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NEW ALBIAN (EARLY CRETACEOUS) OPHIUROIDS FROM THE TLAYÚA QUARRY, PUEBLA, MEXICO

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Abstract: On the basis of six articulated individuals from the middle to late Albian lithographic limestone at Tlayúa near Tepexi de Rodríguez (Puebla, Mexico), a new species of ophiuroid, *Ophiactis applegatei*, is described. The material adds to the rather poor record of Early Cretaceous brittlestars and represents the oldest known member of the family Ophiactidae, being based on well-preserved and articulated specimens and thus reasonably well defined morphologically. The rarity of ophiuroids, their complete preservation as well as the unnatural contortions of their arms suggest these specimens to be allochthonous, having been transported into a hostile environment where burial was rapid.

Key words: Albian, Tlayúa Formation, Mexico, Ophiuroidea, taxonomy, palaeoecology.

OFTEN referred to as the 'Mexican Solnhofen', the Tlayúa Quarry near Tepexi de Rodríguez (State of Puebla, Mexico) ranks amongst the more important fossil localities in the New World. Strata exposed there have yielded a vast array of biota, which are remarkable in view of their diversity and exceptional preservation, inclusive soft tissues in fish (Alvarado-Ortega *et al.* 2007). Over the past few decades, the highly fossiliferous lithographic limestone at Tlayúa has been the focus of studies which aim to characterize the biota and reconstruct their palaeoecology. To date, only 5 per cent of all biota represented at Tlayúa have been described, which means that a majority (>6500 specimens) remain largely unassessed taxonomically. The presence of brittlestar remains has been noted previously by Applegate and Espinosa-Arrubarrena (1982), Applegate (1987, 1996), Buitrón and Malpica-Cruz (1987), Feldmann *et al.* (1998), Applegate *et al.* (2000), Martin-Medrano (2003, 2006), Alvarado-Ortega (2005), Applegate *et al.* (2006) and Martin-Medrano and García-Barrera (2006).

In Mexico, fossil ophiuroids are rare in comparison to other echinoderms and echinoids in particular (Nieto-López and García-Barrera 2006). To date, brittlestar remains have been recorded from strata of Late Carboniferous (Pennsylvanian) to Pliocene age (Buitrón *et al.* 1994; Quiroz-Barroso and Sour-Tovar 1995), at just a handful (seven in all) of localities. Amongst these, the Cretaceous accounts for three sites, namely the Tlayúa Quarry (Puebla; the present record), Redoma in the State of Coahuila and Altares in Chihuahua (Martin-Medrano 2006), with the first-named being the richest locality in terms of individuals. The present paper, in which a new species, *Ophiactis applegatei*, is erected, constitutes the first formal description of fossil ophiuroids from Mexico.

Similar to other biota from Tlayúa, these brittlestars are well preserved and reveal hardly any sign of disintegration. As such, they offer a unique insight into skeletal structure and the species' palaeobiology. This is of special note, because little is known about Early Cretaceous brittlestars in comparison to the well-documented Late Jurassic and Late Cretaceous ophiuroid diversity (Hess 1975; Kutscher and Jagt 2000). Here, we assess the present faunule taxonomically and briefly discuss its taphonomy and palaeoecology.

GEOLOGICAL AND PALAEONTOLOGICAL CONTEXT

The Albian Tlayúa Formation, introduced by Pantoja-Alor (1992), comprises a succession of carbonates in the Tlayúa Ravine area, near the city of Tepexi de Rodríguez (Text-fig. 1), which is subdivided into three members. About 50 m of massive white limestone constitutes the Lower Member which yields miliolid foraminifera and small-sized molluscs; the occurrence of the rudist *Toucasia polygyra* Alencáster, 1973 and the bivalve genus *Chondrodonta* Stanton, 1901 dates this member as early Albian (Pantoja-Alor, 1992). The Middle Member (thickness *c.* 35 m; Text-fig. 2) comprises mainly micritic, yellowish brown lithographic limestone with intercalated, hematite-rich clayey layers,

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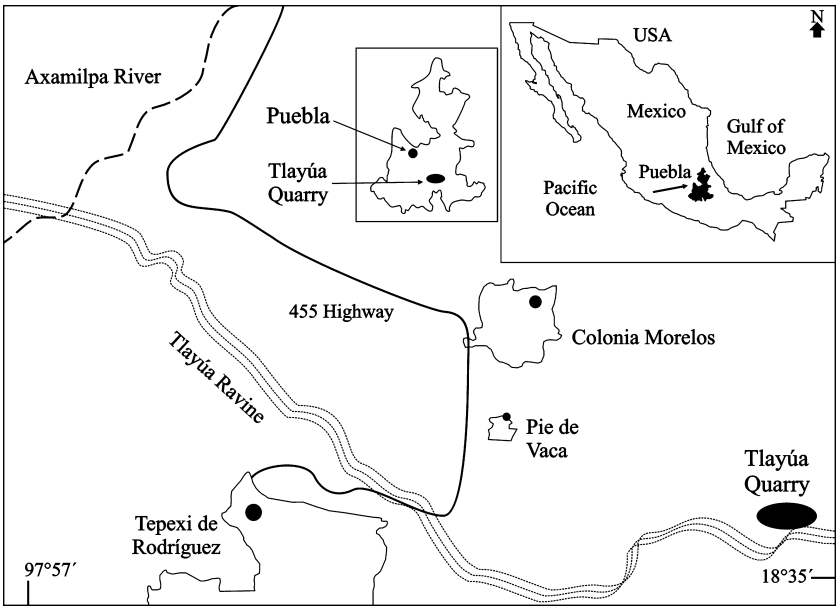


TEXT-FIG. 1. Location of the Tlayúa Quarry, near Tepexi de Rodríguez, Puebla.

parallel to bedding, which outcrop over a stretch of some 700 m (Pantoja-Alor 1992; Applegate *et al.* 2006). Magnetostratigraphic data strongly suggest a middle to late Albian age for these highly fossiliferous limestones (Benammi *et al.* 2006); this age assignment is supported by the presence of the ammonite genera *Hysteroceras* Hyatt, 1900, *Mortoniceras* Meek, 1876 and cf. *Anisoceras* Pictet, 1854 (Cantú-Chapa 1987; Applegate *et al.* 2006). Finally, the Upper Member (40 m thick) comprises grey dolomitic limestones dated as Cenomanian on the basis of the miliolid foraminiferan *Dicyclina schlumbergeri* Munier-Chalmas, 1887 (Fernández-Becerra 1985).

