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Brittle stars from the Lower Cretaceous of Patagonia: first ophiuroid articulated remains for the Mesozoic of South America

*Diana E. Fernández^{1,2}, Luciana Giachetti¹, Sabine Stöhr³, Ben Thuy⁴, Damián E. Pérez⁵, Marcos Comerio⁶, Pablo J. Pazos^{1,2}

¹ Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Geológicas, Buenos Aires, Argentina. elizabeth@gl.fcen.uba.ar; giachetti.luciana@gmail.com; pazos@gl.fcen.uba.ar

² CONICET-Universidad de Buenos Aires, Instituto de Estudios Andinos Don Pablo Groeber (IDEAN), Buenos Aires, Argentina.

³ Swedish Museum of Natural History, Department of Zoology, Box 50007, 104 05 Stockholm, Sweden.

sabine.stohr@nrm.se

⁴ Natural History Museum Luxembourg, Department of Palaeontology, 25, rue Münster, 2160 Luxembourg-City, Luxembourg.

bthuy@mnhn.lu

⁵ Museo Argentino de Ciencias Naturales Bernardino Rivadavia, División Paleoinvertebrados, Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina.

trophon@gmail.com

⁶ Centro de Tecnología de Recursos Minerales y Cerámica (CETMIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), camino Centenario y 506 s/n, C.C.49 (B1897ZCA), M.B. Gonnet, Argentina.

comerio@gl.fcen.uba.ar

* Corresponding author: elizabeth@gl.fcen.uba.ar; arkhamdryad@gmail.com.

ABSTRACT. The first articulated remains of ophiuroids for the Mesozoic of South America are described from the Lower Cretaceous of Neuquén Basin, Argentina. The taxonomic analysis allows the assignment of the material described herein to the extinct genus *Ophiopetra*. The specimens belong to a new species, but considering the poor preservation, a new name is not introduced, as it would be based on an incomplete diagnosis. Certain characteristics (e.g., the diameter of the disc, the width/height ratio of the vertebrae) suggest that these ophiuroids are paedomorphic specimens. In light of the latest classification of the Ophiuroidea, and new insights on the spine articulation microstructure of *Ophiopetra lithographica* presented herein, a transfer of *Ophiopetra* to the family Ophionereididae within the order Amphilepidida is proposed. This material expands the palaeogeographic record of this genus, since it represents the first remains of *Ophiopetra* described in the Southern Hemisphere. It is also the first Cretaceous record of the genus worldwide.

Keywords: Ophiuroidea, Early Cretaceous, Southern Hemisphere, *Ophiopetra*, Ophionereididae.

RESUMEN. Ofiuroideos del Cretácico Inferior de Patagonia: primer registro fósil articulado para el Mesozoico de América del Sur. Se describen los primeros registros fósiles de ofiuroideos articulados del Mesozoico de América del Sur, provenientes del Cretácico Inferior de Cuenca Neuquina, Argentina. El análisis taxonómico permite asignar el material descrito al género extinto *Ophiopetra*. Los especímenes pertenecen a una nueva especie, pero no se propone un nuevo nombre porque, debido a la pobre preservación, estaría basado en una diagnosis incompleta. Ciertas características (e.g., el diámetro del disco, la relación ancho/alto de vértebras, etc.) sugieren que estos ofiuroideos son especímenes pedomórficos. Se propone la transferencia de *Ophiopetra* a la familia Ophionereididae del orden Amphilepidida teniendo en cuenta la última clasificación de ofiuroideos y nuevas evidencias sobre la microestructura de las articulaciones espinales de *Ophiopetra lithographica* presentadas en este trabajo. Este material expande el registro paleogeográfico del género, ya que es la primera descripción de *Ophiopetra* en el hemisferio sur. Además, es el primer registro cretácico del género a nivel mundial.

Palabras clave: Ophiuroidea, Cretácico Temprano, Hemisferio Sur, *Ophiopetra*, Ophionereididae.

1. Introduction

Ophiuroids (Echinodermata: Ophiuroidea), commonly known as brittle stars, are a diverse group of echinoderms. Their extant representatives are cosmopolitan and contribute significantly to species diversity in many marine benthic communities (Gerdes *et al.*, 1992; Dahm, 1996; Stöhr *et al.*, 2012). Despite their early appearance in the Phanerozoic (Early Ordovician), the fossil record of ophiuroids is relatively scarce, mainly due to post-mortem disarticulation of their skeletal elements. Specimens with articulated and largely complete skeleton are extremely rare (Spencer and Wright, 1966; Aronson, 1989; Kerr and Twitchett 2004; Martínez *et al.*, 2010). Systematic assessment of fossil ophiuroids has recently received increasing attention (Ewin and Thuy, 2017). Yet, knowledge of the fossil record of ophiuroids, particularly in the Lower Cretaceous, is still limited (Thuy *et al.*, 2014).

