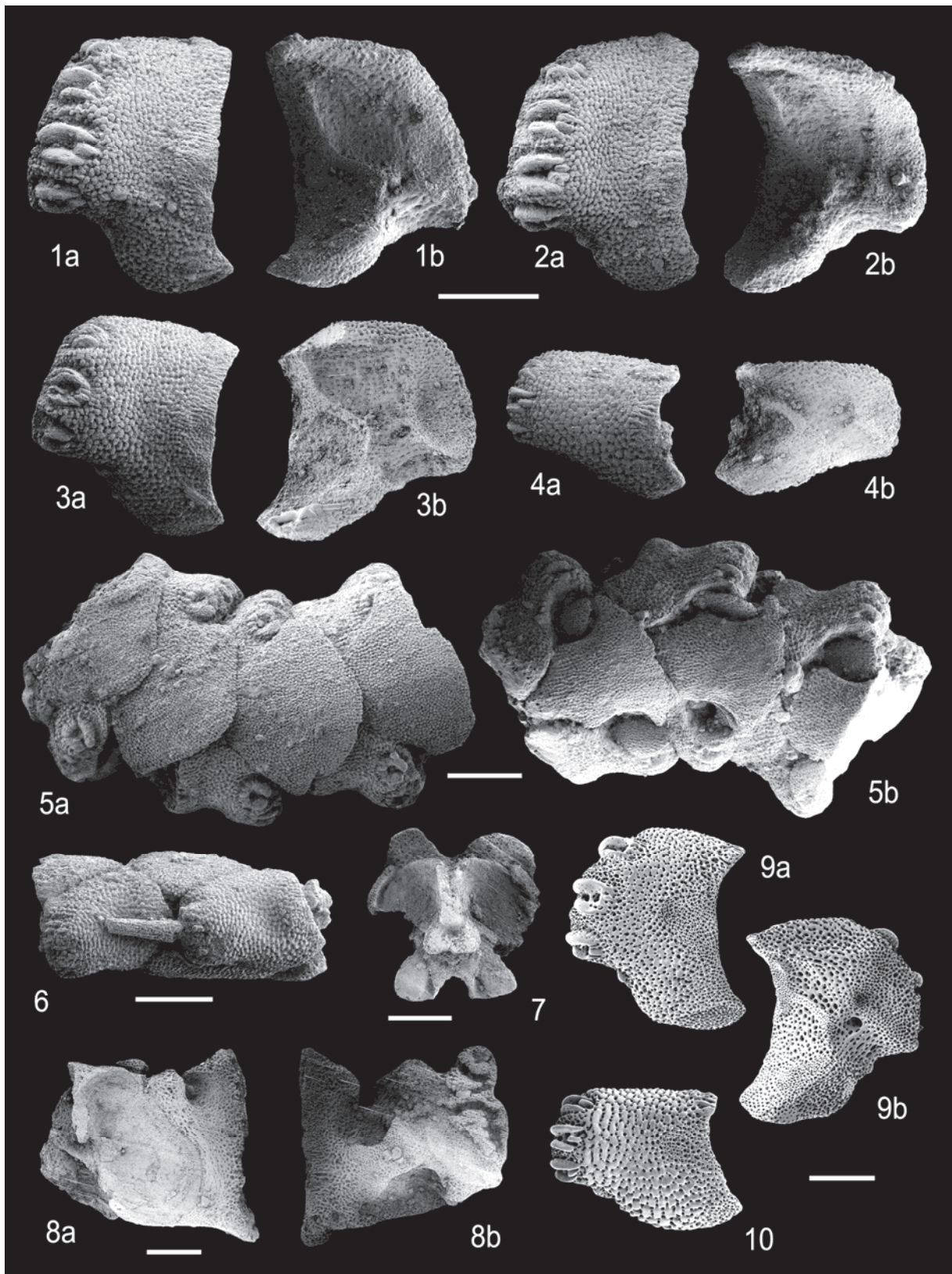
**Description of holotype.** – GZG.INV.78853 is a small, dissociated proximal LAP, slightly higher than wide; dorsal edge nearly straight; dorso-proximal tip truncated in external

view; distal edge gently convex; proximal edge weakly concave, with very weak, slightly prominent, poorly defined central protrusion; narrow band of fine, irregular horizontal striation lining proximal edge except for ventral quarter, widest around central protrusion; small, poorly defined, weakly prominent and non-protruding, horizontally elongate, thin spur near ventro-proximal tip of LAP; ventral quarter of LAP conspicuously protruding ventro-proximalwards; outer surface with coarse, tightly packed, slightly vertically elongate tubercles, coarsest around and between spine articulations, less densely packed on ventral portion of LAP. Four large, conspicuous, nearly equidistant spine articulations composed of a smooth, vertically elongate, slightly bent dorsal lobe and a smaller, smooth, vertically elongate and nearly straight ventral lobe; both lobes separated proximally by single, large knob; spine articulations in very shallow notches of weakly bulging distal portion of LAP; second ventralmost spine articulation largest, dorsalmost one smallest; gap between spine articulations and distal edge of LAP very narrow. Tentacle notch very large and deep.