The ophiuroid material described herein originates from the Middle Member which is also referred to by the informal name 'Tlayúa Quarry', and it is these levels that have produced numerous algae, plants, foraminifera, sponges, cnidarians, molluscs, insects, spiders, crabs, echinoderms, reptiles and osteichthyan fish. The last-named group is represented best amongst macrofossil taxa and accounts for 80 per cent in current collections (>6500 specimens) from Tlayúa Quarry (Applegate *et al.* 2006).

MATERIAL AND METHODS

The faunule studied comprises six articulated specimens, all preserved on slabs of lithographic limestone. Seven additional specimens are known, but these are not considered further because of insufficient preservation. Unfortunately, the exact provenance of the specimens studied within the quarry has not been noted and consequently, we cannot determine whether this lot represent isolated, scattered occurrences or was found concentrated at one or more levels. Similar to all macrofossils from the Middle Member, these brittlestars are preserved within thin clayey deposits on bedding planes. We used water and soft brushes to remove the adhering clay from the specimens; subsequently, immersion in a solution of 3 per cent acetic acid for 5 min proved necessary to get rid of more consolidated carbonate encrustations, although this procedure slightly damaged the ophiuroid skeletal microstructure.

Five specimens were carbon coated for SEM observation, while the sixth, which is preserved on a slab together with an aspidorhynchid fish, was left uncoated. In the descriptions, the use of morphological terms follows Stöhr (2005), while higher-level classification is adopted from Smith *et al.* (1995).

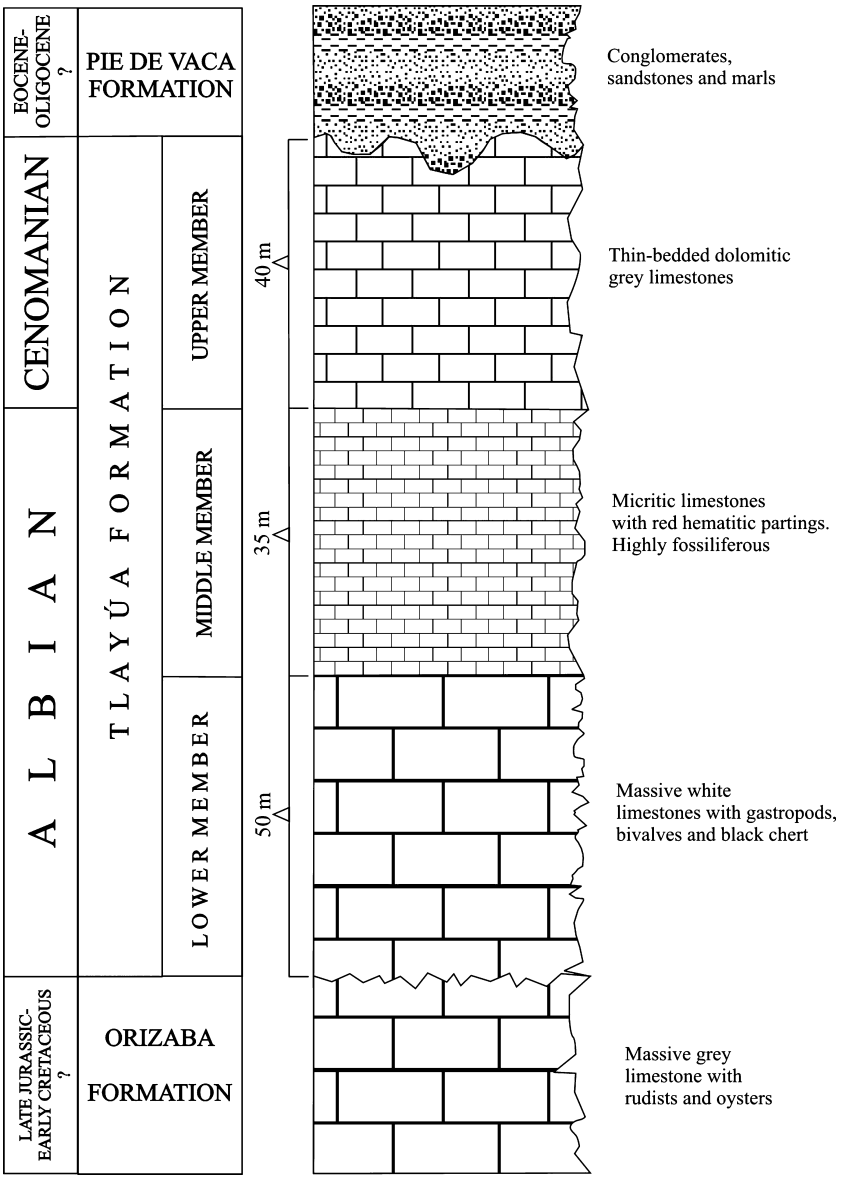
Institutional abbreviations. FCMP, Museum of Palaeontology, Faculty of Sciences, Universidad Nacional Autónoma de México (UNAM), Mexico City; IGM, National Collection of the Institute of Geology, Universidad Nacional Autónoma de México (UNAM), Mexico City.

SYSTEMATIC PALAEONTOLOGY

Order OPHIURIDA Müller and Troschel, 1840
Suborder OPHIURINA Müller and Troschel, 1840
Family OPHIACTIDAE Matsumoto, 1915

Genus OPHIACTIS Lütken, 1856

Type species. Ophiactis krebsii Lütken, 1856 (= *Ophiolepis savignyi* Müller and Troschel, 1842), by subsequent designation of H. L. Clark (1915).



TEXT-FIG. 2. Generalized lithostratigraphic section of the Tlayúa Ravine (modified after Martin-Medrano 2006).

Ophiactis applegatei sp. nov.
Plates 1–4

Derivation of name. In honour of Dr Shelton Pleasants Applegate (1928–2005), for his indefatigable enthusiasm and promotion of palaeontology in Mexico and for the great vision and creativity that brought him to lead the Tlayúa Quarry research project from 1981 until his death.

Types. Holotype is IGM 9298; paratypes are IGM 9290 and FCMP 602.

Other material. Three additional specimens, preserved on slabs; IGM 9296 (ventral side exposed; disc diameter 4.97 mm), IGM 9299 (ventral side exposed; disc diameter 4.78 mm, and IGM 9301 (ventral side exposed, disc diameter 4.07 mm).

Locality and horizon. Tlayúa Quarry (Puebla, Mexico); lithographic limestone of the Middle Member of the Tlayúa Formation of middle to late Albian age.

Diagnosis. Five-armed ophiactid with indented disc; radial shields contiguous, except distally; short, blunt and slightly flattened spines at least in ventral interradial areas close to disc edge; one tiny plus one large operculiform scale covering second tentacle pore in angle of mouth slit; three to four flat, elongate oral papillae; single tentacle scale on all pores, up to four tapering and erect spines not exceeding the length of an arm segment.