The ophiuroid fossil record in South America is scarce (Martin-Medrano and García-Barrera, 2013). Recently, ophiuroid remains were reported for the first time in the lowermost part of the Lower Cretaceous Agua de la Mula Member of the Agrio Formation, Neuquén Basin, Patagonia (Pérez *et al.*, 2011). The purpose of this work is twofold: **i.** to present a detailed description of this material; and, **ii.** to provide a taxonomic assignment in the light of the latest classification of the Ophiuroidea. The material presented here represents the first articulated remains of ophiuroids for the Mesozoic of South America.

2. Geological setting, study area and paleoenvironmental context

The Neuquén Basin (Fig. 1A) is located in west-central Argentina (northern Patagonia) between 34° and 41°S. It contains marine and continental sedimentary deposits of Late Triassic to Paleogene age (Vergani *et al.*, 1995; Legarreta and Uliana, 1999). Most of the Jurassic and Lower Cretaceous sedimentary deposits are composed of diverse, highly fossiliferous marine facies associated with transgressions (Howell *et al.*, 2005). During the Early Cretaceous, the basin was connected to the paleo-Pacific Ocean to the west by a gateway, accentuated by a roughly N-S oriented island arc chain, and the basin was affected by eustatic and relative sea level

variations (Zapata and Folguera, 2005). Close to the Late Hauterivian, the Neuquén basin was rapidly flooded, and the basin-wide style of ramp deposition had resumed, represented by a calm open marine basin with deposition of organic-rich shales and mudstones (Legarreta and Uliana, 1991).

The Agrio Formation, in the Neuquén Basin, is the youngest unit of the Mendoza Group (Tithonian-Barremian), exposed in Neuquén Province (Weaver, 1931). The upper member, or Agua de la Mula Member (Leanza *et al.*, 2001), of the Agrio Formation is late Hauterivian to early Barremian in age (Aguirre-Urreta *et al.*, 2007, 2015; Aguirre-Urreta and Rawson, 2012). It comprises mixed carbonate-siliciclastic marine and marginal-marine deposits (Spalletti *et al.*, 2001a; Lazo *et al.*, 2005; Pazos and Fernández, 2010; Fernández and Pazos, 2012). The uppermost part of the unit was tidally influenced (Pazos *et al.*, 2012; Fernández and Pazos, 2013), while the lowermost levels have been interpreted as an open marine ramp under fluctuating rates of siliciclastic input and carbonate productivity (Spalletti *et al.*, 2001b; Comerio *et al.*, 2018). This highly fossiliferous unit presents varied and abundant evidence of invertebrate fauna (*e.g.*, Aguirre-Urreta, 2003; Cichowolski, 2003; Lazo *et al.*, 2005, 2009; Rodríguez, 2007; Taylor *et al.*, 2009; Aguirre-Urreta *et al.*, 2011; Luci *et al.*, 2013; Fernández and Pazos, 2013; Cataldo, 2014). However, ophiuroids were never before described in the unit. The bed of interest in this work is within the lowermost levels of the Agua de la Mula Member (Fig. 1B) at Loma La Torre (37°19-20' S, 69°50-51' W), in the Neuquén Province (Fig. 1A). The ophiuroid-bearing bed is a mudstone level, located approximately 12 m above the contact with the underlying Avilé Member (Fig. 1B). The logged section comprises three main lithofacies: massive mudstones, marlstones, and laminated shales. In this section, two intervals are distinguished based on their lithology and stacking pattern. Within the first 10 m, outcrops comprise moderately to highly indurated beds where mudstones and marlstones dominate over shales. In the second interval, shales dominate over mudstones and marlstones. In nearby localities, these two intervals were identified and have been interpreted as deposited in a distal to proximal outer ramp setting (Comerio *et al.*, 2018). A similar paleoenvironmental interpretation is envisaged here. The ophiuroid-bearing level lies within the proximal outer ramp deposits.