Inner side of LAP with conspicuous, sharply defined, relatively narrow ridge composed of three parts; dorsal part slightly oblique, almost vertical, with widened ventralwards pointing extension on ventral tip; median part oblique, connected with dorsal and ventral parts by gentle kinks; ventral part well defined dorsally, becoming decreasingly prominent and well defined ventralwards but not merged with ventral edge of LAP; dorso-proximal tip pointed in internal view; inner side of distal edge devoid of spurs; single, medium-sized perforation distally bordering kink between median and ventral parts of ridge, with poorly defined, shallow, vertical furrow projecting dorsalwards from perforation; inner side of tentacle notch well defined, with coarsely meshed, slightly horizontally elongate stereom, encompassed distally and proximally by thickened edges.

**Paratype supplements and variation.** – GZG.INV.78854 is a small, dissociated proximal LAP; very well in agreement with holotype; dorsal and ventral lobes of spine articulations proximally separated by two medium-sized knobs rather than a single large one. Inner side as in holotype.

GZG.INV.78855 is a small, dissociated median LAP, nearly as high as wide; dorsal edge gently convex; proximal edge and outer surface ornamentation as in holotype, except for better defined, more strongly prominent small spur near ventro-proximal tip of LAP; ventral third of LAP protruding ventro-proximalwards. Three spine articulations similar in shape and position to those of holotype, except for two medium-sized knobs proximally separating dorsal and ventral lobes of spine articulations; median spine articulation slightly larger than ventral and dorsal ones. Inner side as in holotype, except for larger perforation but almost indiscernible vertical furrow dorsalwards projecting from the perforation.



**Fig. 4:** (1–8) *Ophiodoris holterhoffi* sp. nov. from the latest Aptian of Wizard Way, Texas. (1) proximal LAP (holotype, GZG.INV.78853), (2) proximal LAP (paratype, GZG.INV.78854), (3) median LAP (paratype, GZG.INV.78855), (4) distal LAP (paratype, GZG.INV.78856) [all in external (a) and internal (b) views], (5) proximal arm fragment (paratype, GZG.INV.78857) in dorsal (a) and ventral (b) views, (6) distal arm fragment (paratype, GZG.INV.78858) in lateral view, (7) vertebra (paratype, GZG.INV.78859) in dorso-distal view, (8) oral plate (paratype, GZG.INV.78860) in adradial (a) and abradial (b) views. (9–10) *Ophionereis porrecta*, recent; (9) proximal LAP in external (a) and internal (b) views, (10) distal LAP in external view. All scale bars equal 250 µm.

**Table 1:** Faunal spectra of the three assemblages described herein and of the Blake Nose assemblage described by Thuy et al. (2012) with additional data from Thuy (2013).

Family	Cuchía 1 & 2 (early Aptian)	Texas (latest Aptian)	Blake Nose (latest Aptian)
Ophiacanthidae	<i>Ophiacantha</i> sp. nov. <i>Ophiojagtus</i> sp. nov. <i>Dermocoma</i> sp. nov.	<i>Ophiojagtus acklesi</i>	<i>Ophiologimus martynovi</i> <i>Ophiologimus aiodipius</i> <i>Ophiotoma incredibilis</i> <i>Ophiolimna kucerai</i> <i>Ophiacantha</i> sp. nov. 1 <i>Ophiacantha</i> sp. nov. 2 <i>Ophiotreta</i> sp. nov. Ophiacanthid indet. <i>Ophiotholia</i> sp. nov.
Ophiomycetidae			
Ophiolepididae	<i>Ophiozonella eloy</i>	<i>Ophiozonella thomasi</i>	<i>Ophiomusium</i> sp. nov.
Ophiuridae	<i>Ophioleuce sanmigueli</i>		<i>Ophioleuce</i> sp. nov.
Ophiodermatidae	<i>Ophiotitanos?</i> sp.		
Amphiuridae	<i>Amphilimna</i> sp. nov.		
Ophionereididae	<i>Ophiodoris?</i> sp. nov.	<i>Ophiodoris holterhoffi</i>	