Description of holotype. Disc round to subpentagonal with indented interradial areas; disc diameter 5.2 mm. Dorsal side of

disc not exposed; ventral side with small, rounded plates, bearing short, blunt and flattened spines at least on disc margin (Pl. 1, figs 1–2); no bursal slit observable. Oral shield approximately as long as broad, arrow shaped, with slightly obtuse proximal angle and rounded convex distal edge. Adoral shields abutting in front of oral shield, not extending around lateral angles of oral shield or hardly so (Pl. 2, figs 1–2). Apical papilla very large, heart shaped and flat (Pl. 2, figs 1–3). Second tentacle pore opens within the mouth slit and bears a tiny distal scale and a large, operculiform proximal one encompassed by the rounded pentagonal first ventral arm plate and the angle formed by the oral plate and adoral shield (Pl. 2, figs 1–2). Three to four flat, elongate oral papillae occur on the lateral edges of the oral plates, increasing in size distally. Five arms, more or less complete and comprising >60 segments, total length of the longest arm as preserved 26.1 mm. Tentacle pores developed throughout the arm (Pl. 2, figs 4–5), with one flat, rounded tentacle scale on all pores. Ventral arm plate rather thick, widest distally and generally longer than wide, except in proximalmost arm segments; with convex distal edge, strongly concave lateral indentations for the tentacle pore, and narrower and straight proximal edge (Pl. 2, figs 4–5). Adjacent ventral arm plates are contiguous at least in proximal arm segments. Lateral arm plate of stout aspect, with distinct notch for tentacle pore. One slightly displaced median lateral arm plate, higher than wide, shows coarse outer surface, a slight constriction parallel to the strongly concave proximal edge of the plate, and large spine articulations in shallow notches of the distal edge of the plate, with two parallel horizontal articulation ridges (Pl. 2, figs 4–5). Three to four, thick and tapering arm spines, coarsely striated, widest at their base, pointed, erect, not exceeding the length of one arm segment (Pl. 2, figs 4–5). Some spines, especially the ventralmost, seem to be slightly flattened, but it cannot be ruled out though that this is a preservational artifact.

Two of the arms present a sudden and more or less obvious change in arm segment size, suggesting that arm tips were in the process of regeneration (Pl. 3, fig. 1). The two completely preserved arms show a distinct curvature in their median portion which clearly exceeds the maximum horizontal coiling capacity of the arms.

Paratype supplements and variation. Specimen IGM 9290 exposes the dorsal disc and attribution to *O. applegatei* sp. nov. is based on similarities in disc indentation and arm structure (Pl. 3, fig. 2). Recrystallization tends to blur details of disc plating; disc subpentagonal, slightly indented. No spines or granules are present on disc, their absence presumably being due to insufficient preservation. The radial shield is of stout aspect, length about a quarter of the disc diameter, proximal tip covered by small imbricating disc scales (Pl. 4, fig. 6). Paired radial shields contiguous, separated close to their distal tip by a gap forming an acute angle between radial shields. The gap is occupied by at least one plate, sunken probably as a result of preservation, consistent with the dorsal arm plates of the first segments outside the disc.

Dorsal arm plates rather thick, fan shaped, with convex distal edge and slightly concave proximal edges forming an obtuse angle. Adjacent dorsal arm plates contiguous in proximal arm segments (Pl. 4, fig. 5) separated by lateral arm plates in distal arm segments.

Specimen FCMP 602 exposes the ventral disc, and generally fits with the description of the holotype well; however, a few details are better preserved and provide supplementary morphological data. Disc indented, scales of interradial areas with small, blunt and slightly flattened spines, smaller than spines on the edge of the interradial area. Larger spines of disc edge slightly extending into interradial notch. Bursal slit visible, abutting oral frame but not reaching edge of disc; no genital papillae discernible. Three flat and blunt oral papillae on oral plate, flanked by large round scale of second oral tentacle pore. Five arms, more or less complete (Pl. 3, fig. 3), maximum arm length (as preserved) is 17.5 mm. Ventral arm plates contiguous throughout the arm. Tentacle pores present on all arm segments.

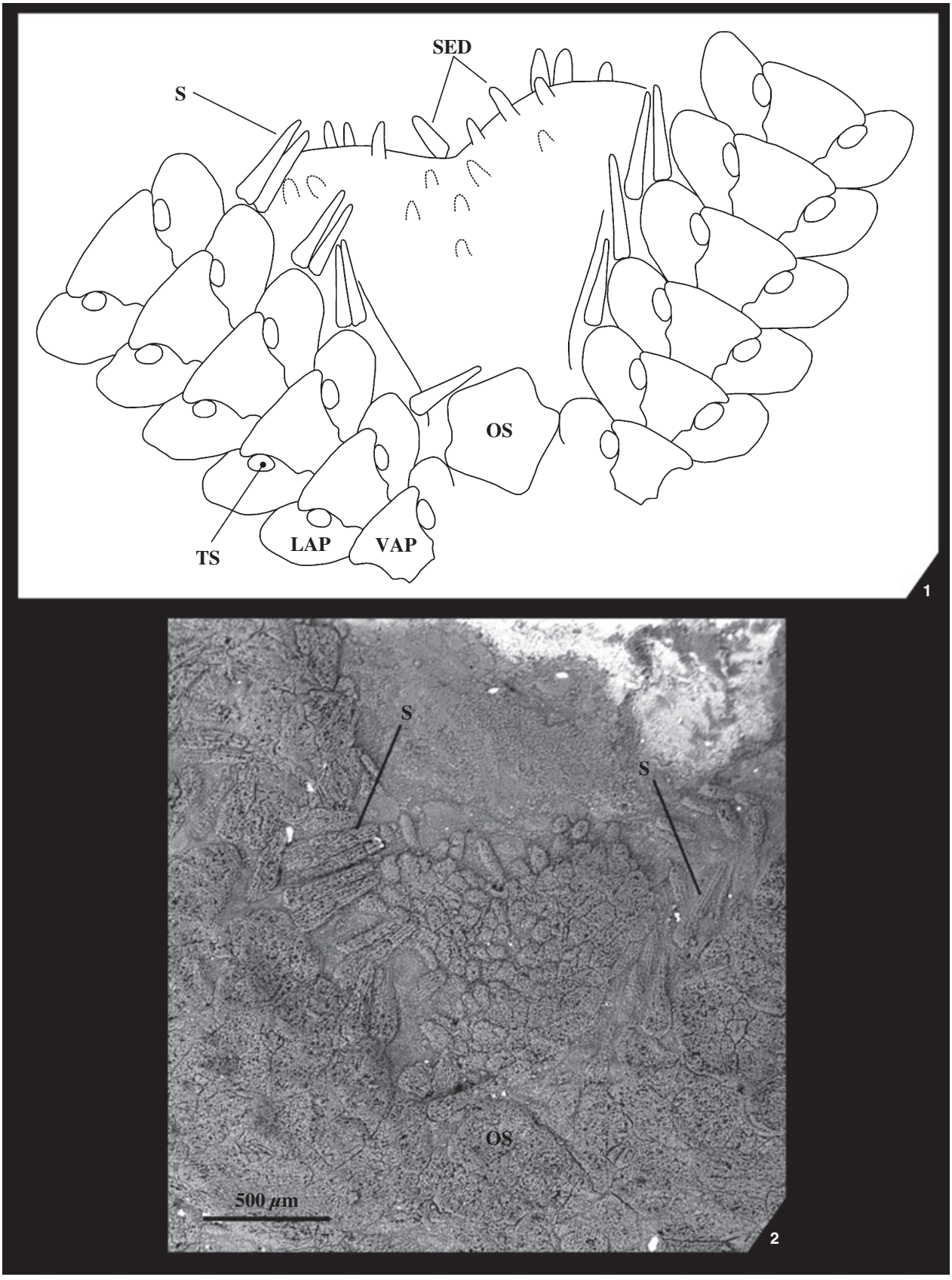
Discussion. Early Cretaceous ophiuroid taxa described to date clearly differ from *O. applegatei* sp. nov., in particular with regard to disc appendages and plating of the oral frame. *Ophiura graysonensis* (Alexander, 1931; lower Cenomanian of Texas), *Ophiura texana* (W. B. Clark, 1893; upper Albian of Texas), *Ophiolancea swartkopensis* Shone, 1986 (Valanginian of South Africa), *Ophiopeza buehleri* Hess, 1970 (upper Hauterivian of Switzerland) and *Xanthamphiura hauteriviensis* Hess, 1970 (upper Hauterivian of Switzerland) have different mouth plating and lack spines on the ventral side of the disc. The poorly known *Ophiura*? *straini* Cornell *et al.*, 1991 (Albian of New Mexico) has clearly separated radial shields, while *Geocoma libanotica* König, 1825 (Cenomanian of Lebanon) is not clearly defined (Hess 1960; Kutscher 1997).

