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Observations on *Onychaster* Meek & Worthen, 1868 (Ophiuroidea: Onychasteridae) (Famennian – Visean age)*

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Contribution dedicated to the memory of Dr. John H. Dearborn (1933–2010)

Abstract

Onychaster is prominent in discussions on the ancestry of crown group ophiuroids because about half of researchers have classified *Onychaster* as a Palaeozoic representative of the living Order Euryalida. With this classification there is a Mississippian to Cretaceous gap in the euryalid fossil record. Other researchers have classified *Onychaster* as non-euryalid, in which case there is no such gap. This undecided status is an important reason to review the classification of *Onychaster* using new observations. In *Onychaster* the lateral plates are strictly on the underside of the arm where they form a double row and nearly touch midventrally; there are no mid-ventral underarm plates. The undersurface-laterals bear a transverse row of spines that point proximally (in retro-direction). The disk in large specimens bulges interradially such that the arms insert subambitally. The morphology of *Onychaster* vertebrae is documented anew in SEM stereo-pair images. Distinctive features include: a median dorsal cleft or circular pit on the upper surface; an auluroid canal; paired epanapophyses; a zygosphene dorsal to the auluroid canal; exceptionally spacious fossae for the ventral longitudinal muscles; and an undersurface plastron that is dimensioned like a waist belt. These features are transformationally close to eospondylid/furcasterid vertebrae and progressively/increasingly distant from zygospondylous, transpondylous, and streptospondylous vertebrae. Classification of *Onychaster* as an euryalid is not supported. We reclassify the Onychasteridae next to the Furcasteridae.

Key words: Ophiuroidea, Furcasteridae, *Onychaster*, Palaeozoic, Classification, ophiuroid vertebrae

Introduction

Onychaster flexilis Meek & Worthen, 1868, lived epizoic on the crowns of stalked crinoids. Whereas most bottom-dwelling ophiuroids bend their arms into sideways curves for movement or bend them upward to feed from the water column, *Onychaster* bent its arms ventrally into coils that grasped the calyx and arms of its crinoid host. *Onychaster* may have gathered food from the water column from this perch, or stolen the food of the crinoid, or fed upon the anal wastes or the flesh of the crinoid (Wachsmuth & Springer 1897; Clarke 1908, 1921; Dacqué 1921; Meyer & Ausich 1983). Because of its life habits, *Onychaster* has been compared with living euryalid ophiuroids that also curl their

arms ventrally and perch epizoic on gorgonians, pennatulids, or other tall organisms or on seafloor promontories (Macurda 1976; Mosher & Watling 2009).

Spencer (1927: 334) saw *Onychaster* as being in the direct line of ancestry to the Recent Euryalae, with the lineage having retained its epizoic habits since the Carboniferous period (p. 338): “The vertebrae of *Onychaster* show a transition between the double ‘pegged’ type found in *Hallaster* [Stürtz, 1886a] to the simple hinged type found in *Gorgonocephalus* [Leach, 1815] and the Recent *Astrophyton* [Fleming, 1828]-like Ophiurans. The act of ‘striking’, which compelled the arm to hit the ground and so caused propulsion seems to have been abandoned, and the modern *Astrophyton*-like Ophiurans can no longer use their arms to propel themselves along the sea bottom, but live sessile, frequently with the arms coiled round branches of sea fans, *etc.* It would appear that *Onychaster* was also a sessile form associated with Crinoidea.” He emphasized as resemblances between *Onychaster* and the Recent Euryalae: (A) the concentration of the intervertebral articulations in one area, (B) the small size of the cups for the tube feet, (C) the narrow high vertebrae, (D) branching in the arms (which he noted as rare in *Onychaster*), and (E) the mode of life. He noted (p. 334) the open ambulacral groove in *Onychaster* as “the only difference.” This analysis was reaffirmed by Spencer & Wright (1966: U90).

Glass (2006: 226) and Hotchkiss *et al.* (2007) began to express doubts about *Onychaster* as a euryalid. Cladistic analysis of body-fossil morphologies aligned *Onychaster* with the Furcasteridae and not with euryalids (Glass 2006); the Furcasteridae now includes *Furcaster* Stürtz, 1886b, *Eospondylus* Gregory, 1897, and *Kentrospondylus* Lehmann, 1957 (Glass 2005, 2006: 224). Importantly, the arm vertebrae of *Onychaster* do not have euryalid-type hour-glass articulations (confirming Bell 1892: 182; Schöndorf 1909; Sollas 1913; Spencer 1927; Haude & Thomas 1983).

