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## Barremian ophiuroids from the Serre de Bleyton (Drôme, SE France)

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(With 4 plates and 1 figure)

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### Abstract

Two turbiditic beds of Barremian (Early Cretaceous) age from Serre de Bleyton, Drôme, Southern France, yielded disarticulated brittle-star remains. The material mainly consists of lateral arm plates, most of which are sufficiently well preserved to allow for a taxonomic interpretation following comparison with modern equivalents. A total of nine species were found, including two undescribed species (*Ophiozonella stoeckerae* nov. spec. and *Ophiotitanos pilleri* nov. spec.). The remaining seven species are probably also undescribed, but the limited available material precludes establishing new taxa. The strong dominance in abundance of lateral arm plates of *Ophiotitanos* in the studied material seems to reflect preservation and/or collecting bias due to the size, robustness and conspicuousness of the lateral arm plates assignable to *Ophiotitanos*. The Serre de Bleyton fauna is the most diverse in the Early Cretaceous known to date and fills at least part of a major stratigraphic gap between well known and comparably diverse Late Jurassic and Late Cretaceous brittle-star assemblages. The faunal spectrum at Serre de Bleyton is reminiscent of Late Jurassic equivalents. Amphiuroid, ophiocomid, ophiotrichid and ophiactid species, common in Latest Cretaceous assemblages and dominant in most modern shallow water communities, could not be found at Serre de Bleyton, suggesting that the studied fauna predates at least part of the shift in Cretaceous brittle-star assemblages towards a more modern composition.

**Keywords:** Echinodermata, Ophiuroidea, Early Cretaceous, Tethys, New Taxa

### Zusammenfassung

Zwei turbiditische Lagen barremischen Alters (Frühe Kreide), von Serre de Bleyton, Drôme, Südfrankreich, lieferten disartikulierte Skelettreste von Schlangensternen. Das Material besteht zum

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größten Teil aus Lateralschilder, von denen die meisten ausreichend erhalten sind um eine taxonomische Interpretation, basierend auf Vergleichen mit rezenten Äquivalenten, durchzuführen. Es wurden insgesamt neun Arten gefunden, von denen zwei unbeschrieben sind (*Ophiozonella stoehræ* nov. spec. und *Ophiotitanos pilleri* nov. spec.). Die restlichen sieben Arten sind vermutlich ebenfalls unbeschrieben, wurden hier jedoch mangels geeigneten Materials nicht benannt. Die große, relative Häufigkeit der Lateralschilder von *Ophiotitanos*-Arten liegt wahrscheinlich an deren Größe, Robustheit und Auffälligkeit, dank derer sie erhaltungsfähiger waren und vermutlich häufiger aufgesammelt bzw. ausgelesen wurden. Die Schlangensternefauna aus Serre de Bleyton ist die bisher diverseste, die man aus der Frühen Kreide kennt und füllt zumindest einen Teil einer großen, stratigraphischen Lücke zwischen gut untersuchten und ähnlich diversen Vergesellschaftungen aus dem Späten Jura und der Späten Kreide. Amphiuride, ophiocomide, ophiiothricide und ophiactide Arten sind recht häufig in Vergesellschaftungen der Spätesten Kreide und dominieren heute Flachwasservergesellschaftungen, fehlen in Serre de Bleyton jedoch komplett. Dies lässt vermuten, dass die Vergesellschaftung von Serre de Bleyton zumindest einem Teil der Veränderung kretazischer Schlangensternefaunen zu einer moderneren Zusammensetzung vorausgeht.

**Schlüsselwörter:** Echinodermata, Ophiuroidea, Unter-Kreide, Tethys, Neue Arten

## Introduction

The fossil record of ophiuroids is extremely poor when estimated in terms of intact skeletons. In fact, rapid post-mortem disintegration prevents the preservation of articulated ophiuroid skeletons in most cases (KERR & TWITCHETT 2004). In contrast, the isolated and mostly microscopic, calcitic plates of the ophiuroid skeleton have an excellent fossilisation potential, and often occur in great numbers in the sieving residues of sediments (WOLBURG 1939). Efforts have thus been made to taxonomically assess disarticulated skeletal parts of ophiuroids (e. g. BERRY 1938; WOLBURG 1939; RASMUSSEN 1950, 1951), and soon converged to the use of the spine-bearing lateral arm plates for species identification (HESS 1962a). In fact, among all types of plates of an ophiuroid skeleton, lateral arm plates have been considered to display the highest morphological variation (HESS 1962a). Based upon this assumption, many new ophiuroid species were erected on the basis of disarticulated lateral arm plates (e. g. KUTSCHER 1996; KUTSCHER & JAGT 2000; THUY 2005), accounting for more than 60 percent of all currently known Jurassic and Cretaceous ophiuroid species.

Very recently, the intra- and interspecific variability of lateral arm plates was systematically evaluated on the basis of lateral arm plates isolated from macerated specimens of 58 Recent species (THUY & STÖHR 2011), complementing the assessment of the lateral arm plate spine articulation structure as a basis for brittle-star taxonomy (MARTYNOV 2010). Although it corroborates the use of lateral arm plates in ophiuroid micropalaeontology, the study by THUY & STÖHR (2011) clearly highlights that a meaningful morphological assessment of fossil lateral arm plates requires detailed SEM-supported examination based on plates of which the diagnostic characters are sufficiently well supported to be

unequivocally discernible. In fact, differences in lateral arm plate morphology between closely related species are often smaller than previously acknowledged and commonly pertain to morphological features overlooked in earlier species descriptions exclusively based on fossil isolated lateral arm plates.

In spite of the revised taxonomic assessability of isolated skeletal parts, knowledge of Early Cretaceous ophiuroid diversity is comparatively low and exclusively based on the much more scarcely occurring intact skeletons (KÖNIG 1825; W. B. CLARK 1893; ALEXANDER 1931; TAYLOR 1966; HESS 1970; SHONE 1986; CORNELL et al. 1991; MARTIN-MEDRANO et al. 2009). Here, we describe an ophiuroid assemblage preserved as completely disarticulated skeletal parts from Barremian turbidite beds of the Serre-the-Bleyton, Southern France. It is the first detailed report of ophiuroids from the Early Cretaceous of France, and from the Barremian worldwide. It is by far the most diverse Lower Cretaceous brittle-star assemblage known to date and thus considerably adds to a better understanding of brittle-star diversity between the comparatively well-known Upper Jurassic and Lower Cretaceous ophiuroid assemblages (e. g. HESS 1975; JAGT 2000)

### Study area and geological setting

The studied section “Serre de Bleyton” is located in the Commune d’Aranyon (Drôme provençale), and is exposed on the southern side of the Serre de Bleyton ridge, east of Col de Perty. It lies about 20 km north-east of Nyons and 2 km south-east of Arnyon (Fig. 1). There, fossiliferous Barremian sediments occur in form of siliciclastic and turbiditic beds, the so-called “*coulées boueuses*”. These beds were interpreted as channels and fan-structures terminating in the Vocontian Through (ADATTE et al. 2005; ARNAUD 2005). Fossils are generally rare in the pelagic deposits of the “*coulées boueuses*”. Few other macrofossils are preserved, apart from cephalopods, and even these are rare at most places. At the Serre de Bleyton ridge, however, several turbidite horizons are present, containing abundant micro- and meso-scale bioclasts. Bulk sampling and surface picking of specimens exposed by weathering resulted in a rich invertebrate fauna. The material is interpreted to derive from the near-by Provence Platform and hemipelagic areas to the north-west of the Vocontian Trough.

The studied section is exposed along a gravel road on the southern slope of the Serre de Bleyton ridge. It is partly covered by soil and is affected by local tectonics. The majority of the beds represent light-grey intercalation of marls and limestone beds. Three of fossiliferous turbidite horizons mentioned above have been located in the section. The studied material derived from two of these horizons (Locality 1: N 44°28′55″, E 05°18′00″; Locality 2: N 44°28′54″, E 05°17′58″). For more detail on the study area see KROH et al. (2010).

Biostratigraphical data relating to the “*coulées boueuses*” are scarce. New studies based on material collected from the Serre de Bleyton section indicate a Barremian, possibly

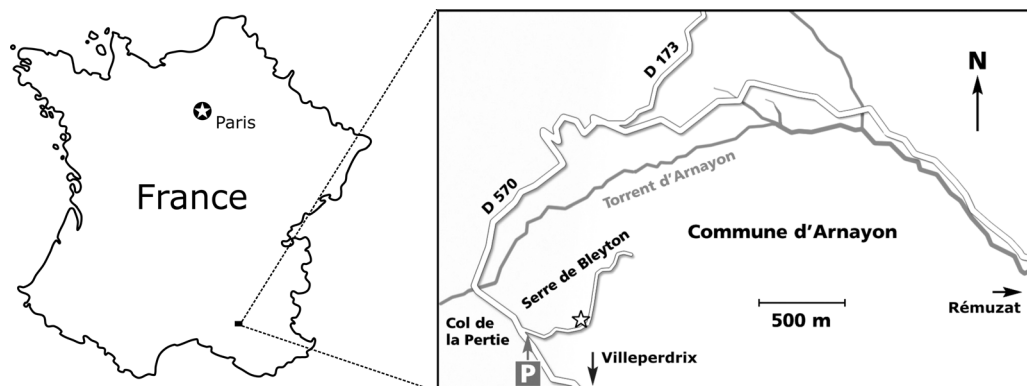


Fig. 1. Location of map of studied sites at Serre de Bleyton. The star indicates the position of the studied section.