Of other ophiuroid species from mid- and Upper Mesozoic deposits, of which discs are known, hardly any bears a closer resemblance to *O. applegatei* sp. nov. with respect to mouth plating, disc indentation and appendages. In addition, very few of these have been attributed to the Ophiactidae. Hess (1965) described isolated arm ossicles and arm segments from the lower Oxfordian of Switzerland as *Ophiopholis*? *trispinosa*; this species has only up to three arm spines and, at least on median arm

EXPLANATION OF PLATE 1

Figs 1–2. *Ophiactis applegatei* sp. nov. from the middle–late Albian Tlayúa Formation, Tlayúa Quarry, Puebla (Mexico). 1, Drawing of ventral disc and proximal arm segments. 2, FCMP 602 (paratype; SEM), ventral disc and proximal arm segments.

Abbreviations: LAP, lateral arm plates; OS, oral shield; S, arm spines; SED, spines on edge of disc; TS, tentacle scales; VAP, ventral arm plates.



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segments, ventrally abutting lateral arm plates. *Ophiactis*? *sulcatus* Kutscher and Jagt (in Jagt 2000) (lower Maastrichtian of Rügen, and possibly upper Campanian of north-east Belgium) is based on isolated lateral arm plates which had up to five arm spines; median lateral arm plates are elongated. *Ophiopholis* sp. 1 of Ishida (2004, p. 37), from the Miocene of Japan, has larger oral shields. Thus, the erection of a new species for the Mexican material appears warranted.

Attribution to the Ophiactidae is based mainly on the presence of disc spinelets, a single, cordiform apical papilla, short erect spines and conspicuous radial shields. There is a certain affinity with members of the Ophiacanthidae, but the arm spines in the new species are atypically short and the lateral arm plates rather massive and not as strongly constricted as in most ophiacanthids. Similarities to the Amphiuridae are only superficial; the Mexican specimens lack the typical paired infradental papillae of amphiurids.

According to Paterson (1985, p. 76), the Recent *Ophiactis abyssicola* (Sars, 1861) has a round or indented disc, spinelets of variable distribution on interradial disc areas, a cordiform apical papilla and a single tentacle scale. As far as number and arrangement of oral papillae are concerned, there are greater similarities to the extant ophiactid *Histampica duplicata* (Lyman, 1875) (see Paterson 1985, fig. 32), even though other characteristics (i.e., number of tentacle scales and disc appendages) clearly differ. *Ophiopholis* has dorsal arm plates surrounded by small plates and thus clearly differs from our specimens. The closest affinities are shared with five-armed species of the genus *Ophiactis*, which justifies the attribution to this genus. However, as long as dorsal disc plating (and possible appendages) and internal disc structure (especially shape of ambulacral part of the oral plate) remain unknown, this assignment is tentative.

Ophiactis applegatei sp. nov. is the oldest known member of the Ophiactidae, and being based on well-preserved, articulated specimens, it is reasonably well-defined. The question of the origin of hexamery, frequently encountered in *Ophiactis*, remains unanswered, as all individuals of the new species have five arms.