GZG.INV.78856 is a small, dissociated distal LAP; almost 1.5 times wider than high; dorsal edge very weakly convex; no spur discernible near ventro-proximal edge of LAP; ventral quarter of LAP protruding ventro-proximalwards. Three nearly equal-sized spine articulations similar in shape and position to those of holotype. Tentacle notch large but very shallow. Ridge on inner side relatively narrow, sharply defined, prominent, composed of an oblique, proximalwards bent dorsal part with a widened dorsal tip displaying a ventralwards projecting extension, and a less well defined ventral part; both parts of the ridge connected by a rounded kink; large, poorly defined perforation between kink and distal edge of LAP; no vertical furrow discernible; inner side of tentacle notch very large, well defined, encompassed distally and proximally by thickened edges.

GZG.INV.78857 is an articulated arm fragment composed of three proximal to median arm segments; LAP morphology well in agreement with holotype and other paratypes; dorsal arm plates very large, slightly wider than long, wider than half the total width of the arm; with rounded obtuse distal angle, pointed right lateral angles, and straight to slightly convex, latero-proximal edges; proximal angle not discernible, covered by neighbouring dorsal arm plates; outer surface of dorsal arm plates uniformly covered by tubercles, slightly smaller than tubercles covering outer surface of LAPs; neighbouring dorsal arm plates overlapping. No accessory dorsal arm plates. Ventral arm plates large, slightly longer than wide, widest distally, with weakly convex distal edge, pointed latero-distal tips, deeply concave tentacle notches on lateral edges, slightly concave latero-proximal edges and pointed proximal angles; outer surface of ventral arm plates uniformly covered by tubercles slightly smaller than those covering the outer surface of the LAPs; tentacle openings covered by a large, leaf-like, very weakly longitudinally striated scale; at least one much smaller additional scale on lateral edge of ventral arm plate. No arm spines preserved.

GZG.INV.78858 is an articulated arm fragment composed of two distal segments; LAP morphology well in agreement with distal paratype LAPs; dorsal arm plates slightly longer than wide, fan-shaped, with an evenly convex distal edge and an acute proximal angle; neighbouring dorsal arm plates separated by LAPs; ventral arm plates as in above described paratype except for higher length/width ratio; no tentacle scales discernible; one arm spine preserved, conical, with fine, irregular longitudinal striation; tip broken; preserved part of spine as long as half an arm segment; original spine length not exceeding the length of an arm segment.

GZG.INV.78859 is a small, dissociated vertebra with large, dorso-distal and dorso-proximal muscular fossae, and small ventro-proximal and small, distalwards protruding ventro-distal fossae; well developed keel projecting distalwards, associated with a deep groove on the proximal face.

GZG.INV.78860 is a dissociated oral plate, nearly as high as wide; very large, entire, kidney-shaped abradial muscular area forming a weak wing distally; adradial muscular area nearly half as high as oral plate, entire, narrow, ventro-proximalwards bent; ring nerve notch deep.

**Remarks.** – The highly distinctive spine articulation morphology combined with the coarse tuberculation of the outer surface, the single large perforation and the ridge on the inner side composed of three parts, and the large but rather shallow tentacle notch unequivocally place the above described LAPs in the family Ophionereididae (Figs. 5.9–10). The presence of distinctively keeled vertebrae (Stöhr et al. 2012) and oral plates strongly reminiscent of those of recent *Ophionereis variegata* Duncan, 1879 (Murakami 1963) co-occurring with the LAPs in question further endorse the ophionereidid affinities. The fortunate presence of articulated arm fragments leaves no doubt as to the genus-level placement of the material in question. In fact, *Ophiodoris* is the only extant ophionereidid genus lacking accessory dorsal arm plates. The here described fossil material thus either belongs to *Ophiodoris* or to a very



closely related yet unknown fossil genus. In the light of the striking similarities in dorsal and ventral arm plate morphology and tentacle scale pattern shared with the type species *Ophiodoris malignus*, assignment to *Ophiodoris* seems to be the best option at the present state of knowledge.