Late Barremian age for the horizons containing the ophiuroid fauna [based on ammonite (LUKENEDER 2010) and belemnite (JANSSEN 2010) evidence]. Other co-occurring organism groups [asteroids (VILLIER 2010), bryozoans (TAYLOR 2010), corals (LÖSER 2010), crinoids (JÄGER 2010), rhyncholites (RIEGRAP & MOOSLEITNER 2010)] did not include age-indicative taxa. The exceptionally rich ostracod fauna (BABINOT & COLIN 2011, this volume), documented by several thousand specimens in 67 taxa supports the Barremian age of the Serre de Bleyton deposits, but fails to provide a more refined age assessment due to the fact that only about one third of the species could be attributed to previously known species, many of which have a wide stratigraphic range (Hauterivian to Aptian).

## Material & Methods

The ophiuroid material studied here derives from the two outcrops (locality 1 and locality 2) discussed above. There bulk samples have been taken from marly sediments by Gero MOOSLEITNER (Salzburg) and processed by disaggregation facilitating hydrogen superoxide and wet sieving. Afterwards the specimens were cleaned by using an ultrasonic bath and the tenside Rewoquat (LIERL 1992). Selected specimens were mounted on aluminium stubs and gold-coated for SEM-examination.

The ophiuroid material studied herein almost exclusively consists of isolated lateral arm plates (LAPs). A small number of vertebrae and ventral and dorsal arm plates are also among the material. As, however, they could not be convincingly assigned to the different types of LAPs or otherwise taxonomically assessed, they are not treated here. The preservation of the brittle-star plates varies from moderate to very good. Some plates have the fine structure of their stereom beautifully preserved while others display signs of pre-burial abrasion and/or post-diagenetic weathering. Taxonomic procedure and LAP

terminology follow THUY & STÖHR (2011). Higher taxonomic ophiuroid classification is adopted from SMITH et al. (1995).

The material studied here is deposited in the collections of the Department of Geology & Palaeontology at the Natural History Museum Vienna, Austria (NHMW) and in the Geoscientific Museum of the Georg-August-University Göttingen, Germany (GZG. INV.).

## **Systematic Palaeontology**

Class Ophiuroidea GRAY, 1840

Order Ophiurida MÜLLER & TROSCHEL, 1840

Family Ophiacanthidae PERRIER, 1891

**Gen. et spec. indet. A (“Ophiacanthid A”)**

(Pl. 1, Figs 1–2)

**Material:** 4 lateral arm plates from locality 2 (NHMW 2010/0356/0001 to .../0003).

**Description:** Proximal to median lateral arm plates higher than wide, rather fragile; distal plates unknown. All available plates fragmented; ventral third of LAP probably originally protruding; dorsal edge of LAP only slightly concave to straight, constriction weak, if developed at all. Proximal edge of LAP slightly bulging, with enlarged middle part, apart of which no other structures, such as spurs, are discernible. Ornamentation of outer surface of LAP consisting of well developed vertical striation close to proximal edge of spine articulations; stripes developing into small pustules towards proximal edge of LAP. Five large, free-standing, ear-shaped spine articulations, in shallow depressions proximally sharply bordered by notches of striated outer surface; gap between spine articulations slightly increasing in size dorsalwards; row of spine articulations constituting bulging ridge.

Inner side of LAP with prominent, well defined ridge, confluent with the dorso-proximal edge of LAP, with sharp proximal-ward kink towards its ventral tip. At least three perforations on inner side of LAP, rather large and irregular, arranged in vertical row distally bordered by thin, poorly defined ridge. Tentacle notch small, shallowly incising ventro-distal edge of LAP close to ventral kink of ridge on inner side of LAP, sharply separating the ventralmost spine articulation from broken but supposedly protruding ventral third of LAP.

**Remarks:** The rather fragile aspect, the large, ear-shaped spine articulations, the striation of the outer surface and the perforations on the inner side arranged in a vertical row unquestionably place the lateral arm plates described above within the Ophiacanthidae

(THUY & STÖHR 2011). Lateral arm plates with ophiacanthid affinities are a common component of uppermost Triassic (KRISTAN-TOLLMANN et al. 1979; KRISTAN-TOLLMANN & GRAMANN 1992), Jurassic (e. g. HESS 1975 and references therein; KUTSCHER & HARY 1991; KUTSCHER 1996; THUY, 2005) and Upper Cretaceous assemblages (e. g. KUTSCHER & JAGT 2000; JAGT & ODIN 2001) and were almost invariably tentatively assigned to the extant genus *Ophiacantha*. Among the species with a striated outer surface of the lateral arm plates, *Ophiacantha* ? *toarcensis* HESS, 1962b (Early Jurassic, Central Europe) and *Ophiacantha* ? *suprajurassica* HESS, 1966 (Late Jurassic, Switzerland and France) differ from ophiacanthid species A in having well defined spurs on the outer proximal and inner distal edges of the lateral arm plates. Striation in *Ophiacantha* ? *biformis* HESS, 1975 (Late Jurassic, Switzerland and France) is restricted to the distal lateral arm plates and is much finer. *Ophiacantha* ? *subtilirugosa* KRISTAN-TOLLMANN & GRAMANN, 1991 (Latest Triassic, Wombat Plateau) has smaller spine articulations situated in depressions of the finely striated outer surface rather than freestanding on an elevated ridge. Edge proximally bordering the spine articulations in lateral arm plates of *Ophiacantha* ? *striata* KUTSCHER & JAGT, 2000 (Late Cretaceous, Central Europe) is nearly straight rather than forming notches around the spine articulations.

Lateral arm plates of “ophiacanthid A” thus cannot be assigned to any known Mesozoic ophiacanthid species. We nevertheless refrain from formally describing it as a new species here, considering the low number of available lateral arm plates and their fragmentary nature, which does not provide the necessary insights on plate morphology and variability required for the proposal of a new species.

Generic attribution of “ophiacanthid A” poses problems as lateral arm plate morphology did not reflect patterns of classification on genus and subfamily level in the species examined by THUY & STÖHR (2011). Pending a survey on morphological variability of lateral arm plates including more ophiacanthid species, generic attribution of “ophiacanthid A” is left open.

The large, freestanding, ear-shaped spine articulations in combination with the conspicuously striated outer surface preclude any confusion with other types of lateral arm plates from the Serre-de-Bleyton assemblages.

### **Gen. et spec. indet. B (“Ophiacanthid B”)**

(Pl. 1, Figs 3–6)

**Material:** 5 lateral arm plates from locality 1 (NHMW 2010/0356/0004 to .../0006, .../0008); one lateral arm plate from locality 2 tentatively assigned to this species (NHMW 2010/0356/0007).

**Description:** Proximal LAPs large, extremely high and strongly arched; rather stout; median LAPs lower; distal plates unknown; no constriction. No spurs discernible on outer proximal and inner distal edges of LAP. Ornamentation consisting of finely pustulate stereom, developing into faint vertical striation in distal and ventro-distal parts of outer



surface. In proximal LAPs, outer surface almost completely occupied by a row of spine articulations. Up to eight (six in median LAPs) large, ear-shaped spine articulations, free-standing in depressions on strongly elevated ridge; spine articulations and gaps separating them clearly increasing in size dorsalwards.

Inner side of LAP with thin, prominent and rather well defined, nearly vertical ridge with gentle kink in its middle part and proximalward bend in its ventral part. Perforations small and inconspicuous, in shallow but rather well defined furrow distally bordering ridge on inner side. Tentacle notch very small, shallowly incising the ventral edge of the LAP close to the ventral bend of the inner ridge.

**Remarks:** While the large, freestanding, ear-shaped spine articulations clearly place the above described lateral arm plates into Group 1 of THUY & STÖHR (2011), consisting of the Ophiacanthidae and Ophiocomidae, attribution to either of these two families is more difficult. In fact, greatest similarities are shared with the lateral arm plates of the ophiocomid *Ophiocomina nigra* (ABILDGAARD, in O. F. MÜLLER, 1789), especially in respect of the stout, very high and arched aspect of the lateral arm plates as well as the ornamentation of the outer surface. Development of the perforations on the inner side of the plates, however, is more reminiscent of ophiacanthid species (THUY & STÖHR 2011), with the perforations irregularly distributed in a shallow, vertical furrow rather than grouped as single conspicuous opening at the ventral tip of the central ridge. We thus prefer an assignment to the Ophiacanthidae, although the systematic significance of the development of the perforations awaits confirmation. Whatever the systematic position of “ophiacanthid B”, it underpins the similarities in lateral arm plate morphology of *Ophiocomina nigra* and some ophiacanthid species, as already shown by THUY & STÖHR (2011). Whether these similarities reflect a close phylogenetic relationship of the two families or rather resulted from convergent developments in lateral arm plate morphology requires more research.