The Question. Is the genus *Onychaster* properly classified as a Palaeozoic representative of the extant order Euryalida (cf. Spencer & Wright 1966)? ...or is it merely homeomorphic with extant euryalids (cf. Fedotov 1926)? If *Onychaster* is an euryalid, then it is the first and oldest record of this crown group (Hotchkiss *et al.* 2007), and there is a Mississippian to Cretaceous gap in the euryalid fossil record.

Benchmark Systematics. The history of classification of *Onychaster* as euryalid or as non-euryalid is summarized in Table 1. The family Onychasteridae Miller, 1889, contains only the genus *Onychaster* Meek & Worthen, 1868, although Jell (1997) suggested that *Lumectaster* Jell, 1997, may also belong here. *Onychaster flexilis* is the type species; the type locality is the “crinoid beds” of Crawfordsville (see Ausich 1999), Indiana, in the Edwardsville Member of the Muldraugh Formation, Borden Group (upper Osagian). The lectotype specimen is UMMP 6197 (Bjork *et al.* 1968b). Material-based papers on *O. flexilis* morphology are by Meek & Worthen (1868: 526; 1869: 82; 1873: 474), Schöndorf (1909, 1913), Sollas (1913), Spencer (1927, 1930), Bjork *et al.* (1968a, 1968b), Turner (1999), and Glass (2006). Additional species are *O. barrisi* (Hall, 1861), *O. strimplei* Bjork, Goldberg & Kesling, 1968a, and *O. velbertensis* Haude & Thomas, 1983. Species removed from the genus are *O. asper* Miller, 1891, *O. confragosus* Miller, 1891, and *O. demissus* Miller, 1891, which were reevaluated as starfish (Asteroidea) and assigned to the genera *Calliasterella* Schuchert, 1915, and/or *Calyptactis* Spencer, 1930, by Spencer (1930: 396, 400, Text-fig. 252, Pl. 25: Fig. 9), followed by Golden & Niteki (1970), and by Jell (1997). In North America, *Onychaster* has been found in Mississippian rocks in Alabama, Indiana, Iowa, and Missouri (see the materials section; also Horowitz & Waters 1972). In Europe, Spencer (1927: 340; 1930: 393) reported *O. barrisi* from the Pilton Formation

(Famennian-Tournasian), North Devon, based on reidentification of two specimens of *Eugaster perarmatus* Whidborne, 1898 (this reidentification doubted by Bjork *et al.* 1968b: 56; specimens are in the GSM collection according to Owen 1965: 558), and he reported *O. flexilis* from isolated vertebrae from Skateraw Quarry, near Dunbar, in the Scottish Lower Limestones (Visean). *Onychaster velbertensis* is from the Northern Rhenish Slate Massif (Famennian-Tournasian). The oldest occurrence for *Onychaster* is Late Famennian, whether based on *O. velbertensis* or on *O. barrisi* (Spencer 1927: 340; Lane *et al.* 2001: 1044).

Methods

Factors that might have influenced the description, interpretation and classification of *Onychaster* include: the quality and availability of specimens; techniques such as serial sectioning and reconstruction; study of isolated vertebrae; and choice of comparative reference material. Different specimens contribute in different ways, as partially noted in the materials list.

Ophiuroid vertebrae form the central “backbone” of the arms of brittlestars, and the flexibility and arm motions of brittlestars are constrained and enabled by the details of the articulations between the vertebrae. Thus the vertebrae are complex and contain information of behavioral, ecological and tax-

TABLE 1. History of classification of *Onychaster* as euryalid or non-euryalid ophiuroid.

Onychaster classified as a euryalid		Onychaster classified as non-euryalid	
Zittel (1880)	Euryaleae	Bell (1892)	Streptophiurae
Steinmann & Döderlein (1888)	Euryaleae	Gregory (1897)	Streptophiurae
Nicholson & Lydekker (1889)	Euryalida	Stürtz (1899)	Protophiureae
Stürtz (1893)	Euryalae	Gregory (1900)	Streptophiurae
Zittel (1895)	Euryaleae	Delage & Hérouard (1903)	Streptophiurida
Broili (1924)	Cladophiurae (Euryalae)	Schöndorf (1909)	non-euryalid
Spencer (1927)	cf. Euryalae	Bather (1910)	Streptophiurae
Cuénot (1948)	Astéronychidés	Clark (1913)	Streptophiuroida
Ubaghs (1953)	Euryalicae	Sollas (1913)	stem zygophiurid
Müller (1963)	Euryalicae	Matsumoto (1913)	Zeugophiurae
Spencer & Wright (1966)	Euryalina	Jaekel (1923)	Zygophiuri
Hotchkiss (1977)	Phrynophiurida (Euryalina)	Fedotov (1926)	non-euryalid Ophiurae
Bjork <i>et al.</i> (1968b)	Euryalina	Fedotov (1934)	Oegophiuroida
Haude & Thomas (1983)	Euryalina	Spencer (1951)	Zeugophiuricae
Litvinova (1989)	euryalid	Owen (1965)	Zeugophiuricae
Simms (1993)	Euryalina	Glass (2006)	non-euryalid
Jell (1997)	Euryalina	Hotchkiss <i>et al.</i> (2007)	probably non-euryalid
Kroh (2003)	Euryalida		