PALAEOECOLOGY AND TAPHONOMY

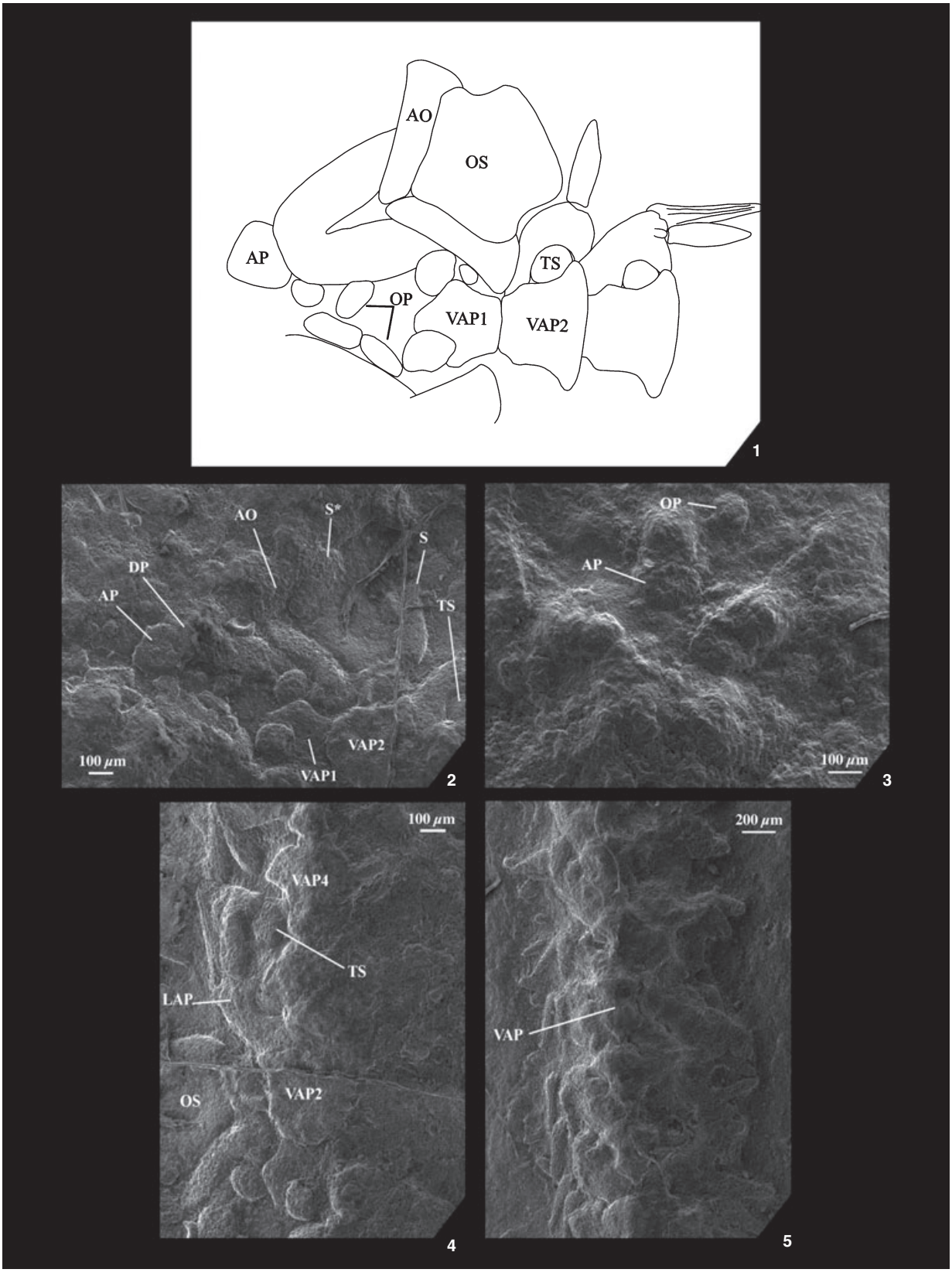
Palaeoecological models published for these lithographic limestone and its exceptionally well-preserved biota favour one of two interpretations: deposition took place in an open-marine basin under storm-dominated conditions and restricted bottom water circulation (Kashiyama *et al.* 2004), or it occurred in a shallow-water, protected back reef lagoon (Applegate 1987). The most convincing piece of evidence comes from well-documented cyanobacterial mats, which imply that water depths did not exceed 60 m (Applegate *et al.* 2006). In their evaluation of the palaeoecology of different biotic groups encountered in the Tlayúa lithographic limestone, Applegate *et al.* (2006) highlighted the considerable percentage of allochthonous forms, originating from either reefal environments, the open sea or nearby terrestrial settings, with life inside the lagoon assumed to have been restricted to nektonic organisms and occasional occurrences of benthic scavengers (Espinosa-Arrubarrena and Applegate 1996; Guerrero-Arenas 2004). There is ample evidence of stagnant conditions inside the lagoon, which led to hypersaline and anoxic conditions (Applegate *et al.* 2006). Miliolids (*Trocholina lenticularis* Henson, 1948, and the genus *Quinqueloculina* d'Orbigny, 1826; (C. Rosales-Domínguez, pers. comm. 2006) are found at some levels in Tlayúa Quarry (Alvarado-Ortega *et al.* 2007), like on slab FCMP 602 and corroborate hypersalinity.

All ophiuroids studied show hardly any sign of decay; only the arm tips of IGM 9299 (Pl. 4, fig. 2) show slight disintegration. Despite their small size, the dislocated arm plates were not subjected to transport and this substantiates stagnant conditions at the time of decay, but the role of possible cyanobacterial mats as sediment traps preventing the plates from further transport must also be considered. Burial of these specimens was probably fairly rapid (Allison 1991; Ausich 2001), as the distalmost segments of an ophiuroid arm are amongst the first skeletal parts to disintegrate (BT, pers. obs.). Most specimens reveal conspicuous contortions of the arms; the tips and median parts of the arms are often unnaturally curled. In IGM 9298, the distal halves of two arms are broken but still adhere to the proximal half (Pl. 3, fig. 1). It is unclear whether these contortions and injuries are because of

EXPLANATION OF PLATE 2

Figs 1–5. *Ophiactis applegatei* sp. nov. from the middle–late Albian Tlayúa Quarry, Puebla (Mexico). IGM 9298 (holotype). 1, Drawing of fig. 2, showing jaw and proximal arm plates. 2, Jaw and proximal arm plates (SEM). 3, Mouth frame (SEM). 4, Proximalmost arm segments (SEM). 5, median arm segments (SEM).

Abbreviations: AO, adoral shield; AP, apical papilla; DP, dental plate; LAP, lateral arm plates; OP, oral papillae; OS, oral shield; S, arm spines; S*, arm spine on oral shield, not drawn as its position is probably an artifact of preservation; TS, tentacle scale; VAP1, first ventral arm plate; VAP2, second ventral arm plate.



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unfavourable conditions shortly prior to the animals' death or rather constitute a *post mortem* effect caused by hypersalinity and comparable to contortions seen in fish and reported on by Applegate *et al.* (2006) for Tlayúa and by Viohl (1990) for Solnhofen. One specimen (IGM 9296) (Pl. 4, fig. 1) displays an arrangement of the arms comparable to the posture of a moving ophiuroid using one leading arm (Ishida and Fujita 2001). Another specimen (IGM 9301) has its ventral side exposed and the arms partly flexed on the dorsal side in a way comparable to the arm-coiling posture mentioned by Emson and Wilkie (1981) (Pl. 4, figs 3–4). Up to now, a total number of thirteen ophiuroid specimens are known from the Tlayúa Quarry. Other echinoderm classes are represented by few specimens only. As the lithographic limestone are being intensely explored for fossils under the supervision of the Geological Institute of UNAM, the paucity of echinoderm remains cannot be explained by a lack of collecting. It seems more probable that the environment was not favourable for echinoderms, which implies that their remains, inclusive of the brittlestars described herein, must all be allochtonous, having been transported from reefal or open marine settings into the hostile depositional environment and mixed with autochthonous, open-marine, reefal, freshwater and terrestrial organisms. Recent species of *Ophiactis* are often associated with coral (S. Stöhr, pers. comm. 2008). Thus, it is quite possible that these specimens were transported into the lagoon after their coral hosts had been broken up during a storm, because remains of gorgonians have been recorded from the Tlayúa lithographic limestones (Applegate *et al.* 2006). Whether the ophiuroids reached their final destination dead or alive is uncertain; the possible moving posture of specimen IGM 9296 (Pl. 4, fig. 1) suggests that at least some individuals were still alive. As the exact provenance of the specimens remains unknown, it cannot be determined whether all originate from a single or from several such transportation events. The mode of occurrence of these ophiuroids fits the model of a back reef lagoon with at least temporarily stagnant water and hypersaline conditions well.