The generic attribution of “ophiacanthid B” is left open pending a more extensive survey on lateral arm plate morphology of extant ophiacanthid genera. In fact, the study by THUY & STÖHR (2011) covered only 5 ophiacanthid genera, none of which is convincingly similar to “ophiacanthid B”.

Among all types of lateral arm plates with large, ear-shaped spine articulations known from Mesozoic strata, none bears a close similarity with “ophiacanthid B”, in particular in respect of the size and the stout, slender aspect of its lateral arm plates. A certain resemblance is shared with lateral arm plates described as *Ophiomyxa* ? *curvata* KUTSCHER & JAGT, 2000 from the Maastrichtian of Germany. “Ophiacanthid B”, however, differs among others in the clear dorsalward increase in spine articulation size and distance. In contrast, LAPs figured as *Ophiomyxa*? cf. *curvata* by ŠTORC & ŽÍTT (2008) from the Late Turonian of Czech Republic display a clear dorsalward increase in size of the spine articulations and the distance separating them. These plates, however, seemingly lack the fine pustules tending towards a faint vertical striation on the outer surface. Although “ophiacanthid B” thus represents a yet undescribed species, we refrain from erecting a new taxon pending the collection of a more representative number of lateral arm plates.

While the large, proximal lateral arm plates of “ophiacanthid B” are highly distinct in the Serre-de-Bleyton assemblages, confusion is possible between its more compact median lateral arm plates and the proximal ones of *Amphiophiura* ? nov. spec. (see below). In the latter, however, spine articulations are not ear-shaped and remain nearly equal in size towards the dorsal edge of the plate.

**Gen. et spec. indet. C (“Ophiacanthid C”)**

(Pl. 1, Fig. 7)

**Material:** 1 fragmentary lateral plate from locality 2 (NHMW 2010/0356/0009).

**Description:** Outline and proportions of plate not discernible because of fragmentary preservation; outer surface with regular, finely meshed stereom; no ornamentation. Proximal edge of LAP not preserved. Three, very large, ear-shaped, spine articulations preserved; of similar size and equidistant; freestanding and individually surrounded by diffuse areoles of slightly more coarsely meshed stereom in very shallow depressions; on strongly elevated ridge, with sharp proximal break.

Inner side of LAP with thin, prominent, moderately well defined vertical ridge with gentle kink. Distal edge of inner side with two to three horizontal, spur-like structures composed of slightly more dense stereom. Perforations on inner side and tentacle notch not discernible.

**Remarks:** The single, fragmentary lateral arm plate described above seems compatible with “ophiacanthid B” at first sight. However, the small portion of the outer surface preserved in the fragmentary lateral arm plate is larger than in any plate of “ophiacanthid B” and is furthermore devoid of pustules, in spite of a sufficient preservation of the plate.

Assignment to the Ophiacanthidae is based on the large, ear-shaped spine articulations in combination with the comparatively delicate plate structure. The fragmentary state of the plate precludes any meaningful comparison with other ophiacanthid species known from Mesozoic brittle-star assemblages. Until the discovery of more complete material, it seems best to mention and figure the only available specimen as an unidentified ophiacanthid.

Family Ophiolepididae LJUNGMAN, 1867

Genus *Ophiomusium* LYMAN, 1869

***Ophiomusium* sp.**

(Pl. 2, Figs 1–2)

**Material:** one lateral arm plate from locality 1 (NHMW 2010/0356/0010) and two from locality 2 (NHMW 2010/0356/0011, .../0012).



**Description:** Distal LAPs rectangular in outline, elongated, with gentle constriction leading to slightly concave dorsal edge. Outer surface with rather coarsely meshed stereom, except for narrow band of more finely meshed stereom on proximal edge of LAP comprising two to three diffuse spur-like structures. At least three small spine articulations on distal edge of LAP, integrated into coarsely meshed stereom of outer surface and thus hardly discernible; spine articulations of similar size and equidistant. Tentacle pore opening below ventralmost spine articulation.

Inner side of LAP with conspicuously enlarged dorsal contact area with opposite LAP. Ridge on inner side reduced to a short, round, well defined and prominent, slightly oblique knob. No perforations discernible on inner side. Tentacle pore perforating LAP, opening on inner side distal from knob.

**Remarks:** The two plates from the Serre-de-Bleyton assemblages share great similarities with the distal lateral arm plates of extant *Ophiomusium lymani* WYVILLE-THOMSON, 1873 figured in THUY & STÖHR (2011) and are thus assigned to the genus *Ophiomusium*. Comparably massive, compact lateral arm plates with tentacle openings predominantly developed as pores rather than indentations are widespread in the Late Mesozoic, and a number of species described on the basis of such lateral arm plates were attributed to *Ophiomusium* (e. g. HESS 1975b; KUTSCHER & JAGT 2000). Unfortunately, the two plates from Serre-de-Bleyton are rather poorly preserved and originate from distal portions of the arm where diagnostic features of lateral arm plate morphology are likely not to be fully differentiated, thus hampering meaningful comparisons with currently known Mesozoic species of *Ophiomusium*. Greatest similarities are shared with *Ophiomusium lux* JAGT, 2000, Maastrichtian of the Netherlands. A certain resemblance can also be found with *Ophiomusium gagnebini* (THURMANN, 1851), Late Jurassic of Europe, and *Ophiomusium granulosum* (ROEMER, 1841), although these two species have well developed, distinct spurs on the outer proximal and inner distal edges of the lateral arm plate. Pending the discovery of more diagnostic material, it seems best to describe the two plates from Serre-de-Bleyton as *Ophiomusium* sp..

Genus *Ophiozonella* MATSUMOTO, 1915

***Ophiozonella stoechrae* nov. spec.**

(Pl. 2, Figs 3–6)

**Derivatio nominis:** Name formed in honour of Sabine STÖHR, curator and researcher at the Naturhistoriska Riksmuseet, Stockholm, for her outstanding contributions to brittle-star systematics.

**Diagnosis:** Species of *Ophiozonella* with rounded triangular lateral arm plates displaying pustules merged into weak vertical striation on the outer surface of proximal plates; up to four large spine articulations; sharply defined, slender, dorsally pointed ridge on inner side; large, irregular perforation on inner side of LAP.

**Holotype:** Natural History Museum Vienna, Department of Geology & Palaeontology, NHMW 2010/0356/0013 (from locality 2)

**Paratypes:** NHMW 2010/0356/0014, NHMW 2010/0356/0015, GZG.INV.30570 from locality 2.

**Additional material:** six plates from locality 2 (NHMW 2010/0356/0016; GZG.INV.30571).

**Locus typicus:** Locality 2 of KROH et al. (2010), Serre de Bleyton, SW of Arnavon village, Department Drôme, France.

**Stratum typicum:** “*coulées boueuses*”, Barremian, Early Cretaceous.

**Description of holotype** (Pl. 2, Fig. 3): Proximal LAP, slightly higher than wide, of rounded triangular aspect; ventral third of LAP protruding; no constriction; dorsal edge of LAP uniformly convex; distal part of LAP weakly bulging. Ornamentation consisting of fine pustules, merging into a faint and irregular vertical striation in the middle of the outer surface; proximal edge of LAP with strongly prominent, sharply defined spur composed of almost compact stereom. Four spine articulations consisting of two horizontal, nearly parallel ridges separated by two small knobs and slightly bent to form a horseshoe-like structure; spine articulations of similar size and equidistant, sunken into shallow depressions of distal edge of LAP.

Inner side of LAP with conspicuous, prominent, sharply defined oblique ridge with pointed dorsal tip and gentle, ventralward kink; ventral part of ridge becoming increasingly diffuse and merging with thickened ventral edge of LAP. Single large, oblique, drop-shaped perforation on inner side close to kink of ridge. Tentacle notch large and conspicuous, bordered by thickened ventral edge of LAP.

**Paratype supplements:** Median LAP (Pl. 2, Fig. 4; NHMW 2010/0356/0014) nearly as high as wide; ornamentation consisting almost exclusively of pustules not merged into vertical stripes; three spine articulations grouped ventrally; two parallel ridges composing spine articulation separated by a single knob.

Distal LAP (Pl. 2, Fig. 5; NHMW 2010/0356/0015) elongate; pustules on outer surface not merged into vertical stripes but showing tendency to arrange in vertical rows, especially close to spine articulations; three spine articulations each composed of two parallel ridges separated by a single knob.