onomic significance (Litvinova 1989, 1994). We present new observations based on institutional and newly acquired body fossils, isolated vertebrae, and SEM imaging. The concept for the morphospace analysis of vertebral types is based on Litvinova (1989, 1994). *Onychaster* vertebrae were collected and donated by Dr. F. Rudolf Turner of Indiana University (Turner 1999).

Scanning electron microscopy (SEM). Vertebrae were sputter coated with 10 nm platinum in a Leica EM MED020 high vacuum coating system, and imaged with a Zeiss SMT SUPRA 40VP SEM by Louis M. Kerr, Marine Biological Laboratory, Woods Hole, MA. Stubs were tilted six degrees between image captures for stereo-pair images. Images are mounted 63.5 mm apart for stereo viewing.

Measurements and Abbreviations. Measurements on body fossils used a millimeter ruler or a plastic caliper with 0.1 mm vernier. Measurements of figured isolated vertebrae are from SEM images. Abbreviations are: disk diameter (DD), arm width near base of arm (W), arm width at thickest region away from the disk (WW), balled-up largest dimension (BD), and balled-up thickness (BT). We suggest $L = 2BD$ is a plausible estimate of arm length and/or major radius (R). Estimate interbrachium extent as an angular sector: $72^\circ[(\pi DD - 5W)/\pi DD]$.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum (formerly British Museum [Natural History]), London; FMNH, Field Museum of Natural History, Chicago; GSM, Geological Survey and Museum, London (the GSM collection is now at the British Geological Survey, Keyworth, Nottinghamshire); MCZ, Museum of Comparative Zoology, Harvard University; MPRI, Marine and Paleobiological Research Institute, Vineyard Haven, MA; ROM, Royal Ontario Museum, Toronto; UMMP, University of Michigan Museum of Paleontology; USNM, National Museum of Natural History, Smithsonian Institution; WUSTL, Washington University, St. Louis, MO; YPM, Peabody Museum of Natural History, Yale University.

Terminology and other Abbreviations. leg. for legit = collected by. Descriptive terms of ophiuroid vertebrae follow Hotchkiss *et al.* (2007). Abbreviations: ctf = cup for tube foot; rwc = radial water canal; vlm = ventral longitudinal muscles. The term “auluroid canal” is used for the tubular passage through a vertebra for the radial water vessel (the radial water vessel is completely enclosed by the vertebrae). Although the class name Auluroidea has been rejected (Fell & Pawson 1966: 34 footnote), we find the terms “auluroid canal” and “auluroid condition” descriptive and useful. In this paper, the term “undersurface-lateral plates” is preferred over the terms “lateral arm plates” and “laterals” because in *Onychaster* these plates are distinctly on the underside of the arm and do not embrace the sides of the arms.

Specimens

Isolated vertebrae. YMP.227918, YPM.227928-YPM.227932, *Onychaster* sp., isolated vertebrae. Edwardsville Formation. Approx. 0.5 miles from Boy Scout camp on Lake Monroe reservoir, Monroe County, IN; F. Rudolf Turner leg.

Body fossils. ALABAMA: YPM.227921 *Onychaster* sp. on *Platycrinites penicillus*; distinctive

integument of abutting tumid granules (or tumid plates that lack granules?), two arms lost at edge of disk, 6.7 mm DD, 3.0 mm W, 3.8 mm WW, Monteagle Limestone, Huntsville, Madison County, AL.

YPM.227922 *Onychaster* sp., 10.0 mm DD, 4.2 mm W, tumid granules on tile-like weathered plating in geometric-lattice array, some vertebrae exposed, Bangor Limestone (Chester). Colbert County, AL, R. Keyes leg.

YPM.224022–YPM.224023, *Onychaster* sp., Lower Monteagle Limestone, Shade Street (Weatherly Mountain), SE¼ NW¼ SE¼ sec. 5, T5S., R1E. Huntsville TVA Quadrangle, Madison County, AL.

YPM.224024, *O. flexilis*, Lower Bangor Limestone, E½ SE¼ SE¼ sec. 35, T5S., R11W., Russellville Quadrangle, Colbert County, AL.