**Occurrence.** – Latest Aptian of Wizard Way, Texas, U.S.A.

## Faunal analysis

The assemblages described herein include a total of eleven species, eight in the two Spanish assemblages and three in the Texan one (Table 1). Ten of the species reported herein are new. The two Spanish assemblages seemed to yield the same faunal spectrum, albeit in slightly different relative abundances. They are thus treated as one assemblage (Cuchía 1 & 2) when presence/absence data are concerned, but are considered separately (Cuchía 1 and Cuchía 2) in the relative abundances analysis. Cuchía 1 & 2 is one of the most diverse Lower Cretaceous ophiuroid assemblages known to date, only outmatched by the Barremian shallow-water assemblage from France described by Thuy & Kroh (2011) (nine species) and the Aptian bathyal assemblage described by Thuy et al. (2012) and Thuy (2013) (eleven species).

Surprisingly, Cuchía 1 & 2 and the Texan assemblage do not have a single species in common. On genus level, however, all genera found in the Texan assemblage also occur in Cuchía 1 & 2. In the present-day North Atlantic, it is not uncommon that ophiuroid genera which occur on both sides of the ocean fall into eastern and western species (Paterson 1985). Thus, it could be that the here described Aptian records document a similar longitudinal separation on species level of genera occurring on both sides of the ancient North Atlantic. Other factors than longitude, in particular time (early Aptian versus latest Aptian ~4 Ma) or differences in depositional setting (silty basal marls *versus* peri-reefal debris), however, might have contributed at least as much to the differences in species-level composition. In any case, the similarities on genus level clearly show that the eastern and western North Atlantic shallow-water ophiuroid communities were not fundamentally different in the Aptian.

In contrast, the latest Aptian middle bathyal ophiuroid assemblage from Blake Nose (western North Atlantic) described by Thuy et al. (2012) and Thuy (2013) displays a strikingly different faunal spectrum. Not a single species is shared with the Aptian shallow-water assemblages, and only two of the eight genera (*Ophiacantha* and *Ophioleuce*) in total also occur in Cuchía 1 & 2. The case of the Texan assemblage is particularly intriguing. In fact, it is stratigraphically and geographically closest to the Blake Nose assemblage but fails to share a single genus with latter.

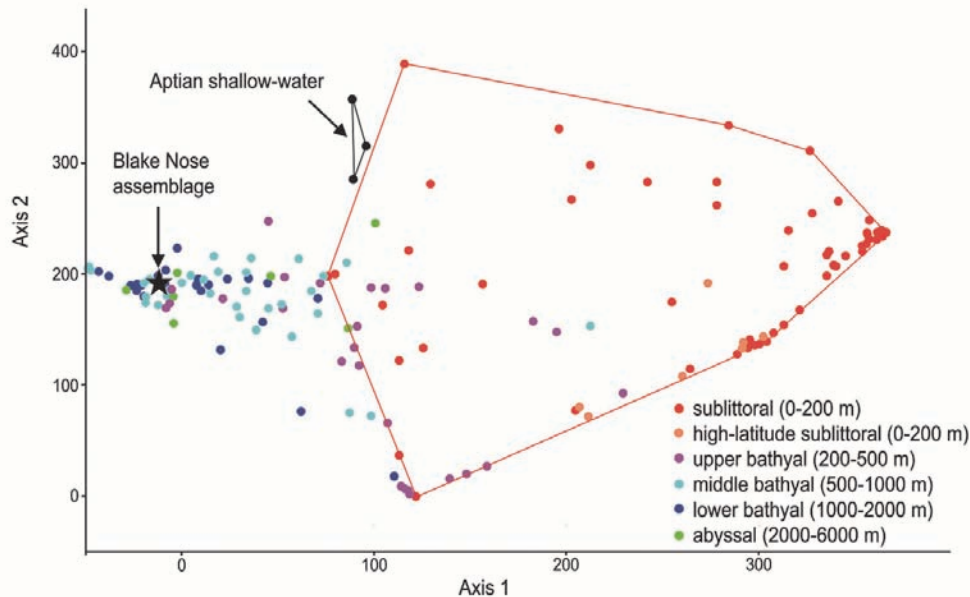
While, for Cuchía 1 & 2, concurrence of time and longitude cannot be ruled out, the faunal differences between

the Texan and the Blake Nose assemblages most probably reflect a true bathymetric signal between mid-shelf (sublittoral) and mid-slope (middle bathyal). Depth-related patterns in faunal composition are only rarely detectable as such in the fossil record because taxonomically assessable deep-sea assemblages are extremely scarce (Thuy et al. 2012), and even if they occur they have to be paralleled with stratigraphically and geographically close shallow-water equivalents. To our knowledge, the here described bathymetric gradient, although limited to two data points, is the first for the ophiuroid fossil record.