**Remarks:** While the LAPs described above display no convincing resemblance to any of the extant brittle-star species figured in THUY & STÖHR (2011), a striking similarity turned out to be shared with the LAPs of extant *Ophiozonella longispina* (CLARK, 1908) (Pl. 2, figs 13–14; pictures kindly provided by Sabine STÖHR, Naturhistoriska Riksmuseet, Stockholm). The plates from Serre-de-Bleyton thus seem best placed in the genus *Ophiozonella*.

Comparable LAPs are known from *Ophiopetra lithographica* ENAY & HESS, 1962, Latest Jurassic of Central Europe, and *Ophiacantha? francojurassica* HESS, 1975, Late Jurassic of Central Europe, which, however, differ in lacking any distinct ornamentation and spurs on the outer proximal and distal inner edges. *Ophiopetra bathonica* HESS, 1964, Middle Jurassic of Europe, has smaller spine articulations. *Ophiocten? seeweni* KUTSCHER & HARY, 1991, Early Jurassic of Central Europe, lacks the distinct spur on the outer proximal and inner distal edges. The same holds true for *Ophiocoma? senonensis* (VALETTE, 1915), *O.? rasmusseni* HESS, 1960 and *O.? ishidai* KUTSCHER & JAGT, 2000, all from the Maastrichtian of Central Europe, of which lateral arm plates are figured by KUTSCHER and JAGT (2000). The LAPs of *Ophiopetra? oertlii* HESS, 1965 from the Toarcian/Aalenian of Germany figured by KUTSCHER (1996) share greatest similarities with those from Serre-de-Bleyton, differing, however, most notably in the ornamentation of their outer surface. In contrast, the holotype of *Ophiopetra? oertlii* from the Late Jurassic of France, figured in HESS (1965), is much less similar to the Serre-de-Bleyton plates, having conspicuously smaller spine articulations grouped ventrally.

The material from Serre-de-Bleyton is thus incompatible with any known Mesozoic brittle-star. Considering the amount and quality of the available material, allowing for a diagnostic characterisation, it seems appropriate to erect a new species. The assignment of the new species from Serre-de-Bleyton to the extant genus *Ophiozonella* within the family Ophiolpididae adds a new perception to the higher taxonomic position of forms like *Ophiopetra lithographica*, *O. bathonica*, *O.? oertlii* and *Ophiacantha? francojurassica*, all sharing superficial similarities in LAP morphology and so far assigned to families as little related as the extinct Aplocomidae (e.g. HESS & MEYER 2008) and the Ophiacanthidae (HESS 1975b). The taxonomic interpretation, both on higher level and on species-concept level, of this widespread and long-lived group of ophiuroids is obviously in need of a detailed re-evaluation paying more attention to lateral arm plate morphology of extant species.

Family Ophiuridae MÜLLER & TROSCHEL, 1840

Subfamily Ophiurinae LYMAN, 1865

Genus *Ophiotitanos* SPENCER, 1907

***Ophiotitanos pilleri* nov. spec.**

(Pl. 3, Figs 1–6)

**Derivatio nominis:** Name formed in honour of Werner E. PILLER, head of the Institute of Earth Sciences at the Karl-Franzens-University Graz, for his outstanding dedication to the promotion of palaeontological and stratigraphical research in Austria and abroad.

**Diagnosis:** Species of *Ophiotitanos* with a clearly striated outer surface of proximal lateral shields.

**Holotype:** Natural History Museum Vienna, Department of Geology & Palaeontology, NHMW 2010/0356/0017 (from locality 2).

**Paratypes:** NHMW 2010/0356/0018, NHMW 2010/0356/0019 from locality 2, and GZG.INV.30572 from locality 1.

**Additional material:** 180 plates from locality 1 (NHMW 2010/0356/0020–0022; GZG.INV.30573) and 39 plates from locality 2 (NHMW 2010/0356/0023; GZG.INV.30574).

**Locus typicus:** Locality 2 of KROH et al. (2010), Serre de Bleyton, SW of Arnanon village, Department Drôme, France.

**Stratum typicum:** “*coulées boueuses*”, Barremian, Early Cretaceous.

**Description of holotype** (Pl. 3, Fig. 1): Proximal lateral arm plate of thick and massive aspect, higher than wide, uniformly bent; only small ventral portion of LAP protruding; no constriction. Proximal edge of LAP with two large, well defined, prominent and protruding spurs; dorsal spur larger and more strongly protruding than ventral one. Ornamentation consisting of fine and moderately regular vertical striation covering almost the entire outer surface of the LAP; stripes strongly decreasing in size towards the proximal, dorsal and ventral edges of the LAP. Nine spine articulations sunken into notches of the distal edge of the LAP; similar in size and nearly equidistant; the two or three dorsalmost spine articulations separated by slightly larger gaps than the remaining ones.

Inner side of LAP bearing prominent, well defined, oblique ridge with rounded, broader dorsal tip; gentle kink in lower third of ridge; ventral tip of the ridge well defined, not confluent with ventral edge of LAP. Single perforation on the inner side of the LAP close to tentacle notch; shallow, very weakly defined furrow radiating dorsalwards from perforation, probably bearing more perforations of smaller size. Inner distal edge of LAP with two large, conspicuous spurs composed of more massive stereom, corresponding to spurs on outer proximal edge. Tentacle notch small but well developed.

**Paratype supplements:** Median to proximal LAP (Pl. 3, Fig. 2; NHMW 2010/0356/0018) nearly as high as wide; distance between two spurs on outer proximal edge greater than in proximal LAP; seven spine articulations.

Distal LAP (Pl. 3, Fig. 3; NHMW 2010/0356/0019) elongate, rounded rectangular and of tumid aspect; spurs on outer proximal edge prominent and protruding but rather poorly defined. Four spine articulations; equal in size and equidistant. Ridge on inner side of LAP strongly reduced but sharply defined; oblique, with pointed dorsal tip and broad rounded ventral tip. Perforations not discernible. Tentacle opening developed as conspicuous pore entirely within LAP.

**Remarks:** The LAPs described above belong to a group commonly found in Triassic (KRISTAN-TOLLMANN et al. 1979), Jurassic (e.g. HESS 1975b and references therein; KUTSCHER 1996; THUY 2005) and Cretaceous (RASMUSSEN 1950; JAGT 2000; KUTSCHER & JAGT 2000) brittle-star assemblages. Species of this group have LAP which share a relatively large size, numerous spine articulations sunken into notches of the distal edge and a variable number of generally well developed spurs on the outer proximal and inner distal edges. *Ophioderma* ? *waliabadensis* KRISTAN-TOLLMANN et al., 1979, Uppermost Triassic of Iran, and *Ophioderma* ? *delsatei* THUY, 2005, Hettangian of Central Europe, both have more than two spurs. *Ophiarachna* ? *liasica* KUTSCHER, 1996, Toarcian/Aalenian of Germany, has larger and fewer spine articulations. *Ophioderma* ? *spectabilis* HESS, 1966, from the Oxfordian of France, differs in lacking the vertical striation on the outer surface and in having a longer, less oblique ridge on the inner side.

Greatest similarities are shared with the LAPs of *Ophiotitanos serrata* (ROEMER, 1841) from the Maastrichtian of Rügen, Germany, figured by KUTSCHER & JAGT (2000: Pl. 26, Figs 8–11) and from the Turonian of Czech Republic, figured by ŠTORC & ŽIT (2008). In these plates, however, the vertical striation is much weaker than in those from Serre-de-Bleyton. In contrast, LAPs from the Maastrichtian and Danian of Belgium and the Netherlands, figured by JAGT (2000) as belonging to *Ophiotitanos serrata*, clearly differ from the material from Serre-de-Bleyton in being much more tumid and lacking the vertical striation (JAGT 2000: Pl. 16, Figs 1–3; Pl. 19, Figs 1–2), in having a much stronger ventral protrusion and less well defined spurs (JAGT 2000: Pl. 17, Fig. 3) or in being constricted (Pl. 21, Figs 1–4). Chances are high that the material figured as *Ophiotitanos serrata* by JAGT (2000) and KUTSCHER & JAGT (2000) in fact falls into several different species sharing superficially similar lateral arm plate morphology. What is relevant at this point is that none of these plates, whatever their taxonomic interpretation, are compatible with the Serre-de-Bleyton material. Other species of the genus *Ophiotitanos*, known from partly articulated specimens and/or arm fragments from the Upper Cretaceous of Great Britain, namely *O. tenuis* SPENCER, 1907, *O. laevis* SPENCER, 1907 and *O. magnus* SPENCER, 1907, differ from the Serre-de-Bleyton material in lacking the vertical striation and, at least in the case of *O. tenuis*, in having a significantly lower number of spine articulations. It therefore seems justified to propose a new species for the Serre-de-Bleyton LAPs described above.