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REFERENCES

ALENCÁSTER, G. 1973. Una nueva especie de *Toucasia* en el Cretácico medio de los Estados de Oaxaca y Puebla. *Universidad Nacional Autónoma de México, Instituto de Geología, Paleontología Mexicana*, **36**, 4–20.

ALEXANDER, C. I. 1931. A new Lower Cretaceous ophiuroid. *Journal of Paleontology*, **5**, 152–153.

ALLISON, P. A. 1991. Variation in rates of decay and disarticulation of Echinodermata: implications for the application of actualistic data. *Palaios*, **5**, 432–440.

ALVARADO-ORTEGA, J. 2005. *Sistemática de los peces Ichthyodectiformes de la Cantera Tlayúa, Puebla, México*. Unpublished PhD thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 302 pp.

—— ESPINOSA-ARRUBARRENA, L., BLANCO, A., VEGA, F. J., BENAMMI, M. and BRIGGS, D. E. G. 2007. Exceptional preservation of soft tissues in cretaceous fishes from the Tlayúa Quarry, Central México. *Palaios*, **22**, 682–685.

APPLEGATE, S. P. 1987. A preliminary study of the Tlayúa Quarry near Tepexi de Rodríguez, Puebla. *Sociedad Mexicana de Paleontología, Revista*, **1**, 40–50.

—— 1996. An overview of the Cretaceous fishes of the quarries near Tepexi de Rodríguez, Puebla, México. 529–538. *In* ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes. Systematics and paleoecology*. F. Pfeil, München, 576 pp.

—— and ESPINOSA-ARRUBARRENA, L. 1982. Lithographic limestone-like deposits in Tepexi de Rodríguez, Puebla, México. *Society of Vertebrate Paleontology, Universidad Nacional Autónoma de México, Instituto de Geología, Field Trip Guidebook*, 42nd Annual Meeting, 39 pp.

—— GONZALEZ-RODRÍGUEZ, K. and ALVARADO-ORTEGA, J. 2000. Fish fauna of the Tlayúa quarries. 97–130. *In* ESPINOSA-ARRUBARRENA, L., MONTELLANO-BALLESTEROS, M. and APPLEGATE, S. P.

EXPLANATION OF PLATE 3

Figs 1–3. *Ophiactis applegatei* sp. nov. from the middle–late Albian Tlayúa Formation, Tlayúa Quarry, Puebla (Mexico). 1, IGM 9298 (holotype), ventral surface; the regenerating arm tip is marked by a thick arrow; the two arms broken in the distal half are marked by thin arrows. 2, IGM 9290 (paratype), dorsal surface. 3, FCMP 602 (paratype), ventral surface. Scale bar represents 2 mm.

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(eds). *Paleontological highlights of the Mixteca Poblana in Central Mexico*. Society of Vertebrate Paleontology, Universidad Nacional Autónoma de México and Universidad Autónoma del Estado de Hidalgo, Field Trip Guidebook, 60th Annual Meeting. Universidad Autónoma del Estado de Hidalgo, Publicatión Especial, 172 pp.

—— ESPINOSA-ARRUBARRENA, L., ALVARADO-ORTEGA, J. and BENAMMI, M. 2006. Revision of recent investigations in the Tlayúa Quarry. 275–304. *In* VEGA, F. J., NYBORG, T. G., PERRILLIAT, M. C., MONTELLANO-BALLESTEROS, M., CEVALLOS-FERRIZ, S. R. S. and QUIROZ-BARROSO, S. A. (eds). *Studies on Mexican paleontology*, **24**. Springer, Berlin, 308 pp.

AUSICH, W. I.. 2001. Echinoderm taphonomy. 171–227. *In* JANGOUX, M. and LAWRENCE, J. M. (eds). *Echinoderm studies*, 6. A. A. Balkema, Rotterdam, 348 pp.

BENAMMI, M., ALVARADO-ORTEGA, J. and URRUTIA-FUCUGAUCHI, J. 2006. Magnetostratigraphy of the Lower Cretaceous strata in Tlayúa Quarry, Tepexi de Rodríguez, State of Puebla, México. *Earth Planets Space*, **58**, 1295–1302.

BUITRÓN, B. E. and MALPICA-CRUZ, R. 1987. Tepexi de Rodríguez, Puebla, una localidad fosilífera de México. *Sociedad Mexicana de Paleontología, Field Trip Guidebook*, Distrito Federal, México, 24 pp.

—— SOLÍS MARIN, F. A., MIRANDA, J. C. and MIRANDA, J. B. 1994. El hallazgo de un Ofiuroidea Pliocénico de la Región de Vizcaíno, Baja California Sur. *Memorias de la XII Convención Geológica Nacional, Sociedad Geológica Mexicana*, México, D.F., 26–27.

CANTÚ-CHAPA, A. 1987. Las amonitas del Albiano Superior de Tepexi de Rodríguez, Puebla. *Sociedad Mexicana de Paleontología, Revista*, **1**, 159–160.

CLARK, H. L. 1915. Catalogue of Recent ophiurans: based on the collection of the Museum of Comparative Zoology. *Memoirs of the Museum of comparative Zoölogy, Harvard College*, **25**, 163–376.

CLARK, W. B. 1893. The Mesozoic Echinodermata of the United States. *Bulletin of the United States Geological Survey*, **97**, 1–207, pls 1–50.

CORNELL, W. C., LeMONE, D. V. and NORLAND, W. D. 1991. Albian ophiuroids from Cerro de Cristo Rey, Dona Ana County, New Mexico. *Journal of Paleontology*, **65**, 1009–1012.

EMSON, R. H. and WILKIE, I. C. 1981. The arm coiling response of *Amphipholis squamata* (Delle Chiaje). 11–18. *In* LAWRENCE, J. (ed.). *Echinoderms: Proceedings of the International Conference*. A. A. Balkema, Rotterdam, 234 pp.