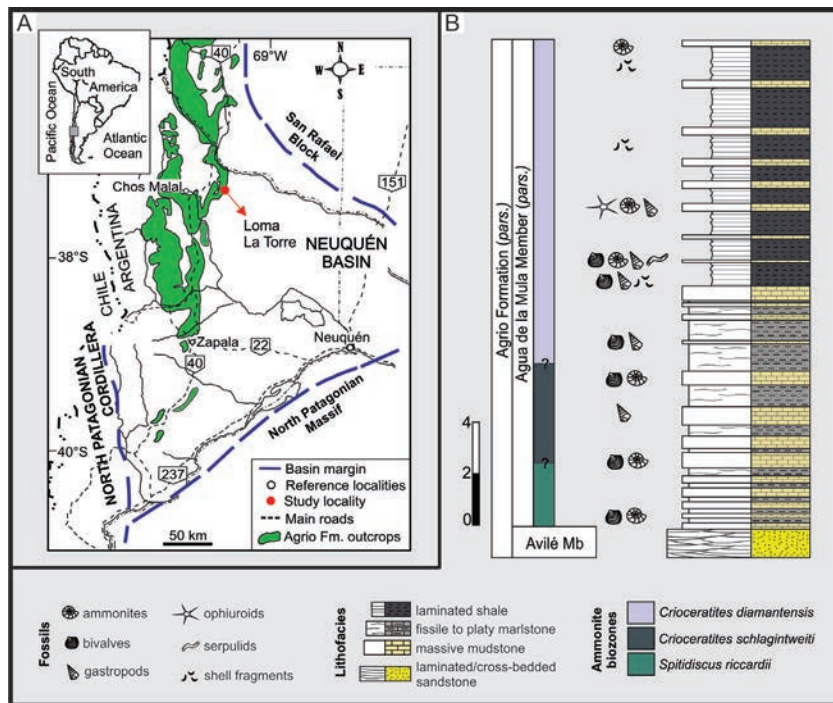


FIG. 1. A. Map of the Neuquén Basin and its location in Argentina and South America. Note the location of the Agrio Formation outcrops and the study site. Modified from Aguirre-Urreta *et al.* (2007). B. Logged section of the lowermost part of the Agua de la Mula Member, Agrio Formation, in Loma La Torre. Note the ophiuroid-bearing level. Ammonite biozones from Aguirre-Urreta *et al.* (2007, 2015).

3. Material and methods

The logged section included here (Fig. 1B) comprises only the lowermost part of the Agua de la Mula Member, *i.e.*, the interval of interest where the ophiuroid-bearing level is found. Three specimens preserved on slabs were examined under scanning electron and light microscopy. For SEM images, a microscope FEI Quanta 200 was used after standard sample preparation (thin gold coat). Light photographs were taken with a Leica M165C microscope and DFC295 camera and combined using Combine ZP stacking software. The studied samples are housed in the Collection of the Área de Paleontología (Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires) under the prefix CPBA with the numbers 20455.1, 20455.2 and 20455.3. The specimens from the type locality (Kimmeridgian of France) are housed in the palaeontological collection of the Luxembourg Natural History Museum under the prefix MnhnL. Morphological terminology follows Stöhr

et al. (2012) for skeletal plates, and Thuy and Stöhr (2011) for features of lateral arm plates. Higher-level classification is adopted from O'Hara *et al.* (2017).

4. Results

4.1. Systematic paleontology

Order Amphilepidida O'Hara *et al.*, 2017
Suborder Ophionereidina O'Hara *et al.*, 2017
Superfamily Ophionereidoidea Ljungman, 1867
Family Ophionereididae Ljungman, 1867

Diagnosis. Granules along the genital slit, extending onto disc edge. Accessory dorsal arm plates (*Ophionereis*). Scale-like, flat, oval to round tentacle scales. Tooth sockets dorsally as large fenestrations with septum. Arm spine articulation horse-shoe shaped, with parallel dorsal and ventral lobes proximally separated by vertical row of knobs or merged by ribbed border, framing nerve and muscle openings of almost equal size. Internal of

lateral arm plate with large pore close to the dorsal edge of the tentacle pore excavation, at the ventral tip of a large ridge along the inner proximal edge that bends ventro-distalwards. Vertebrae with distally protruding dorsal keel and proximal dorsal groove (from O'Hara *et al.*, 2018).

Genus *Ophiopetra* Hess in Enay and Hess, 1962

Diagnosis. Small species. Disc with granules on both sides (including radial shields). Granules covering small imbricated disc scales. Radial shields and genital plates articulate with two condyles and a facet present in both the radial shield and the corresponding genital plate. Radial shields of moderate width, those of the same radius do not touch each other. Oral plates without large, wing-like flange. Double peristomial plates. Approximately six oral papillae contiguous on each side. Probably no tooth papillae. Teeth blunt, not very strong. Adoral shields meeting at proximal edge of oral shield. Arm spines in groups of three, erect, slightly longer than one arm segment. Ventral arm plates pentagonal, longer than wide, contiguous only on the proximal half of the arm. Dorsal arm plates triangular, with a strongly convex distal edge. Tentacles pores on almost the entire length of the arms, two tentacle scales per pore. Vertebrae with zygospondylous articulation (from Hess in Enay and Hess, 1962).