The LAPs of the new species have a certain resemblance with LAPs of extant species of *Ophioderma* and *Ophioplithus* figured by THUY & STÖHR (2011), differ, however, in having tentacle pores perforating the LAPs in distal arm portions, in contrast to tentacle pores perforating also proximal and median LAPs in *Ophioplithus*, and tentacle notches rather than pores in all LAPs in *Ophioderma*. The development of the tentacle openings in *Ophiotitanos* is not mentioned by SPENCER (1907) in the original description of *O. tenuis*, the type species of the genus, and the holotype of *O. tenuis* is an articulated specimen not exposing the ventral side. Isolated lateral arm plates from Upper Cretaceous assemblages, which are superficially compatible with those observed in the type specimens of SPENCER'S (1907) *Ophiotitanos* species (e.g. JAGT 2000), however, invariably

have tentacle openings developed as perforations in distal LAPs only. It therefore seems best to assign the new species from Serre-de-Bleyton to the genus *Ophiotitanos*, albeit with tentativeness pending a detailed re-examination of the type material of *O. tenuis*. *Ophiotitanos* is considered to be closest to extant Ophiodermatidae (JAGT 2000), as are almost all other Mesozoic species with similar LAP morphology (see above), whereas HESS (1960) placed it in the vicinity of the Ophiolepididae. Tentacle openings developed as perforations within the LAPs are known from *Ophioplinthus* (Ophiuridae) and *Ophiomusium* (Ophiolepididae) (THUY & STÖHR 2011). As similarities in LAP morphology are greatest with *Ophioplinthus*, it seems best to assign the genus *Ophiotitanos*, including the new species *O. pilleri*, to the subfamily Ophiurinae within the Ophiuridae.

***Ophiotitanos* sp.**

(Pl. 4, Figs 1–3)

**Material:** 93 lateral arm plates from locality 1 (NHMW 2010/0356/0024–0027) and seven from locality 2 (NHMW 2010/0356/0028).

**Description:** Lateral arm plates of tumid and massive aspect; proximal ones higher than wide, moderately bent; median and distal LAPs nearly as high as wide, of compact aspect; ventral part of LAP only very slightly protruding; no constriction. Proximal edge of LAP with two very large, moderately well defined, prominent and slightly protruding spurs; dorsal spur clearly larger than ventral one; spurs in median and distal LAPs weakly defined, prominent but hardly protruding. Ornamentation consisting of very fine granulation covering almost the entire outer surface of the LAP except for a broad band of slightly more coarsely meshed stereom on the proximal edge comprising the two spurs. Twelve spine articulations in proximal LAPs (eight in median and six in distal ones) sunken into shallow notches at the very tip of the distal edge of the LAP; similar in size and nearly equidistant; the two or three dorsalmost spine articulations separated by slightly larger gaps than the remaining ones.

Inner side of LAP with prominent, poorly defined, oblique ridge; gentle kink in lower third of ridge; ventral tip of the ridge rather diffuse. Inner distal edge of LAP with two large, conspicuous spurs composed of more massive stereom, corresponding to spurs on outer proximal edge. Very small, hardly discernible perforations between the spurs and the oblique ridge on the inner side of the proximal LAPs; no perforations discernible in median and distal LAPs. Tentacle notch small but well developed in proximal and median LAPs; distal LAPs with tentacle pore rather than notch, perforating the ventral edge of the plate.

**Remarks:** The LAPs described above from both Serre-de-Bleyton localities bear a superficial resemblance with those of *Ophiotitanos pilleri* nov. spec., differ, however, in the finely granulated rather than vertically striated outer surface, the more tumid aspect and the less well defined oblique ridge on the inner side and the spurs on the outer proximal and inner distal edges. Nevertheless, confusion is possible in strongly worn specimens.



Unlike the LAPs of *Ophiotitanos pilleri* nov. spec., the ones described above have no conspicuous morphological feature which would clearly set them apart from other similar species.

*Ophioderma* ? *spectabilis*, Oxfordian of France, has LAP which are very similar to those described above. At present it remains unclear if the more diffuse ridge on the inner side and the less sharply defined spurs on the outer proximal and inner distal edges in the Serre-de-Bleyton material justify distinction on species level. A detailed, SEM-supported examination of the type material of *O.?* *spectabilis* is necessary to tackle this question. As for species of *Ophiotitanos* other than *O. striatulus* nov. spec., only *O. tenuis* seems to be meaningfully distinguishable from the Serre-de-Bleyton material in having a significantly lower number of spine articulations. The original descriptions of *O. laevis* and *O. magnus*, in contrast, provide no morphological basis on which to base a sound distinction. To make matters worse, the LAPs figured as *Ophiotitanos serrata* by JAGT (2000) obviously fall into different groups, as already mentioned in the discussion of the taxonomic interpretation of *O. pilleri* nov. spec. (see above). One of these groups, characterised as being more tumid and having better developed spurs on the outer proximal edge (JAGT 2000: Pl. 16, Figs 1–3; Pl. 19, Figs 1–2), bear greatest similarities with the Serre-de-Bleyton material described above.

Pending a detailed revision of the group of LAPs, including *O.?* *spectabilis*, *O. laevis*, *O. magnus* and, in part, *O. serrata*, all characterised by a relatively large size, numerous small spine articulations in notches of the distal edge, two well developed spurs on the outer proximal and the inner distal edges and the lack of any conspicuous ornamentation on the outer surface, it is impossible to clarify the position on species level of the Serre-de-Bleyton material. Assignment to the genus *Ophiotitanos* within the Ophiuridae follows the same argumentation than in *Ophiotitanos pilleri* nov. spec. (see above).

#### Genus *Amphiophiura* MATSUMOTO, 1915

##### *Amphiophiura* ? sp. (Pl. 4, Figs 4–5)

**Material:** three lateral arm plates from locality 1 (NHMW 2010/0356/0029 to .../0031).

**Description:** Proximal to median LAPs higher than wide, of very thick and tumid aspect and conspicuously bent. Proximalmost part of LAP slightly constricted and, especially in ventral half of LAP, clearly separated from remaining plate by furrow, enhancing the tumid aspect of the LAP. No spurs discernible on outer proximal edge. Ornamentation of outer surface consisting of coarse pustules tending to merge into very short, irregular vertical stripes; covering the entire outer surface except for the proximalmost part including the furrow. Six to nine spine articulations; moderately large, approximately

horseshoe-shaped; near equal in size and equidistant; sunken into notches of the distal edge of the LAP.

Inner side of LAP with broad, poorly defined, prominent and strongly bent ridge; broadest dorsally; best defined and most prominent ventrally. Inner side of ventral edge of LAP thickened; with large central knob and smaller, prominent knob near ventro-proximal tip. Clearly discernible perforation distal from ventral third of ridge; shallow furrow radiating dorsalwards from basal perforation and bearing more perforations of variable size. Tentacle notch distal from central knob on ventral edge of LAP; very shallow and hardly discernible.

Remarks: Lateral arm plates superficially comparable to those described above are known as *Hemieuryale? lunaris* HESS, 1962, from the Toarcian of Switzerland. They clearly differ, however, in lacking the coarse pustules on the outer surface and in having different spine articulation morphology. A certain resemblance can also be found with LAPs of *Ophiomyxa? curvata* KUTSCHER & JAGT, 2000, from the Maastrichtian of Germany, which have ear-shaped rather than horseshoe-shaped spine articulations not sunken into notches of the distal edge, and the ventral tip of the LAP strongly protruding. Although the LAPs described cannot be assigned to any presently known Mesozoic brittle-star species, the limited available material precludes establishing of a new species.

In spite of the aforementioned superficial similarities with fossil hemieuryalid and ophiomyxid species, greatest affinities among extant species are shared with the ophiurid *Amphiophiura insolita* (KOEHLER, 1904) (Pl. 4, fig. 6; pictures kindly provided by Sabine Stöhr, Naturhistoriska Riksmuseet, Stockholm), especially in terms of general shape, ornamentation of the outer surface, ridge and perforation on the inner side of the LAP and development of the tentacle notch. It therefore seems best to assign the Serre-de-Bleyton material to the extant genus *Amphiophiura*.

Confusion with other types of LAP from the Serre-de-Bleyton localities is only possible with the median LAPs of ophiacanthid B (see above). *Amphiophiura* nov. spec., however, differs in having horseshoe-shaped rather than ear-shaped spine articulation, which are almost equal in size and equidistant.

### **Gen. et spec. indet. (“Ophiurid nov. spec.”)**

(Pl. 4, Fig. 7)

Material: a single lateral arm plate from locality 2 (NHMW 2010/0356/0032).

Description: The single proximal to median LAP is slightly higher than wide, gently bent, moderately stout and of rounded aspect. Ventro-proximal part of LAP protruding. No constriction. Five conspicuous, sharply defined, prominent knobs on proximal edge of LAP; three dorsal knobs rounded squarish; two ventral knobs elongate. Outer surface with fine, vertically elongated pustules resulting in a faint, irregular vertical striation covering

entire outer surface except for narrow band along proximal edge bearing the spurs. Five small spine articulations sunken into deep notches of the distal edge.