ESPINOSA-ARRUBARRENA, L. and APPLEGATE, S. 1996. A possible model for the paleoecology of the vertebrate bearing beds in the Tlayúa quarries, near Tepexi de Rodríguez, Puebla, México. 539–550. *In* ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes. Systematics and paleoecology*. F. Pfeil, München, 576 pp.

FELDMANN, R. M., VEGA, F., APPLEGATE, S. P. and BISHOP, G. 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology*, **72**, 79–90.

FERNÁNDEZ-BECERRA, S. 1985. *Levantamiento a detalle de columnas estratigráficas en el área de Tepexi de Rodríguez, Puebla-"Cantera Tlayúa"*. Petróleos Mexicanos, Superintendencia General de Exploración, Zona Centro, Distrito Poza Rica, 31 pp.

GUERRERO-ARENAS, R. 2004. *Icnofósiles de invertebrados de la Formación Tlayúa en Tepexi de Rodríguez, Puebla, México*. Unpublished MS thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 49 pp.

HENSON, F. R. S. 1948. *Larger imperforate foraminifera of south-western Asia. Families Lituolidae, Orbitolinidae and Meandropsinidae*. British Museum (Natural History), London, 127 pp.

HESS, H. 1960. Neubeschreibung von *Geocoma elegans* (Ophiuroidea) aus dem unteren Callovien von La Voulte-sur-Rhône (Ardèche). *Eclogae geologicae Helvetiae*, **53**, 335–385.

——1965. Mikropaläontologische Untersuchungen an Ophiuren. IV. Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapois (Jura) und Longecombe (Ain). *Eclogae geologicae Helvetiae*, **58**, 1059–1082.

——1970. Schlangensterne und Seesterne aus dem oberen Hauterivien «Pierre jaune» von St-Blaise bei Neuchâtel. *Eclogae geologicae Helvetiae*, **63**, 1069–1091.

—— 1975. Die fossilen Echinodermen des Schweizer Juras. *Veröffentlichungen aus dem Naturhistorischen Museum Basel*, **8**, 1–130, pls 1–48.

HYATT, A. 1900. Cephalopoda. 502–604. *In* VON ZITTEL, K. A. (ed). *Textbook of palaeontology*. Macmillan, London/New York, 890 pp.

ISHIDA, Y. 2004. Ophiuroids. *The Association for the Geological Collaboration in Japan, Monograph*, **51**, 1–80. [in Japanese, English summary].

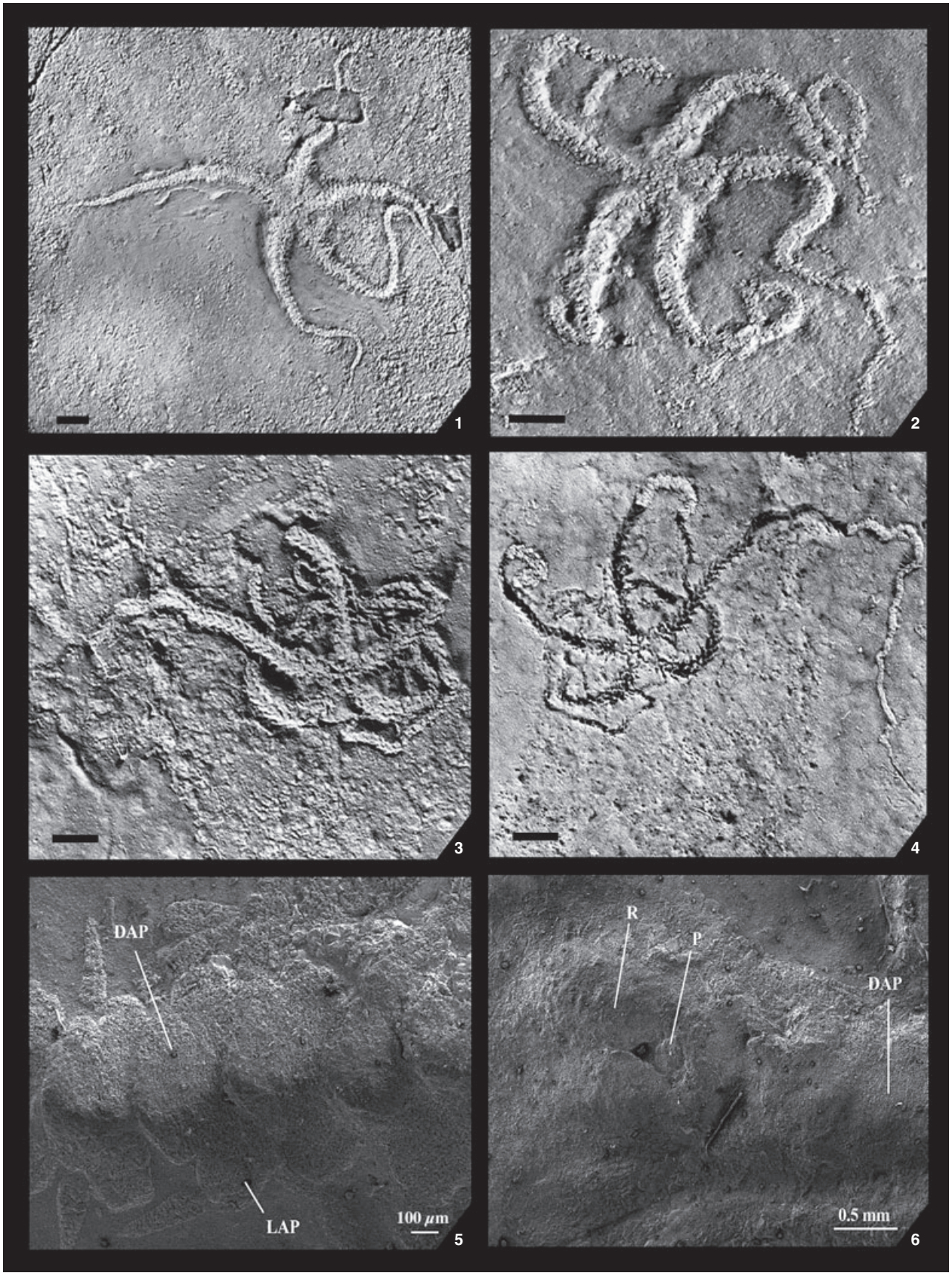
—— and FUJITA, T. 2001. Escape behavior of epibenthic ophiuroids buried in the sediment: observations of extant and fossil *Ophiura sarsii sarsii*. 285–292. *In* BARKER, M. (ed.). *Echinoderms 2000*. A.A. Balkema Publishers, Lisse, 590 pp.