On family-level composition, all three shallow-water assemblages studied herein are dominated by the Ophionereididae (Cuchía 1: 60.1 %; Cuchía 2: 44.5 %; Texas: 84.0 %) followed by the Ophiolepididae in the Spanish assemblages (Cuchía 1: 29.4 %; Cuchía 2: 42.1 %) and the Ophiacanthidae in the Texan one (15.6 %). All other families identified account for less than 6 % each in all three assemblages. This differs markedly from the family-level composition of the middle bathyal Blake Nose assemblage (Thuy et al. 2012) dominated by the Ophiacanthidae (54.9 %), followed by the Ophiuridae (35.6 %) and the Ophiolepididae (9.5 %). It thus seems as if shelf and slope ophiuroid communities, in general clearly distinct in present-day oceans (Stöhr et al. 2012), were differentiated already in the Aptian.

While the middle bathyal Blake Nose ophiuroid assemblage was astonishingly similar to its present-day equivalents (Thuy et al. 2012), the here described shallow-water assemblages seem to lack modern counterparts in terms of family-level composition. In fact, a detrended correspondence analysis reveals that the three Aptian shallow-water assemblages studied herein plot outside the present-day ophiuroid communities, on the margin of the mid- to low-latitude shallow (0–200 m) ones (Fig. 5). The non-analogue composition of the shallow-water Aptian assemblages is due to the co-dominance of the Ophionereididae and the Ophiolepididae. In spite of the low palaeo-latitudes of the assemblages in question (Fig. 1), the Ophiocomidae, Ophiotrichidae and Ophiactidae, which commonly dominate present-day equivalent communities (Stöhr et al. 2012), completely lack, and the Amphiuroidae, another typical and abundant component of modern shallow assemblages (Stöhr et al. 2012), are very rare.

A more detailed analysis of the composition of the shallow-water Aptian assemblages further endorses their non-analogue composition: the Ophiolepididae are represented by the extant genus *Ophiozonella* which, in present-day oceans, typically occurs at bathyal depths (e.g., H. L. Clark 1911; Matsumoto 1915). Even the representative of the otherwise typically shallow Ophionereididae (e.g., Hendlér et al. 1995) in the Aptian assemblages, the extant genus *Ophiodoris*, almost exclusively occurs at bathyal depths in modern seas (Koehler 1904; H. L. Clark 1911). Thus, the Aptian shallow-water ophiuroid communities are in no way comparable to their modern counterparts, in spite of the dominance of typically shallow families.



**Fig. 5:** Detrended correspondence analysis of the three shallow-water (<200 m) Aptian assemblages from Spain and Texas in comparison with modern ophiuroid assemblages and the middle bathyal Aptian assemblage from Blake Nose, western North Atlantic, described by Thuy et al. (2012). The shallow-water Aptian assemblages differ markedly from the Blake Nose one, and plot outside the modern communities, next to the mid- to low-latitude shallow ones. The analysis is based on the relative abundances of the 17 extant ophiuroid families minus the Ophiuridae. Modern community and Blake Nose data from Thuy et al. (2012).