Inner side with conspicuous, well defined, strongly prominent ridge; dorsal tip of ridge pointed; ventral part confluent with ventro-proximal edge of LAP; ridge vertical and nearly straight, with very gentle kink in its middle part. Five well defined, oval spurs on the inner distal edge, corresponding to spurs on the outer proximal edge; spurs on the inner distal edge prominent with shallow depression in the middle. Large, conspicuous perforation close to the ventro-proximal edge of the LAP; no other perforations unambiguously discernible. Tentacle notch very large and deeply incising ventral edge of LAP.

**Remarks:** Among Mesozoic brittle-star assemblages, lateral arm plates with small spine articulations and numerous well defined spurs on the outer proximal and inner distal edges are primarily known from species assigned to *Ophiomusium* (e. g. HESS 1964, 1966; JAGT 2000) and to extinct *Palaeocoma* (e. g. HESS 1961, 1962). The single LAP from Serre-de-Bleyton, however, is incompatible with either. Similarities are greatest with the holotype of *Ophiura? astonensis* HESS, 1964, a proximal LAP from the Lower Jurassic of Great Britain which, however, has a much less protruding ventro-proximal part and a broader and more central ridge on the inner side. The LAP from Serre-de-Bleyton obviously cannot be convincingly included within any known Mesozoic brittle-star species. In spite of its novel character, the single available LAP is an inappropriate basis for the erection of a new species.

The higher taxonomic assignment of the LAP from Serre-de-Bleyton is more problematic as no extant species with satisfyingly similar LAP morphology could be found yet. LAPs with small spine articulations and numerous spurs on the outer proximal and inner distal edges are known from extant representatives of the ophiolipidid *Ophiomusium* and from the ophiurid *Stegophiura*. As the plate from Serre de Bleyton lacks the typically massive aspect combined with very large contact areas with the opposite LAP of *Ophiomusium*-species, we prefer an assignment, albeit with question mark, to the Ophiurinae within the Ophiuridae.

## Discussion

The material described herein constitutes by far the two most diverse brittle-star assemblages from the Early Cretaceous known to date, comprising five and eight species respectively (nine species altogether). All other reports of Early Cretaceous brittle stars are based on intact skeletons with the assemblages each comprising only one or two species (KÖNIG 1825; W. B. CLARK 1893; ALEXANDER 1931; TAYLOR 1966; HESS 1970; SHONE 1986; CORNELL et al. 1991; MARTIN-MEDRANO et al. 2009). The stratigraphically closest, more diverse brittle-star assemblages are the fauna described by SPENCER (1907) from the Lower Chalk (Cenomanian) of England, comprising six currently accepted species, and the fauna described by ŠTORC & ŽITŤ (2008) from the Late Turonian of Czech Republic,

comprising ten species. Comparatively diverse, stratigraphically older brittle-star assemblages are known from the Oxfordian of Switzerland and France (HESS 1975b and references therein). The Serre de Bleyton assemblages thus fill at least part of a major gap between Upper Jurassic and Upper Cretaceous brittle-star assemblages and, in contrast to reports of single species, allow for a preliminary assessment of the community-level changes the brittle-star assemblages underwent in late Mesozoic times.

Judging from the abundance of lateral arm plates, both Serre de Bleyton assemblages are strongly dominated by *Ophiotitanos pilleri* nov. spec. (64 % of the LAPs in locality 1 and 63 % in locality 2). LAPs assigned to the genus *Ophiotitanos* (*O. pilleri* and *O. sp.*) account for more than 70 % of the LAPs in both assemblages. This might be a primary ecological signal, documenting another case of apparent dominance of *Ophiotitanos*-like forms in a fossil brittle-star assemblage, comparable to faunas reported on by HESS (1975a) and ŠTORC & ŽITT (2008) for example. In the present case, however, especially in the light of the turbiditic nature of the beds producing the Serre de Bleyton assemblages, it is more likely that the size and robustness of the *Ophiotitanos*-like LAPs positively biased the preservation potential and thus the abundance of these plates. In addition, the size and conspicuousness of the *Ophiotitanos*-like LAPs might have produced a collecting bias to the disadvantage of smaller LAPs.

The composition of the Serre de Bleyton assemblages is reminiscent of many Late Jurassic communities, comprising one or several ophiacanthid species, forms with supposed ophirolepidid affinities, including species close to extant representatives of *Ophiomusium*, and *Ophiotitanos*-like forms. Amphiurid, ophiocomid, ophiactid and ophiothrichid species are completely lacking, while they are commonly found in Late Cretaceous assemblages (JAGT 2000; ŠTORC & ŽITT 2008). The oldest amphiurid record is the well known *Xanthamphiura hauteriviensis* HESS, 1970 from the Hauterivian of Switzerland, based on several articulated specimens. The generic assignment of *Ophiocoma ? nereida* (WRIGHT, 1880), from the Oxfordian of Great Britain, is highly questionable considering the poor preservation of the only known specimen (HESS 1964). Ophiocomid records from the Late Cretaceous of Central Europe, in contrast, seem to be more reliable (e.g. HESS 1960; JAGT 2000). *Ophiothrix ? royeri* (DE LORIO, 1872) from the Oxfordian of France and Switzerland has spine articulations which are very untypical of ophiothrichids (MARTYNOV 2010; THUY & STÖHR 2011) but rather reminiscent of ophiacanthids instead. The next oldest ophiothrichid records are disarticulated remains from the Late Cretaceous of Central Europe (e.g. JAGT 2000). The oldest unquestionable ophiactid is *Ophiactis applegatei* MARTIN-MEDRANO, THUY & GARCÍA-BARRERA, 2009 from the Albian of Mexico.

The Serre de Bleyton assemblage suggests that the Amphiuridae, Ophiocomidae, Ophiactidae and Ophiothrichidae played at most a minor role in Early Cretaceous brittle-star assemblages, if, in case of the latter three, they had originated by the Barremian at all. By the latest Cretaceous, these four groups had developed into relatively common and diverse elements of brittle-star assemblages, increasingly showing affinities with recent shallow-water communities most of which are dominated by amphiurids, ophiocomids,

ophiothrichids and/or ophiactids (e. g. KOEHLER 1922; HENDLER et al. 1995). During the Cretaceous, brittle-star communities thus underwent a significant, gradual shift towards modern communities in terms of composition. The Serre de Bleyton assemblage seems to predate at least most of this shift and probably represents one of the youngest currently known assemblages of Jurassic composition.

The turbiditic beds producing the Serre de Bleyton macrofauna are interpreted as basin-floor fans derived from the near-by Provence Platform and hemipelagic areas to the north-west of the Vocontian Trough (ADATTE et al. 2005; ARNAUD 2005). Most of the macrofauna should therefore be derived from shallower settings. Nevertheless, admixture of autochthonous deeper water faunal elements cannot be ruled out. In the case of the brittle-star remains, possible signs of pre-burial transport do not seem to follow any systematic patterns as almost all species include both very well preserved and obviously worn specimens, which impedes the determination of the origin based on the state of preservation. Analogy with modern equivalents must be discouraged in most cases as many taxa experienced dramatic shifts in distribution over time. The Ophiacanthidae for example, which are predominantly deep dwelling in present-day oceans (TYLER 1980), were a common and diverse component of Jurassic shallow-water communities (HESS 1975b). Pending the analysis of brittle-star remains from surrounding non-turbiditic beds, the origin of the Serre de Bleyton ophiuroid material described herein must remain speculative.