INDIANA: YPM.227919 *Onychaster* sp. that is balled up and has a well defined disk, 6.7 mm DD, 2.8 mm W, 13.2 mm BD, 5.8 mm BT, Haney Formation (Mississippian), intersection of Indiana 237 and Interstate 64, Crawford County, IN.

YPM.227920 *Onychaster* sp. on *Scaphocrinus* sp., an arm that bends 180° under itself is notably straight, another arm bends in the horizontal plane as it leaves the disk, bending 90° in nine or ten joints, so bending 9° or 10° horizontally per joint, 4.6 mm W, Glen Dean Formation (Mississippian), Canton, Washington County, IN.

YPM.227923 *O. flexilis* on *Actinocrinites gibsoni*, 5.0 mm WW, L > 34.0 mm, two arms substantially straight, three arms ventrally flexed, two of these revealing a double row of undersurface-laterals, imbricating distally, slightly thickened distally, and bearing a transverse row of at least three spines that abut like a palisade; the spines articulate on the distal thickening (not on the distal edge), spines pointing outward from the underside of the arm and somewhat toward the arm base; in some places the distal thickening gives the laterals a subtle concave surface and a subtle distal ridge, Edwardsville Formation, Corey's Bluff, Crawfordsville, Montgomery County, IN.

YPM.227924 *O. flexilis* on *Agaricocrinus americanus*, 14.4 mm DD, 6.2 mm WW, L > 40.0 mm, disk inflated interradially, the arms insert subambitally, disk plates are smaller on the upper-surface central-region of the disk and larger in each of the bulging interradiol ambital areas, Edwardsville Formation, Indian Creek, Crawfordsville, Montgomery County, IN, T. Witherspoon leg.

YPM.227925 *O. flexilis* that is balled up, 5.5 mm DD, 15.6 mm BD, 5.5 mm BT, 3.2 mm W, mouth vertebra is only vertebra within disk, an arm cross-section shows ventral location of lateral plates, Edwardsville Formation, Indian Creek, Crawfordsville, Montgomery County, IN, T. Witherspoon leg.

YPM.227926 *O. flexilis* partial, 4.9 mm W, L > 30.0 mm, parts of three arms, one in undersurface view showing laterals with five spines that point proximally, spine bases are uniformly just proximal of the distal end of the lateral, but there is no spine articulation ridge, and articulation sockets/bosses for these spines are not detectable, lowermost/adradial spine is longest and might have functioned as a groove-spine, weathering may have altered spine shapes and socket visibility, Edwardsville Formation, Indian Creek, Crawfordsville, Montgomery County, IN, T. Witherspoon leg.

YPM.227927 *Onychaster* sp., 14.8 mm DD, 5.4 mm W, 60.0 mm R, R:r=8.1, exceptional undersurface views of disk and arms, arms preserved almost to tip; teeth, torus, MAPP exposed; arms insert subambitally, disk interradially inflated, two missing arms suggest arm autotomy at the edge of the disk, thin scales overlie arm ossicles (no granules), undersurface-laterals meet midventrally in distal part of arm, Edwardsville Formation, Crawfordsville, Montgomery County, IN, T. Witherspoon leg.

USNM S.4128 *Onychaster* sp., Harrodsburg Limestone, Canton, IN.

USNM S.4100, S.4131, and ROM 41496, *O. flexilis*, Muldraugh Formation, Ramp Creek Limestone Member, Indian Creek, Crawfordsville, Montgomery County, IN.

USNM 59392, 92675, 510097, S.4099, S.4101, S.4132, also ROM 39115, also MCZ 394, 401, 3497, also YPM 26331, 26334, and AMNH 7240, 32253, *O. flexilis*, Muldraugh Formation, Edwardsville Member, Crawfordsville, Montgomery County, IN.

WUSTL 860307 *O. flexilis* excellent detail; good views of arm coiling; unweathered striated spines on the undersurface-lateral arm plates; an arm fragment shows tilted/rotated undersurface-laterals, considerably separated midventrally, forming a matrix-filled slight undersurface groove; a perplexing aspect of this arm fragment is that the proximally-pointing spines of the undersurface-laterals are sandwiched/pressed between successive imbricating laterals; the following features of the arm fragment are difficult to see and may be subject to wishful interpretation: the lifted distal adradial corner of the undersurface-laterals has an indented contour that may have bordered a rounded passage for the emergence of the tube foot; the undersurface-laterals have tilted sufficiently that the indent is in the vicinity of the ctf (see Figs. 5–6 for location of vertebral ctf); the edge of the indent bears a faint suggestion of two small articulation marks, suggesting tentacle scales (modified groove spines); Muldraugh Formation, Edwardsville Member, Crawfordsville, Montgomery County, IN.