Ophiopetra sp. (Figs. 2-5)

Description. CPBA 20455.1 (Figs. 2A, 2C-D, 2F, 4A-F, 5A-C). Deformed disc. Dorsal disc scales not discernible due to insufficient preservation; small granules are visible. Radial shields may be represented by two poorly preserved oval plates (Fig. 2D). Connection between the arms and the central disc is clear in two arms (Fig. 2A). Lateral arm plates stout, subquadrangular to subrectangular with distal edge convex and proximal and lateral edges mostly straight (Fig. 2F). Height/length ratio is approximately 0.62 in proximal lateral arm plates (Figs. 4E and F) while distal ones (Figs. 4A, C and D) are elongated (height/length=0.30). One or two horseshoe-shaped arm spine articulations per lateral arm plate (Figs. 5A, B and C). Arm spines smooth and probably conical with a maximum preserved length 2/3 as long as one arm segment

(Figs. 4E and F). Dorsal arm plates subtriangular with convex distal edge, acute proximal edge and straight to slightly convex lateral edges (Figs. 4C and D). Ventral arm plates subrectangular with concave lateral edges, acute proximal edge and pointed to slightly convex distal edge (Figs. 4A and B). Only one elongated tentacle scale is preserved (Fig. 4A). On all observable arm segments, lateral arm plates separate dorsal and ventral arm plates (Fig. 2F). Outer surface of lateral and dorsal arm plates with coarse tubercles (Figs. 4C and E).

CPBA 20455.2 (Figs. 2E, 3A-D, 5D). The specimen shows a faint outline of the disc, which is circular, approximately 3.5 mm in diameter (Fig. 2E). Oral plates long, relatively slender and slightly curved (Figs. 3A and B). Dental plate and at least one flat subquadrangular tooth are observed (Figs. 3A, B and C). Only one poorly preserved, rod-shaped genital plate (Fig. 3D) and one poorly preserved, much longer than wide/high vertebra are observed (Fig. 5D).

CPBA 20455.3 (Fig. 2B) shows a faint outline of the disc. Five long and slender arms with a maximum preserved length of 9.98 mm, approximately 3 times longer than the disc diameter (Fig. 2B).

5. Discussion and conclusions

Although the here-described specimens are rather poorly preserved (with some deformed areas and fragmented pieces), they show some characters of diagnostic value allowing for a placement in a taxonomic context at least to the genus level. Here, the shape of the spine articulations is of particular interest. According to Martynov (2010), Ophionereididae and Ophiochitonidae, which have recently been synonymized (O'Hara *et al.*, 2017), present horseshoe-shaped arm spine articulations. Among the currently known fossil ophiuroid genera, horseshoe-shaped spine articulations were explicitly mentioned for *Ophiopetra* from the Late Jurassic of France (Hess, 1965a), although the diagnosis of the genus does not include information on the spine articulations (Enay and Hess, 1962) or other characters that are now considered to be diagnostic (Martynov, 2010; Thuy and Stöhr, 2011). *Ophiopetra lithographica* Hess in Enay and Hess, 1962 is currently the only valid species within this genus (Thuy *et al.*, 2013), and we had the chance to study specimens of *O. lithographica* from the type locality (Figs. 5E, F).