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## References

- Aronson, R. B. (1987): Predation on fossil and Recent ophiuroids. *Paleobiology* **13** (2): 187-192.
- Baumiller, T. K. & Gahn, F. J. (2004): Testing predator-driven evolution with Paleozoic crinoid arm regeneration. *Science* **305** (5689): 1453-1455. <http://dx.doi.org/10.1126/science.1101009>
- Bruzelius, N. (1805): *Dissertatio sistens species cognitatas asteriarum, quam, ... sub praesidio D. M. And. J. Retzius*. Lundæ (Literis Berlingianis): 1-37. [formerly known as R. J. Retzius]
- Clark, H. L. (1908): Some Japanese and East Indian Echinoderms. *Bulletin of the Museum of Comparative Zoology* **51**: 279-311.
- Clark, H. L. (1911): North Pacific Ophiurans in the collection of the United States National Museum. *Bulletin of the United States National Museum* **75**: 1-302.
- Collignon, M.; Pascal, A.; Peybernès, B. & Rey, J. (1979): Faunes d'ammonites de l'Aptien de la région de Santander (Espagne). *Annales de Paléontologie (Invertébrés)* **65**: 139-156.
- Donovan, S. K. (1996): Use of the SEM in interpreting ancient faunas of sea urchins. *European Microscopy and Analysis* **54**: 35-36.
- Donovan, S. K. (2001): Evolution of the Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166** (1-2): 177-191. [http://dx.doi.org/10.1016/S0031-0182\(00\)00208-X](http://dx.doi.org/10.1016/S0031-0182(00)00208-X)
- Duncan, P. M. (1879): On some Ophiuroidea from the Korean Seas. *Journal of the Linnean Society, Zoology* **14**: 445-482. <http://dx.doi.org/10.1111/j.1096-3642.1879.tb02443.x>
- Enay, R. & Hess, H. (1962): Sur la découverte d'Ophiures (*Ophiopetra lithographica* n. g. n. sp.) dans le Jurassique supérieur de Haut-Valromey (Jura méridional). *Eclogae Geologicae Helveticae* **55** (2): 657-673.
- Erbacher, J.; Huber, B. T.; Norris, R. D. & Markey, M. (2001): Increased thermohaline stratification as a possible cause for an ocean anoxic event in the Cretaceous period. *Nature* **409** (6818): 325-327. <http://dx.doi.org/10.1038/35053041>
- Gale, A. S. (2011): The phylogeny of post-Paleozoic asteroidea (Neoaasteroidea, Echinodermata). *Special Papers in Palaeontology* **85**: 1-112.
- García-Mondejar, J. (1982): Tectónica sinsedimentaria en el Aptiense y Albiense de la región Vasco-Cantábrica occidental. *Cuadernos de Geología Ibérica* **8**: 23-36.
- Gray, J. E. (1840): A synopsis of the genera and species of the class Hypostoma (*Asterias* Linnaeus). *Annals of the Magazine of Natural History* **6**: 175-184, 275-290.
- Hammer, Ø.; Harper, D. A. T. & Ryan, P. D. (2001): PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4**: 1-9.
- Hendler, G. & Miller, J. E. (1991): Swimming ophiuroids – real and imagined. In: Yanagisawa, T.; Yasumasu, I.; Oguro, C.; Suzuki, N. & Motokawa, T. (eds.): *Biology of Echinodermata*. Rotterdam (A.A. Balkema): 179-190.