IOWA: USNM 510089, also MCZ 108083, 108084, 108085, *O. barrisi*, Burlington Limestone, Burlington, Des Moines County, IA [not MCZ 108082, formerly No. 10, listed as *O. barrisi* by Schuchert (1915) and Bjork *et al.* (1968a), here determined as *Furcaster* sp., cf. *F. cataphractus* Boczarowski, 2001]

USNM S.4082, S.4085, *Onychaster* sp., Burlington Limestone, Burlington, Des Moines County, IA.

USNM S.4129 *Onychaster* sp., Keokuk Limestone, Keokuk, Lee County, IA.

MISSOURI: USNM S.4130 *Onychaster* sp., Warsaw Formation, Booneville, Cooper County, MO.

USNM 111752, 510084, *Onychaster* sp., Warsaw Formation, Quarry 0.5 miles west of Keyes Summit, west edge of St. Louis, Saint Louis County, MO.

Taxonomic data bases. Attribution of authors and dates to living ophiuroid species and genera follows Stöhr & O'Hara (2010). The online Nomenclator Zoologicus database was also consulted. Older bibliographic information was facilitated by use of The AnimalBase in Göttingen [<http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/AnimalBase/search>].

Observations

Body fossils (Figs. 1–2). Arms five, non-branching, long, slender, rounded, flexible, nearly always coiled ventrally (Figs. 1A–B, 2D), “folded together like the claws of a bird when grasping some small object” (Meek & Worthen 1868). Disk small compared to length of arms. The mouth frame is of thick construction (confirming Bjork *et al.* 1968b), with teeth and torus; peristomial plates not found. The mouth frame makes the disk plump, incompressible, and higher than the arm bases. The junction of arm and disk is prone to taphonomic disruption (YPM.227921) and/or edge-of-disk arm autotomy. In small specimens (Fig. 1A) the disk includes only the mouth vertebra, and in large specimens (Fig. 2F) the disk possibly includes a second vertebra (left with the disk following presumed autotomy,