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## Plate 1

### **“Ophiacanthid A”**

Fig. 1: NHMW 2010/0356/0001, proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 2: NHMW 2010/0356/0002, proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

### **“Ophiacanthid B”**

Fig. 3: NHMW 2010/0356/0004, proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 4: NHMW 2010/0356/0005, proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

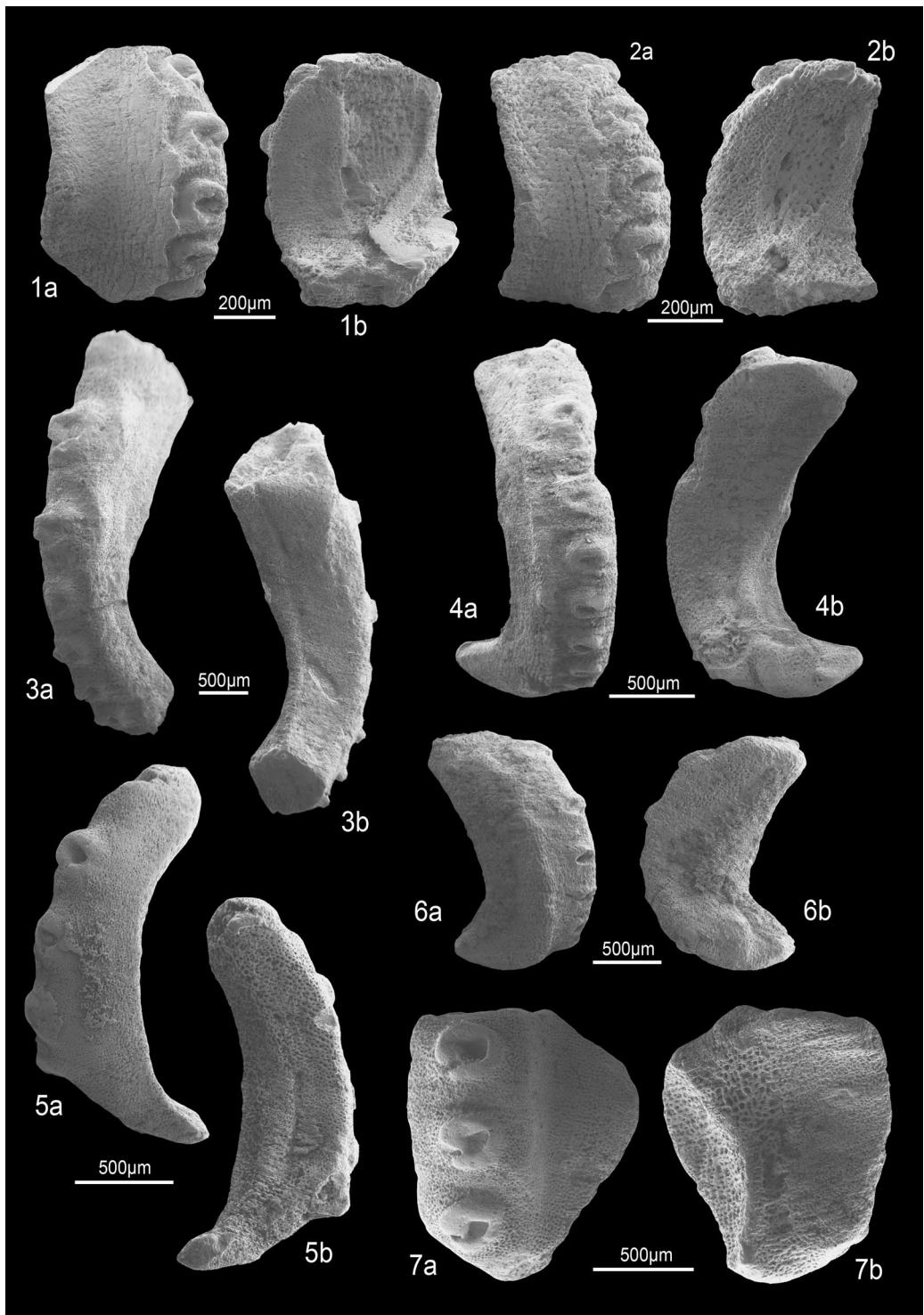
Fig. 5: NHMW 2010/0356/0006, proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 6: NHMW 2010/0356/0007, median lateral arm plate in external (a) and internal (b) view; Locality 1.

### **“Ophiacanthid C”**

Fig. 7: NHMW 2010/0356/0009, fragmentary lateral arm plate in external (a) and internal (b) view; Locality 2.

All specimens from the Barremian of Serre de Bleyton, Drôme, France. Scale bars in  $\mu\text{m}$ .



## Plate 2

### ***Ophiomusium* sp.**

Fig. 1: NHMW 2010/0356/0011, median to distal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 2: NHMW 2010/0356/0010, distal lateral arm plate in external (a) and internal (b) view; Locality 1.

### ***Ophiozonella stoehræ* nov. spec.**

Fig. 3: NHMW 2010/0356/0013 (holotype), proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 4: NHMW 2010/0356/0014 (paratype), median lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 5: NHMW 2010/0356/0015 (paratype), distal lateral arm plate in external (a) and internal (b) view; Locality 2.

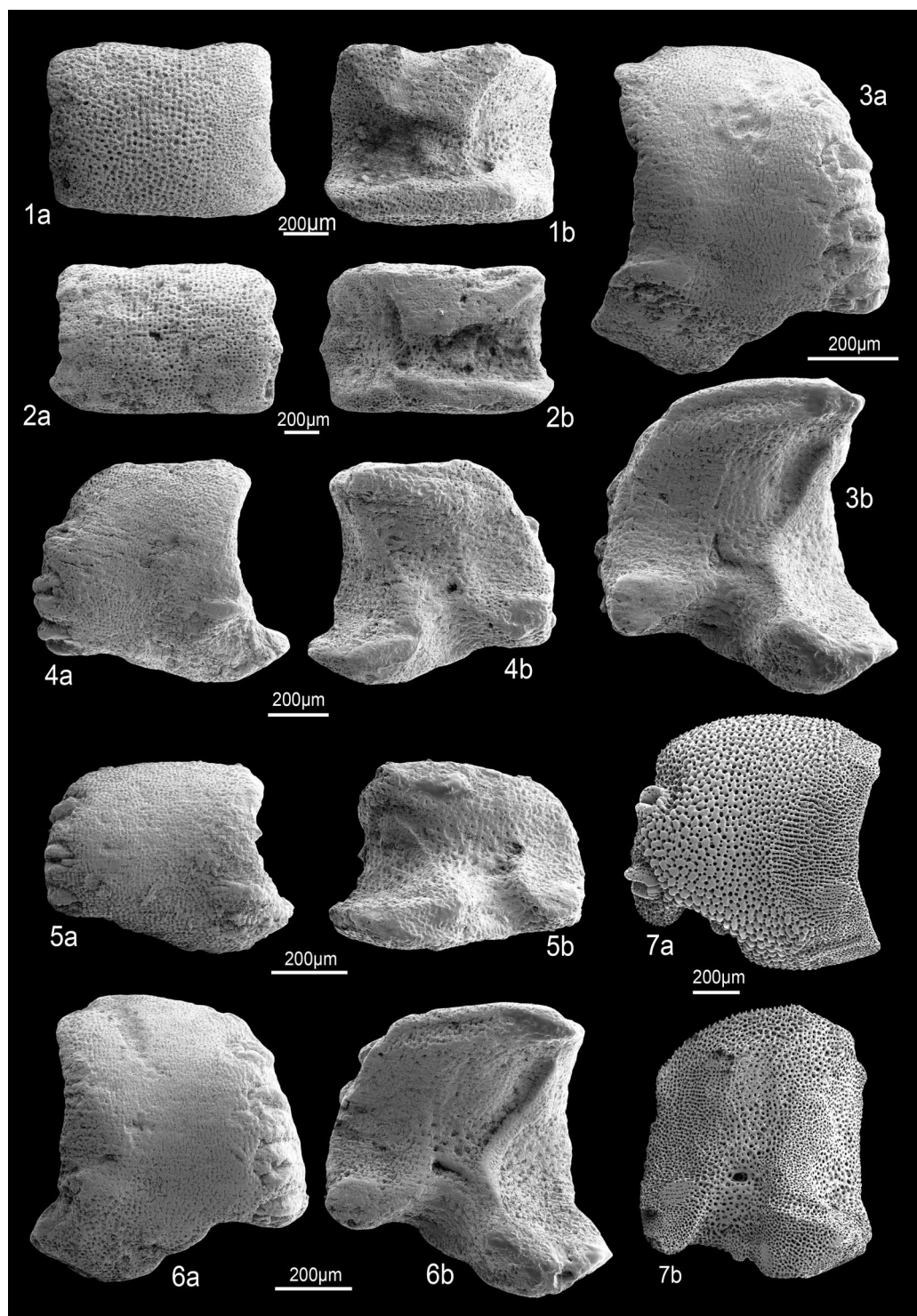
Fig. 6: GZG.INV.30570 (paratype), proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

### ***Ophiozonella longispina* (CLARK, 1908)**

Fig. 7: proximal lateral arm plate in external (a) and internal (b) view; Recent; Saint Kitts, Caribbean. Pictures kindly provided by Sabine Stöhr, Naturhistoriska Riksmuseet, Stockholm.

All specimens from the Barremian of Serre de Bleyton, Drôme, France, except for Fig. 7. Scale bars in  $\mu\text{m}$ .





### Plate 3

***Ophiotitanos pilleri* nov. spec.**

Fig. 1: NHMW 2010/0356/0017 (holotype), proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 2: NHMW 2010/0356/0018 (paratype), median lateral arm plate in external (a) and internal (b) view; Locality 2.