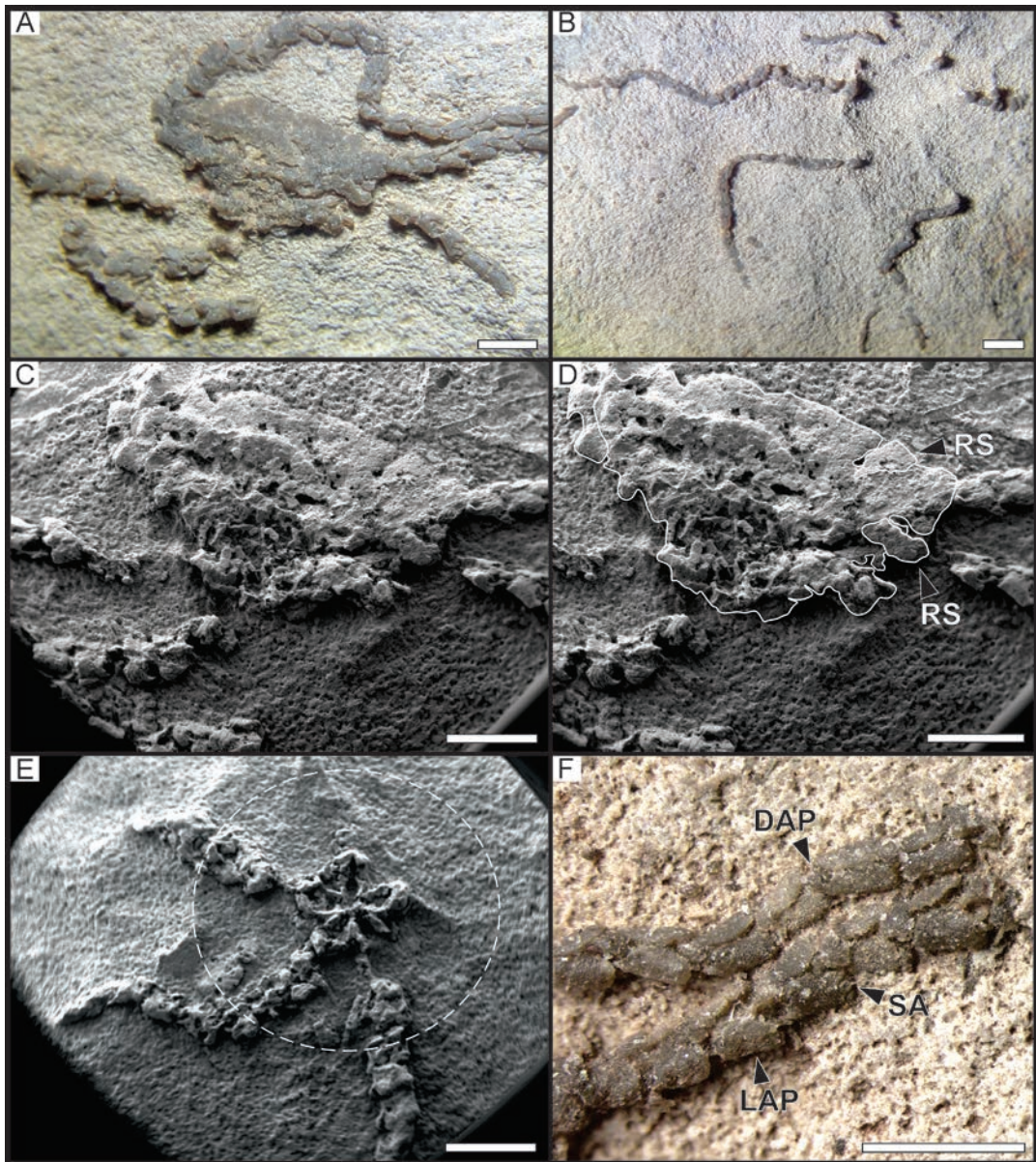


FIG. 2. General view of specimens. **A.** CPBA 20455.1 with partially deformed disc. Two of the arms in connection with the disc and the other three slightly disconnected. **B.** CPBA 20455.3. Only the arms are preserved but a faint outline of the disc is visible. **C.** CPBA 20455.1. Detail of the deformed disc. **D.** CPBA 20455.1. Detail of C, with drawing of the outline of the disc and position of the radial shields. **E.** CPBA 20455.2. Part of the disc and proximal portion of three arms. The outline of the disc is marked with a dotted circle. **F.** CPBA 20455.1. Two arms, showing dorsal arm plates, lateral arm plates and one spine articulation. **RS:** radial shield; **LAP:** lateral arm plate; **DAP:** dorsal arm plate; **SA:** spine articulation; **Scale bars:** 1 mm.

Scanning electron microscopy allowed us to confirm that the spine articulations of *Ophiopetra lithographica* are, indeed, similar to the horseshoe-shaped ones of the material described herein and the ones typical of Ophionereididae in general.