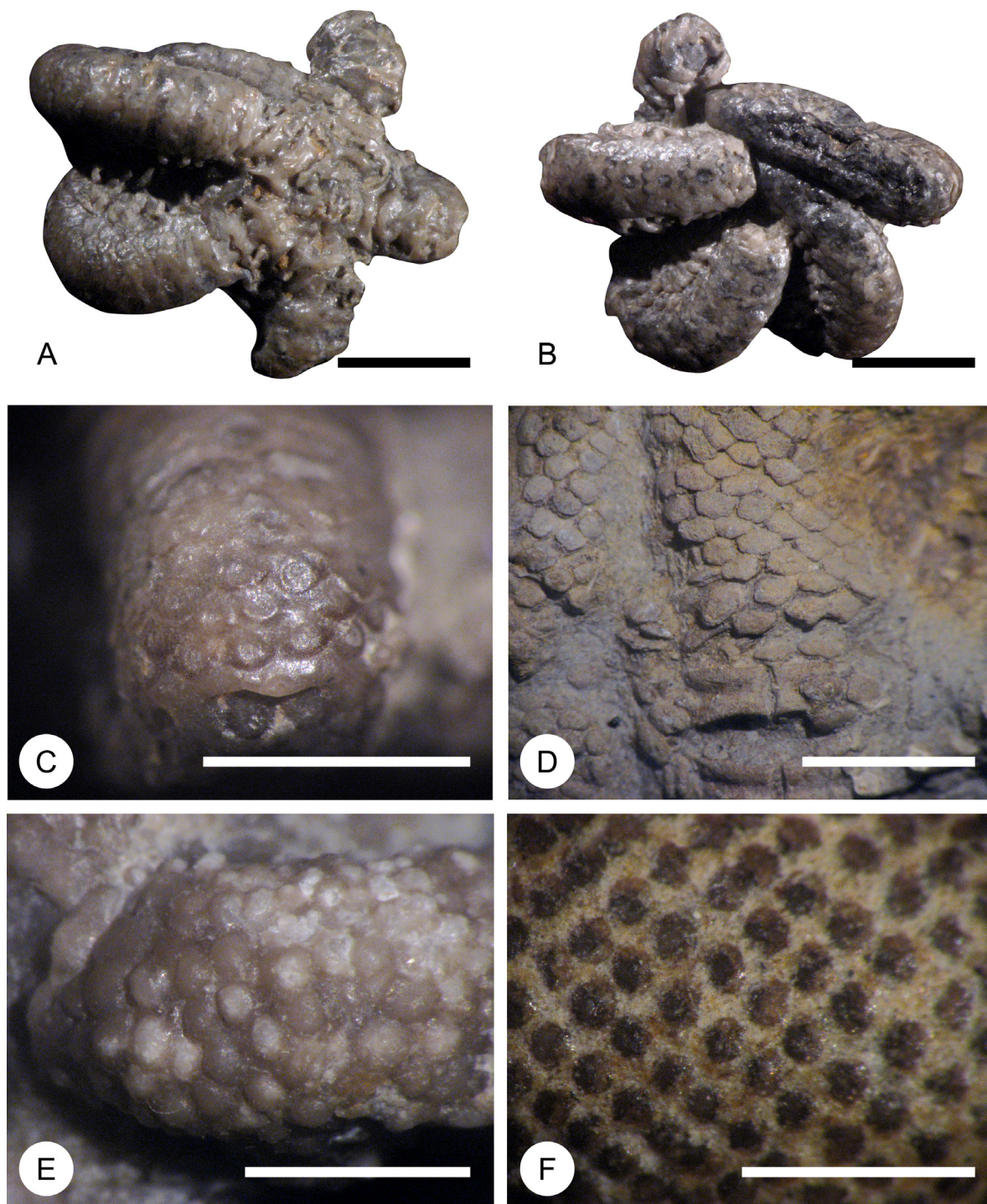


FIGURE 1. A–C: *Onychaster flexilis* (YPM.227925), balled up, 5.5 mm DD. A: aboral view: arms join ambitally at the mouth frame, there is no interbrachial disk: scale bar equals 5 mm; B: undersurface view: arms coiled ventrally: scale bar equals 5 mm; C: integumentary plating: circular indents record lost granules: scale bar equals 3 mm. D: *Onychaster* sp. (YPM.227922): weathered integumentary plating, granules lost to weathering: scale bar equals 3 mm. E: *Onychaster* sp. (YPM.227921): geometric-lattice pattern of abutting tumid granules: scale bar equals 3 mm. F: *Onychaster* sp. (YPM.227920): geometric-lattice pattern of spaced granules: scale bar equals 2 mm.

YPM.227927). In large specimens (Figs. 2E–F) the disk bulges interradially and the arms insert subambitally (YPM.227924, YPM.227927); in smaller specimens (Fig. 2D) the disk does not bulge interradially, the arms insert ambitally, and the interbrachial margin is not as wide as an arm base (YPM.227919); there is no interbrachial margin/disk in the smallest specimen (YPM.227925; Fig.