- Hendler, G.; Miller, J. E.; Pawson, D. L. & Kier, P. M. (1995): *Sea Stars, Sea Urchins, and Allies*. Washington, DC (Smithsonian Institution Press): 390 pp.
- Hess, H. (1962): Mikropaläontologische Untersuchungen an Ophiuren II: Die Ophiuren aus dem Lias (Pliensbachien-Toarcien) von Seewen (Kt. Solothurn). *Eclogae geologicae Helvetiae* **55** (2): 609-656.
- Hess, H. (1964): Die Ophiuren des englischen Jura. *Eclogae Geologicae Helvetiae* **57** (2): 756-801.
- Hess, H. (1960): Neubeschreibung von *Geocoma elegans* (Ophiuroidea) aus dem unteren Callovien von La Voulte-sur-Rhône (Ardèche). *Eclogae geologicae Helvetiae* **53** (1): 335-385.
- Hess, H. (1965a): Mikropaläontologische Untersuchungen an Ophiuren IV: Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapolis (Jura) und Longecombe (Ain). *Eclogae geologicae Helvetiae* **58** (2): 1059-1082.
- Hess, H. (1965b): Trias-Ophiurien aus Deutschland, England, Italien und Spanien. *Mitteilungen der Bayerischen Staatsammlung für Paläontologie und Historische Geologie* **5**: 151-177.
- Hess, H. (1966): Mikropaläontologische Untersuchungen an Ophiuren V: Die Ophiuren aus dem Argovien (unteres Ober-Oxford) vom Guldental (Kt. Solothurn) und von Savigna (Dépt. Jura). *Eclogae geologicae Helvetiae* **59** (2): 1025-1063.
- Hess H (1970): Schlangensterne und Seesterne aus dem oberen Hauterivien „Pierre jaune“ von St-Blaise bei Neuchâtel. *Eclogae Geologicae Helvetiae* **63** (3): 1069-1091.
- Hess, H. (1975a): Mikropaläontologische Untersuchungen an Ophiuren VI: Die Ophiuren aus den Günsberg-Schichten (oberes Oxford) vom Guldental (Kt. Solothurn). *Eclogae geologicae Helvetiae* **68** (3): 591-601.
- Hess, H. (1975b): Mikropaläontologische Untersuchungen an Ophiuren VII: Die Ophiuren aus den Humeralis-Schichten (Ober-Oxford) von Raedersdorf (Ht-Rhin). *Eclogae geologicae Helvetiae* **68** (3): 603-612.
- Hess, H. (2011): *Treatise on Invertebrate Paleontology, Part T, Revised, Echinodermata 2, volume 3, Crinoidea Articulata*. Lawrence (KU Paleontological Institute, University of Kansas): xxix + 261 pp.
- Hess, H. & Meyer, C. A. (2008): A new ophiuroid (*Geocoma schoentalensis* sp. nov.) from the Middle Jurassic of north-western Switzerland and remarks on the family Aplocomidae Hess, 1965. *Swiss Journal of Geosciences* **101** (1): 29-40. <http://dx.doi.org/10.1007/s00015-008-1253-5>
- Hunter, A. W. & Underwood, C. J. (2009): Palaeoenvironmental control on distribution of crinoids in the Bathonian (Middle Jurassic) of England and France. *Acta Palaeontologica Polonica* **54** (1): 77-98.
- Koehler, R. (1904): Ophiures de l'expédition du Siboga. Part 1. Ophiures de mer profonde. *Siboga Expeditie* **45a**: 1-176.
- Kroh, A. (2007): Climate changes in the Early to Middle Miocene of the Central Paratethys and the origin of its echinoderm fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* **253** (1-2): 169-207. <http://dx.doi.org/10.1016/j.palaeo.2007.03.039>
- Kutscher, M. (1996): Echinodermata aus dem Ober-Toarcium und Aalenium Deutschlands II. Ophiuroidea. *Stuttgarter Beiträge zur Naturkunde, Serie B* **242**: 1-33.
- Kutscher, M. & Hary, A. (1991): Echinodermen im Unteren Lias (Bucklandi- und Semicostatum-Zone) zwischen Ellange und Elvange (SE-Luxemburg). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **182** (1): 37-72.
- Kutscher, M. & Jagt, J. W. M. (2000): Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark); In: Jagt, J. M. W., Late Cretaceous-Early Paleocene echinoderms and the K/T boundary in the southeast Netherlands and the northeast Belgium. part 3: Ophiuroids. *Scripta Geologica* **21**: 45-107.
- Kutscher, M. & Villier, L. (2003): Ophiuroid remains from the Toarcian of Sainte-Verge (Deux-Sèvres, France): paleobiological perspectives. *Geobios* **36** (2): 179-194. [http://dx.doi.org/10.1016/S0016-6995\(03\)00005-6](http://dx.doi.org/10.1016/S0016-6995(03)00005-6)
- Ljungman, A. V. (1867): Ophiuroidea vivencia huc usque cognita enumerat. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **23**: 303-336.
- Ljungman, A. V. (1872): Förteckning öfver uti Vestindien af Dr. A Goës samt under korvetten Josefins expedition i Atlantiska Oceanen samlade Ophiurider. *Öfversigt af Kungliga Vetenskaps-Akademiens Förhandlingar* **28**: 615-658.
- Lyman, T. (1869): Preliminary report on the Ophiuroidea and Astrophytidae dredged in deep water between Cuba and the Florida Reef, by L.F. de Pourtales, Assist. U.S. Coast Survey. *Bulletin of the Museum of Comparative Zoology, Harvard University* **1**: 309-354.
- Lyman, T. (1875): Zoological results of the Hassler Expedition. II. Ophiuridae and Astrophytidae. *Illustrated Catalogue of the Museum of Comparative Zoology* **8**: 1-34.
- Martynov, A. (2010): Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. *Zootaxa* **2697**: 1-154.
- Matsumoto, H. (1915): A new classification of the Ophiuroidea, with description of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **68**: 43-92.
- Müller, J. & Troschel, F. H. (1840): Über die Gattungen der Ophiuren. *Archiv für Naturgeschichte* **6**: 327-330.
- Müller, J. & Troschel, F. H. (1842): *System der Asteriden. 1. Asteridae. 2. Ophiuridae*. Braunschweig (Vieweg): 134 pp.
- Murakami, S. (1963): The dental and oral plates of Ophiuroidea. *Transactions of the Royal Society of New Zealand, Zoology* **4**: 1-48.
- Najarro, M.; Rosales, I. & Martín-Chivelet, J. (2010): Major palaeoenvironmental perturbation in an Early Aptian carbonate platform: prelude of the Oceanic Anoxic Event 1a? *Sedimentary Geology* **235** (1-2): 50-71. <http://dx.doi.org/10.1016/j.sedgeo.2010.03.011>
- Najarro, M.; Rosales, I.; Moreno-Bedmar, J. A.; Gea, G. A. de; Barrón, E.; Company, M. & Delanoy, G. (2011): High-resolution chemo- and biostratigraphic records of the Early Aptian oceanic anoxic event in Cantabria (N Spain): Palaeoceanographic and palaeoclimatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **299**: 137-158. <http://dx.doi.org/10.1016/j.palaeo.2010.10.042>
- Paterson, G. L. J. (1985): The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History), Zoology Series* **49**: 1-162.
- Smith, A. B.; Paterson, G. L. J. & Lafay, B. (1995): Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. *Zoological Journal of the Linnean Society* **114**: 213-243. <http://dx.doi.org/10.1006/zjls.1995.0024>
- Smith, A. B. & Rader, W. I. (2009): Echinoid diversity, preservation potential and sequence stratigraphical cycles in the Glen Rose Formation (early Albian, Early Cretaceous), Texas, USA. *Palaeobiodiversity and Palaeoenvironments* **89** (1-2): 7-52. <http://dx.doi.org/10.1007/s12549-009-0002-8>
- Spencer, W. K. (1907): A monograph on the British fossil Echinodermata from the Cretaceous formations 2: The Asteroidea and Ophiuroidea, Part 4. *Monograph of the Palaeontographical Society, London* [1907]: 91-132.
- Stöhr, S.; O'Hara, T. D. & Thuy, B. (2012): Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS ONE* **7** (3): 1-14 [e31940]. <http://dx.doi.org/10.1371/journal.pone.0031940>
- Stricklin, F. L.; Smith, C. I. & Lozo, F. E. (1971): Stratigraphy of Lower Cretaceous Trinity deposits of central Texas. *University of Texas at Austin Bureau of Economic Geology Report of Investigations* **71**: 1-63.
- Taylor, B. J. (1966): Taxonomy and morphology of Echinodermata from the Aptian of Alexander Island. *British Antarctic Survey Bulletin* **8**: 1-18.