The systematic position of *Ophiopetra* has been under debate, ever since the erection of the genus (Enay and Hess, 1962). According to the latest classification of the Ophiuroidea, the Ophionereididae include the genera *Ophiodoris* Koehler, 1904, Paris

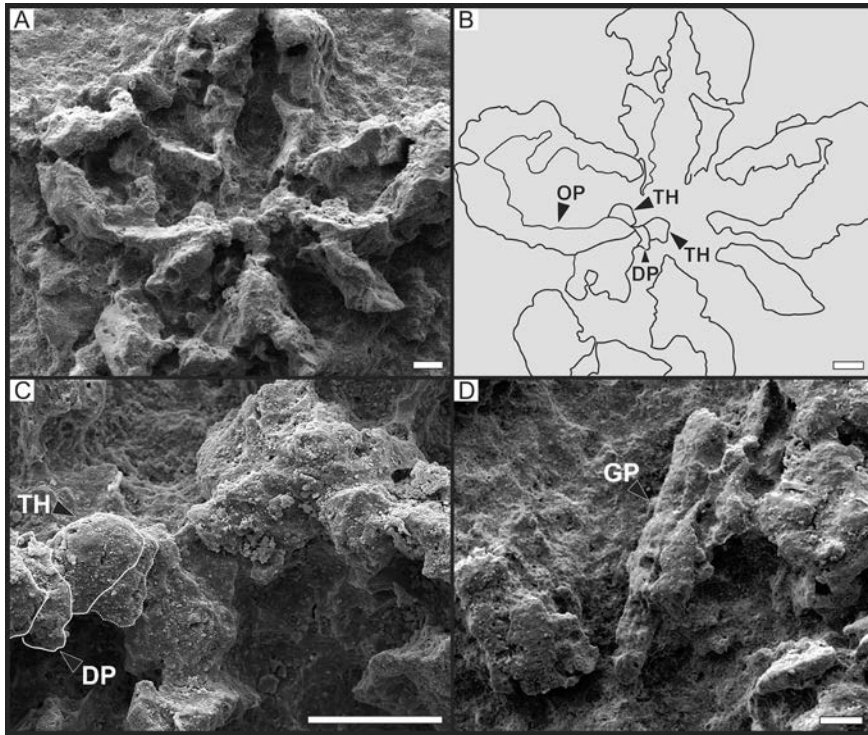


FIG. 3. Details of the disc area. CPBA 20455.2. **A.** Close up of the oral plates. Note they are long, relatively slender and slightly curved. **B.** Line drawing of A, detailing oral plates, teeth and a dental plate. **C.** Detail of A showing teeth and a dental plate. **D.** Poorly preserved, rod-shaped genital plate. **OP:** oral plate; **TH:** teeth; **DP:** dental plate; **GP:** genital plate; **Scale bars:** 100 μm .

Ophionereis Lütken, 1859, *Ophioplax* Lyman, 1875, and *Ophiochiton* Lyman, 1878 (O'Hara *et al.*, 2017, 2018). In *Ophiodoris* and *Ophioplax* the lateral arm plates are ornamented with small tubercles (Lyman, 1875; Koehler, 1904; Numberger-Thuy and Thuy, 2015). The lateral arm plates exhibited by the specimens described herein are similar to what is found in *Ophiodoris* and *Ophioplax* (Lyman, 1875; Koehler, 1904). However, in the disc ornamentation, the present material differs from *Ophiodoris*, in which the disc is naked or bears small spines (Koehler, 1904; Fell, 1960), and from *Ophioplax* which has granules only on the ventral side of the disc (Lyman, 1875; Fell, 1960). In *Ophiopetra*, in contrast, both sides of the disc are densely covered with granules. We therefore place the here-described specimens in the genus *Ophiopetra*, also taking into account similarities in the overall shape of the lateral arm plates.

At the moment, *Ophiopetra* is considered an ophiolpid (Thuy *et al.*, 2012). In the context of the latest progress in ophiuroid systematics, and thanks to the new insights on the spine articulation

microstructure of *Ophiopetra lithographica* presented herein, we propose a transfer of *Ophiopetra* to the Ophionereididae.

Given the lack of preserved diagnostic disc characters, these specimens are not assigned to *Ophiopetra lithographica*. Also, the stratigraphic and palaeo-biogeographic distance to *O. lithographica* (see below) suggest that the here-described specimens belong to a new species. Considering the poor preservation of the currently known material and the lack of disc characters, however, we prefer not to introduce a new name, as it would be based on a highly incomplete diagnosis.