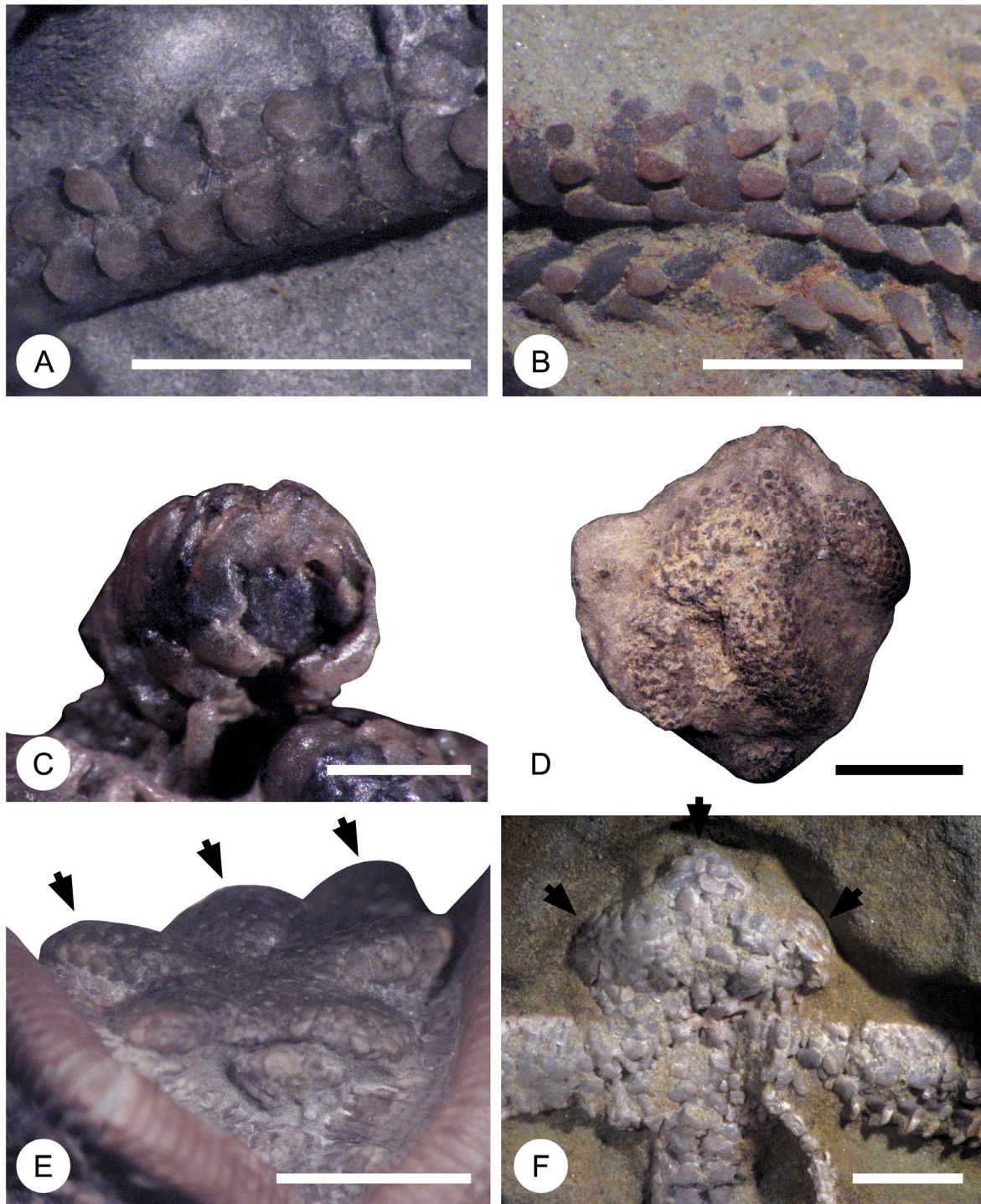


FIGURE 2. A: *Onychaster flexilis* (YPM.227923): undersurface view of arm, distal is to left, showing double row of undersurface-laterals (spines missing): scale bar equals 5 mm. B: *Onychaster flexilis* (YPM.227926): undersurface view of arm, distal is to left, showing double row of spine-bearing undersurface-laterals, spines (altered by weathering) point toward the arm base (proximal/retro-direction): scale bar equals 4 mm. C: *Onychaster flexilis* (YPM.227925): arm cross-section (distal view) shows vertebra with undersurface-laterals: scale bar equals 2 mm. D: *Onychaster* sp. (YPM.227919): balled up, 6.7 mm DD: arms insert ambitally, interbrachial disk present: scale bar equals 5 mm. E: *Onychaster flexilis* (YPM.227924): 14.4 mm DD: tilted edge/aboral view showing five interradial bulges of the disk (three marked with arrows), and subambital to the disk a broken-off arm base (cross-section): scale bar equals 10 mm. F: *Onychaster* sp. (YPM.227927): 14.8 mm DD, oral surface view: two arms are missing at the edge of the disk (upper part of figure) helping to emphasize three of the interradial bulges of the disk, marked with arrows: in the lower part of the figure, the bases of three arms lie below the ambitus of the disk: an arm-tip enters the image (at bottom) and touches the underside of the disk: scale bar equals 6 mm.