- Thuy, B. (2005): Les Ophiures de l'Hettangien inférieur de Vance (B), Bereldange/Bridel et Bourglinster (L). *Memoirs of the Geological Survey of Belgium* **51**: 33-57.
- Thuy, B. (2011): Exceptionally well-preserved brittle stars from the Pliensbachian (Early Jurassic) of the French Ardennes. *Palaeontology* **54** (1): 215-233.
- Thuy, B. (2013): Temporary expansion to shelf depths rather than an onshore-offshore trend: the shallow-water rise and demise of the modern deep-sea brittle star family Ophiacanthidae (Echinodermata: Ophiuroidea). *European Journal of Taxonomy* **48**: 1-242. <http://dx.doi.org/10.5852/ejt.2013.48>
- Thuy, B. & Kroh, A. (2011): Barremian ophiuroids from the Serre de Bleyton (Drôme, SE France). *Annalen des Naturhistorischen Museums in Wien, Serie A* **113**: 777-807.
- Thuy, B. & Meyer, C. A. (2012): The pitfalls of extrapolating present-day depth ranges to fossil communities: new insights from brittle stars (Echinodermata: Ophiuroidea) from the Middle Jurassic of Switzerland. *Swiss Journal of Palaeontology* **132** (1): 5-21. <http://dx.doi.org/10.1007/s13358-012-0048-5>
- Thuy, B. & Stöhr, S. (2011): Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. *Zootaxa* **3013**: 1-47.
- Thuy, B.; Gale, A. S.; Kroh, A.; Kucera, M.; Numberger-Thuy, L. D.; Reich, M. & Stöhr, S. (2012): Ancient origin of the modern deep-sea fauna. *PLoS ONE* **7** (10): 1-11 [e46913]. <http://dx.doi.org/10.1371/journal.pone.0046913>
- Thuy, B.; Gale A. S. & Reich, M. (2011): A new echinoderm Lagerstätte from the Pliensbachian (Early Jurassic) of the French Ardennes. *Swiss Journal of Palaeontology* **130** (1): 173-185. <http://dx.doi.org/10.1007/s13358-010-0015-y>
- Verrill, A. E. (1899): Report on the Ophiuroidea collected by the Bahama expedition in 1893. *Bulletin of the Laboratories of Natural History of the State of Iowa* **5**: 1-88.
- Ward, D. J. (1981): A simple machine for bulk processing of clays and silts. *Tertiary Research* **3**: 121-124.
- Wilmsen, M. (2005): Stratigraphy and biofacies of the Lower Aptian of Cuchía (Cantabria, northern Spain). *Journal of Iberian Geology* **31**: 253-275.

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