5.1. Evidence for pedomorphosis

Ontogenetic studies on post-metamorphic ophiuroids have recently gained more attention (*e.g.*, Stöhr, 2005; Martynov, 2012; Borges *et al.*, 2015). The geometry and proportions of the ophiuroid skeleton gradually and continually change during growth, which complicates an assignment to an

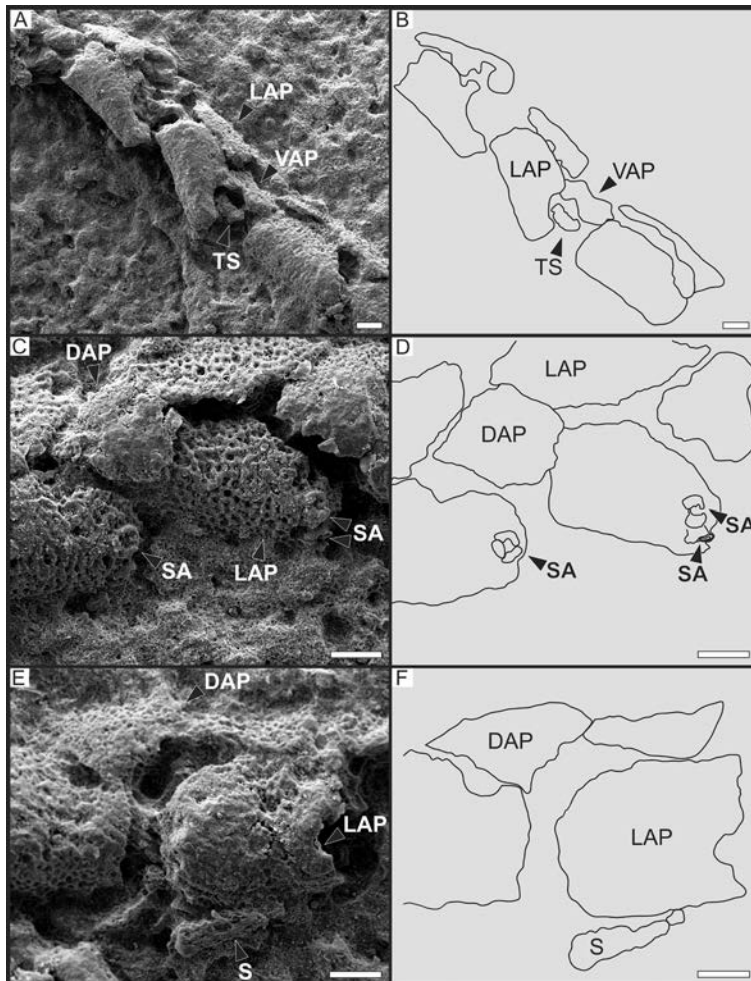


FIG. 4. Articulated arm segments. CPBA 20455.1. **A.** Ventral side of the arm, showing lateral arm plates, one ventral arm plate and one tentacle scale. **B.** Line drawing of A. **C.** Dorso-lateral view of arm showing lateral arm plates, dorsal arm plates and spine articulations. Note the granulated outer surface. **D.** Line drawing of C. **E.** Latero-dorsal view of arm showing lateral arm plates, dorsal arm plates and one spine. **F.** Line drawing of E. **LAP:** lateral arm plate; **VAP:** ventral arm plate; **TS:** tentacle shield; **DAP:** dorsal arm plate; **SA:** spine articulation; **S:** spine; **Scale bars:** 100 μ m.

ontogenetic stage. Some parts of this material present juvenile traits, *e.g.*, small dorsal plates, relatively elongated arm segments even in proximal position (Martynov *et al.*, 2015), and slightly curved jaws (Stöhr and Martinov, 2016). The vertebra (Fig. 5D) in specimen 20455.2 is much longer than wide/high in a very proximal position of the arm, which is an indicator of juvenile/paedomorphic conditions (Stöhr and Martinov, 2016). However, other characteristics, *e.g.*, the diameter of the disc, are not compatible with juveniles (Webb and Tyler, 1985; Borges *et al.*, 2015; Martynov *et al.*, 2015) but may suggest

paedomorphic adults (Stöhr and Martynov, 2016). Hence, the evidence suggests that these ophiuroids are paedomorphic specimens. It is worth to note that this information does not lead to taxonomic uncertainty.

5.2. Ophiuroid fossil remains in South America and the record of Ophiopetra

The findings of articulated and/or nearly complete brittle stars in South America are restricted to Devonian appearances (Ruedemann, 1916; Clarke, 1913; Méndez-Alzola, 1938; Melo, 1988; Rehfeld and