JAGT, J. W. M. 2000. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 3. Ophiuroids; with a chapter on: Early Maastrichtian ophiuroids from Rügen (northeast

EXPLANATION OF PLATE 4

Figs 1–6. *Ophiactis applegatei* sp. nov. from the middle–late Albian Tlayúa Formation, Tlayúa Quarry, Puebla (Mexico). 1, IGM 9296, ventral surface. 2, IGM 9299, ventral surface. 3–4, IGM 9301 (part and counterpart), ventral surface. Scale bar represents 2 mm. 5, IGM 9290 (paratype; SEM), median arm segments. 6, IGM 9290 (paratype; SEM), radial shields and proximalmost arm segments.

Abbreviations: DAP, dorsal arm plates; LAP, lateral arm plates; P, plate between radial shields; R, radial shields.



MARTIN-MEDRANO *et al.*, *Ophiactis applegatei*

Germany) and Møn (Denmark) by Kutscher and J. W. M. Jagt. *Scripta Geologica*, **121**, 1–179.

KASHIYAMA, Y., FASTOVSKY, D. E., RUTHEFORD, S., KING, J. and MONTELLANO, M. 2004. Genesis of a locality of exceptional fossil preservation: paleoenvironments of Tepexi de Rodríguez (mid-Cretaceous, Puebla, México). *Cretaceous Research*, **25**, 153–177.

KÖNIG, C. 1825. *Icones Fossilium Sectiles*. The author, London, 44 pp.

KUTSCHER, M. 1997. Bemerkungen zu den Plattenkalk-Ophiuren, insbesondere *Geocoma carinata* (v. Münster, 1826). *Archaeopteryx*, **15**, 1–10.

—— and JAGT, J. W. M. 2000. Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark). 45–107, pls 22–36. *In* JAGT, J. W. M. (ed.). *Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium- Part 3: Ophiuroids. Scripta Geologica*, **121**, 1–179, 36 pls.

LÜTKEN, F. C. 1856. Bidrag til Kundskab om Slangestjernerne. III. Bidrag til Kundskab om Ophiurerne ved Centralamerikas Vestkyst. *Videnskabelige Meddelelser fra det Naturhistoriske Forenings i Kjobenhavn*, **1856**, 20–26.

LYMAN, T. 1875. Zoological results of the Hassler Expedition. II. Ophiuridae and Astrophytidae. *Illustrated Catalogue of the Museum of Comparative Zoology*, **8**, 1–34.

MARTIN-MEDRANO, L. 2003. *El registro de ofiuroideos fósiles de México y la descripción de dos nuevas formas para el Cretácico y Terciario*. Unpublished Bachelor's thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 55 pp.

——2006. *Análisis paleontológico de los ofiuroideos fósiles de México*. Unpublished MSc thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 140 pp.

—— and GARCÍA-BARRERA, P. 2006. Fossil ophiuroids of Mexico. 115–131. *In* VEGA, F. J., NYBORG, T. G., PERRILLIAT, M. C., MONTELLANO-BALLESTEROS, M., CEVALLOS-FERRIZ, S. R. S. and QUIROZ-BARROSO, S. A. (eds). *Studies on Mexican paleontology*, **24**. Springer, Berlin, 308 pp.

MATSUMOTO, H. 1915. A new classification of the Ophiuroidea: with descriptions of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **67**, 43–92.

MEEK, F. B. 1876. A report of the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country. *In* HAYDEN, F. V. (ed.). *Report of the United States Geological Survey of the Territories*, **9**, i–xvi + 629 pp.

MÜLLER, J. and TROSCHEL, F. H. 1840. Uber die Gattungen der Ophiuren. *Archiv für Naturgeschichte*, **6**, 327–330.

—— 1842. *System der Asteriden*. F. Vieweg & Sohn, Braunschweig, xx + 134 pp.

MUNIER-CHALMAS, E. 1887. Sur la Cyclolina et trois nouveaux genres de foraminifères de couches à Rudistes. Cyclopsina, Dicyclina et Spirocyclina. *Complete Rendus des Séances, Société Géologique de France*, **1887**, xxx–xxxi.

NIETO-LÓPEZ, I. and GARCÍA-BARRERA, P. 2006. Cretaceous echinoids of Mexico. 101–114. *In* VEGA, F. J., NYBORG, T. G., PERRILLIAT, M. C., MONTELLANO-BALLESTEROS, M., CEVALLOS-FERRIZ, S. R. S. and QUIROZ-BARROSO, S. A. (eds). *Studies on Mexican paleontology*, **24**. Springer, Berlin, 308 pp.

ORBIGNY, A. D. d'. 1826. Tableau méthodique de la classe des Céphalopodes. *Annales des Sciences naturelles*, **7**, 245–314.

PANTOJA-ALOR, J. 1992. Geología y paleoambiente de la cantera Tlayúa, Tepexi de Rodríguez, Estado de Puebla. *Revista del Instituto de Geología, Universidad Nacional Autónoma de México*, **9**, 156–169.

PATERSON, G. L. J. 1985. The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum of Natural History (Zoology)*, **49**, 1–162.

PICTET, F. J. 1854. *Traité de paléontologie, Céphalopodes*, **2**, 583–716. J.-B. Baillière, Paris, 896 pp.

QUIROZ-BARROSO, S. A. and SOUR-TOVAR, F. 1995. Nuevo registro de Ophiuroidea (Ophiurinidae) para el Pensilvánico de América del Norte, proveniente de la Formación Ixtaltepec, Oaxaca. *Memorias del V Congreso Nacional de Paleontología, Sociedad Mexicana de Paleontología*, México, D.F., 31.

SARS, M. 1861. *Oversigt of Norges Echinodermer*. Christiania, vi + 160 pp.

SHONE, R. W. 1986. A new ophiuroid from the Sundays River Formation (Lower Cretaceous), South Africa. *Journal of Paleontology*, **60**, 904–910.

SMITH, A. B., PATERSON, G. L. J. and LAFAY, B. 1995. Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. *Zoological Journal of the Linnean Society*, **114**, 213–243.

STANTON, T. W. 1901. *Chondrodonta*, a new genus of ostreiform mollusks from the Cretaceous, with descriptions of the genotype and a new species. *Proceedings of the United States Natural History Museum*, **24** (1257), 301–307.

STÖHR, S. 2005. Who's who among baby brittle stars (Echinodermata, Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society*, **143**, 543–576.

VIOHL, G. 1990. Solnhofen lithographic limestone. 285–289. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology, a synthesis*. Blackwell Scientific Publications, Oxford, 583 pp.