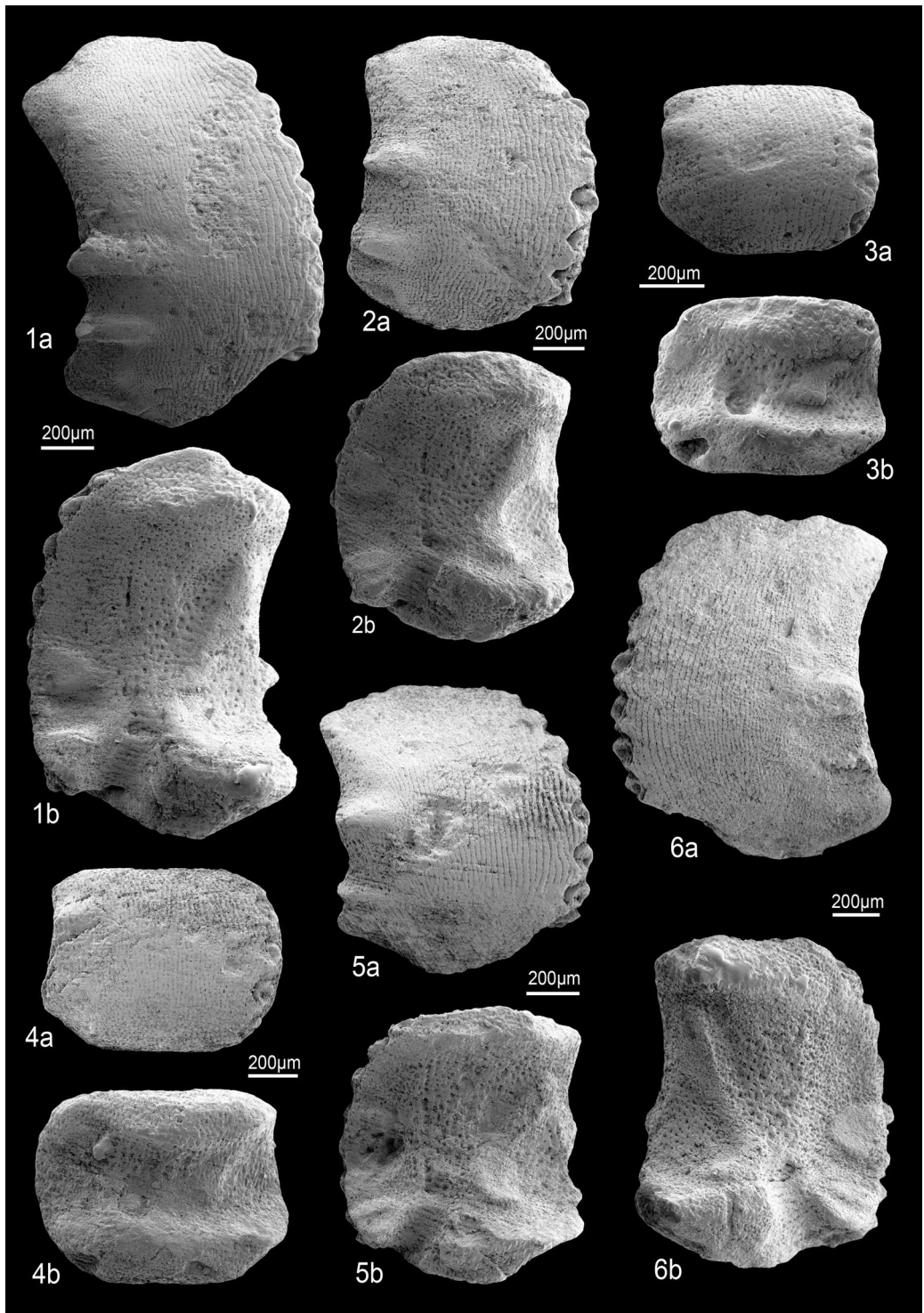
Fig. 3: NHMW 2010/0356/0019 (paratype), distal lateral arm plate in external (a) and internal (b) view; Locality 2.

Fig. 4: NHMW 2010/0356/0021, distal lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 5: NHMW 2010/0356/0022, median lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 6: GZG.INV.30572 (paratype), proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

All specimens from the Barremian of Serre de Bleyton, Drôme, France. Scale bars in  $\mu\text{m}$ .



## Plate 4

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

Fig. 1: NHMW 2010/0356/0024, proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 2: NHMW 2010/0356/0025, median lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 3: NHMW 2010/0356/0026, proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

### ***Amphiophiura* nov. spec.**

Fig. 4: NHMW 2010/0356/0029, proximal to median lateral arm plate in external (a) and internal (b) view; Locality 1.

Fig. 5: NHMW 2010/0356/0030, proximal lateral arm plate in external (a) and internal (b) view; Locality 1.

### ***Amphiophiura insolita* (KOEHLER, 1904)**

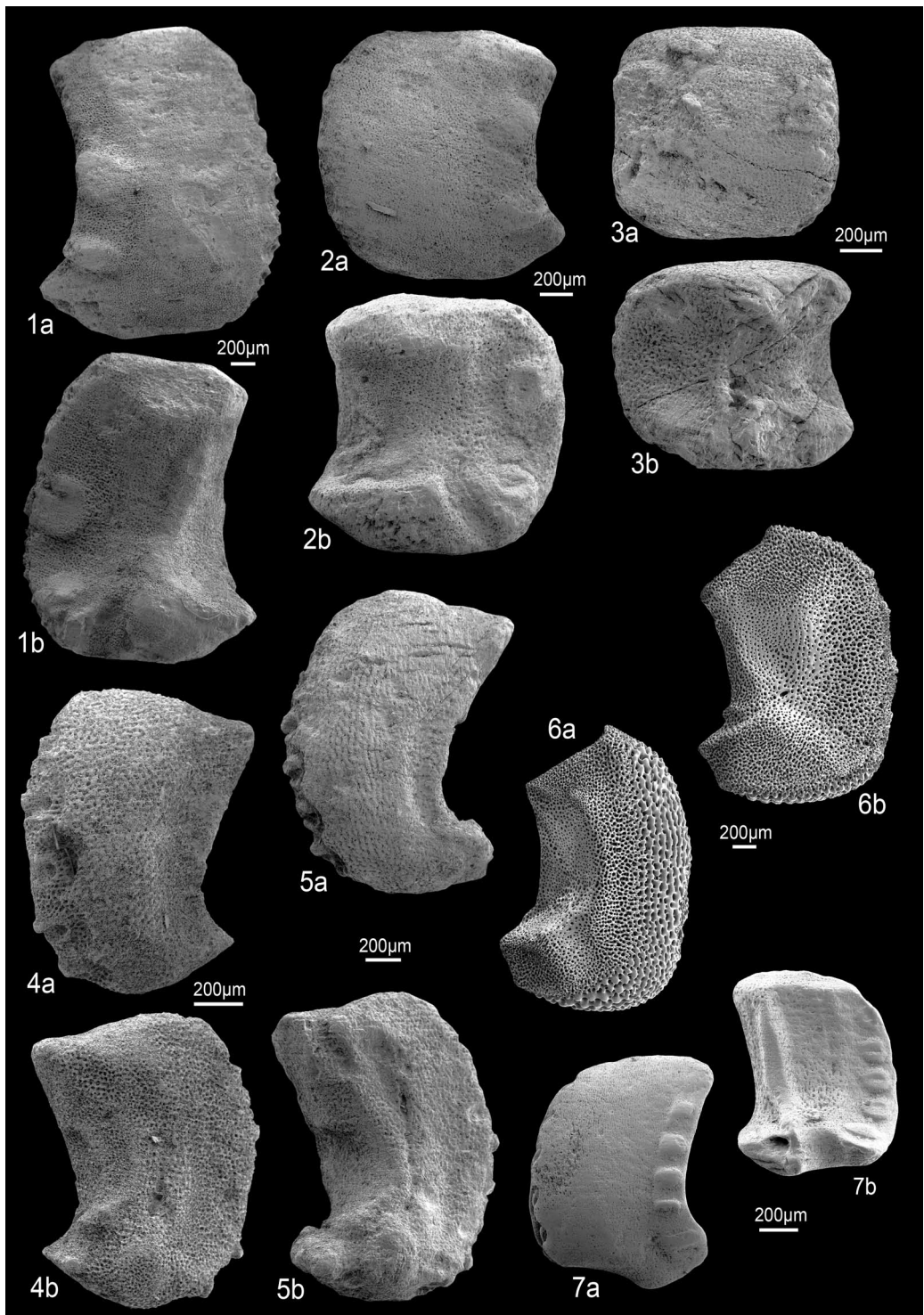
Fig. 6: proximal lateral arm plate in external (a) and internal (b) view; Recent; Lifou, New Caledonia. Pictures kindly provided by Sabine Stöhr, Naturhistoriska Riksmuseet, Stockholm.

### **“Ophiurid nov. spec.”**

Fig. 7: NHMW 2010/0356/0032, proximal lateral arm plate in external (a) and internal (b) view; Locality 2.

All specimens from the Barremian of Serre de Bleyton, Drôme, France, except for Fig. 6. Scale bars in  $\mu\text{m}$ .





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