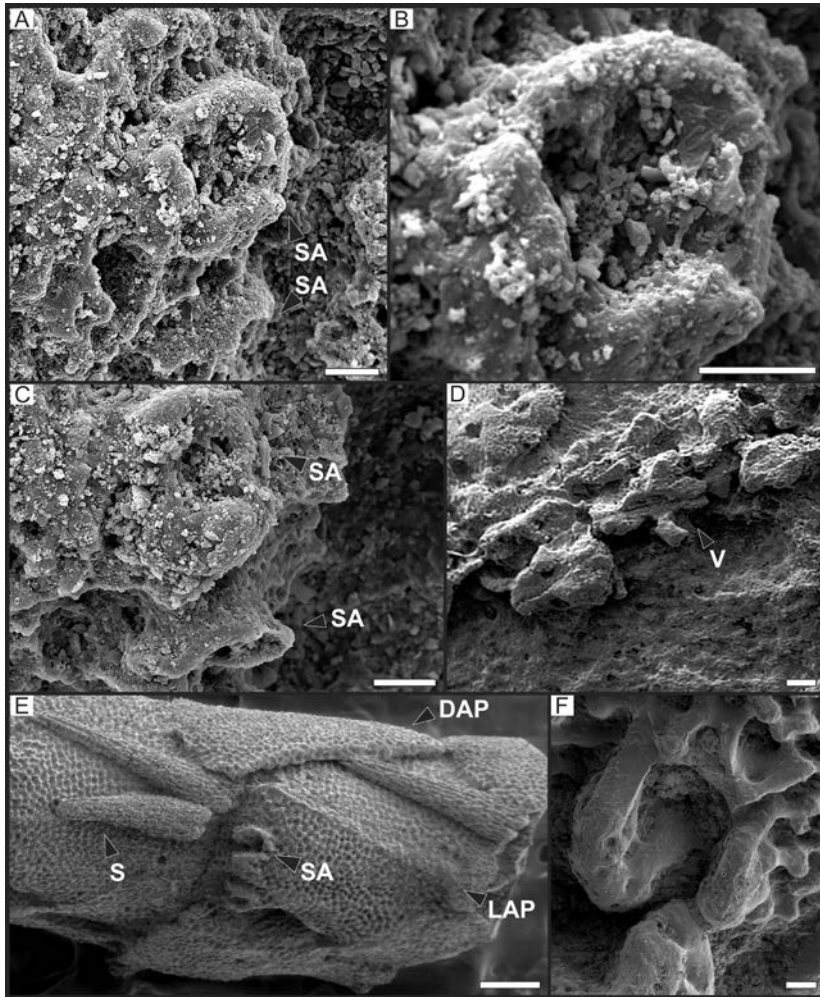


FIG. 5. Spine articulations and a vertebra of the material described herein and specimens of *Ophiopetra lithographica* from the type locality (Kimmeridgian of France), for comparison. **A.** CPBA 20455.1. Detail of lateral arm plate with two horseshoe-shaped arm spine articulation. **B.** CPBA 20455.1. Close up of spine articulation in A. **C.** CPBA 20455.1. Another example of spine articulations. **D.** CPBA 20455.2. A poorly preserved, longer than wide/high vertebra. **E.** MnhnL OPH028. Arm segments of *Ophiopetra lithographica*. Note the granulated outer surface, the general shape of the arm plates and the spine articulation. **F.** MnhnL OPH028. *O. lithographica*. Spine articulation. SA: spine articulation; V: vertebra; DAP: dorsal arm; LAP: lateral arm plate; S: spine; Scale bars: 20 μ m in A, B and C; 0.1 mm in D; 100 μ m in E; 10 μ m in F.

Mehl, 1989; Haude, 1995, 2010), Permian (Sánchez, 1983) and Cenozoic specimens (e.g., Berry, 1941; Furque and Camacho, 1949; Kutscher *et al.*, 2004; Caviglia *et al.*, 2007; Martínez and del Río, 2008). Isolated remains were reported from Devonian (Rehfeld and Mehl, 1989), Jurassic-Cretaceous (Kietzmann *et al.*, 2014) and Cenozoic (Bertels, 1965) sedimentary deposits. For the Mesozoic of South America, the fossil record of ophiuroids is restricted to trace fossils from the Lower Cretaceous

of Argentina and Chile (Bell, 2004; Rodríguez *et al.*, 2007) and isolated ossicles from the deposits of the Tithonian-Valanginian interval in Argentina (Kietzmann *et al.*, 2014). The material presented here includes the first remains of articulated ophiuroids for the Mesozoic of South America.

Ophiopetra lithographica is recorded from the Callovian of Switzerland (Hess, 1963), Kimmeridgian of France (e.g., Bourseau *et al.*, 1991), and Tithonian of Germany (Kutscher and Röper, 1995; Hess, 1999)

and Austria (Hess, 1965b). Isolated ossicles assigned to *Ophiopetra* sp. were reported from the Middle Jurassic of Poland (Gedl et al., 2003). Therefore, these specimens also represent the first record of the genus *Ophiopetra* for the Southern Hemisphere and for the Cretaceous worldwide.

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