1A). Disk merges with the arm bases; disk aboral plating is not substantially different from the aboral plating of the arms. In particular, there are no specially differentiated disk plates: no calycinal plates (primary rosette is not evident in post-juvenile stages but may have been present in early growth stages), no marginal plates, and no radial shields. Also no genital plates, no genital slits, no oral shields, and no adoral shields. No madreporite, stone canal, or periproct has been detected. The disk and arms are covered by many closefitting ossicles in geometric-lattice arrangement (Figs. 2C–F), with or without a stout central granule or thin scales. The arm segments are not detectable (or barely hinted at) through this covering. Arms plump from the contained vertebrae, but may flatten to a crease laterally, indicating a former spacious coelomic cavity in the arm. No specially differentiated carinal/dorsal arm plates. The arms widen slightly before narrowing. The lateral plates are located on the underside of the arm (Figs. 2A–C), where they form a double row of plates that touch or nearly touch midventrally (YPM.227923, YPM.227925); there are no midventral under arm plates. The cup for the tube foot is well covered by the undersurface-lateral plates. In all specimens except WUSTL 860307, the place of emergence of the tube feet with respect to the undersurface-lateral plates is not known; no tentacle scales or groove spines have been observed; and the arm has no undersurface groove. In WUSTL 860307, an arm fragment has undersurface laterals that are tilted/rotated such that they create a slight undersurface groove and possibly create a place of emergence for the tube feet. The undersurface-laterals bear a transverse row of spines that abut like a palisade (YPM.227923, WUSTL 860307); the spines articulate just proximal to the distal edge of the plate (Figs. 2A–B); spine ridge and articulation bosses are present in *O. velbertensis* (Famennian) but absent/vestigial in *O. flexilis* (Visean); the spines point proximally (confirming Sollas 1913), in retro-direction. Unweathered spines show longitudinal striae (WUSTL 860307, confirming Meek & Worthen 1873: Pl. 16: Fig. 3j); weathered spines have smooth surfaces (Fig. 2B). Some studied specimens are clinging to the crowns and anal tubes of crinoids. In such specimens the arms smoothly embrace and flow through and around the arms of the crinoids, emerging, wrapping around, and disappearing again (e.g., YPM.227920, YPM.227923 and YPM.227924). In one case, a small specimen was found clasping a crinoid stem (T. Witherspoon, personal communication, March 2007). Other specimens are found loose. A loose specimen of *O. flexilis* (USNM S.4100) from Indian Creek, Indiana, appears to have its arms stuffed into its mouth (new observation). In the majority of loose specimens, the arms are coiled ventrally, grasping nothing, coiled onto themselves beyond full circle, and are not tangled (e.g., YPM.227919, YPM.227925, WUSTL 860307). This coiling is possibly a balling-up reflex in response to lack of attachment, such as being suspended/tossed in turbulent storm waters (Emson & Wilkie 1982). Balling-up can be a protection from turbulent forces and debris impact. In these specimens it is typical that the disk and all five arms are intact. Only a few loose specimens are found with any arms uncoiled, and the present examples have arm loss and probable autotomy (e.g., YPM.227926, YPM.227927). Uncoiled arms would seem necessary for crawling on the sea floor, for ascending and repositioning onto crinoids, and feeding activities.

Contrary to Spencer (1927), none of the studied specimens has a branched arm. The *Onychaster* specimen with a single branched arm that was reported by Spencer (1927: 331, 333, 335) could be an accident of regeneration (Hotchkiss *et al.* 2007); the specimen was never figured and has been misplaced (Owen 1965). Although Spencer & Wright (1966: U28 referring to Fig. 36) stated that *Onychaster* had small hooked spines that could help it climb up and grip onto hosts such as crinoids, such hooked spines have not been demonstrated in *Onychaster*. The report of under arm plates by

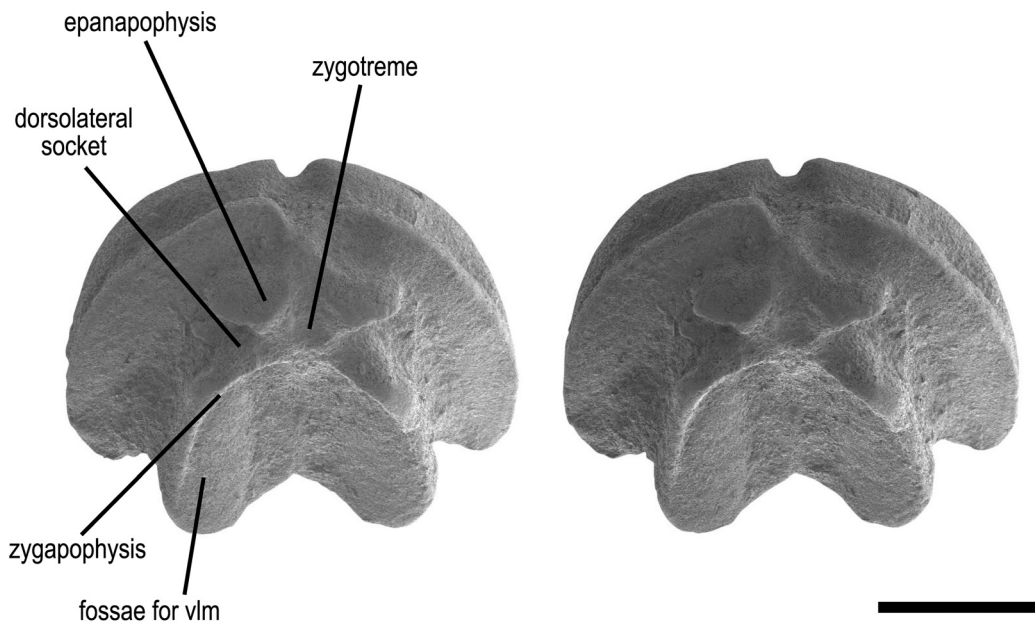


FIGURE 3. *Onychaster* sp. (YPM.227928) vertebra, proximal surface that faces toward the central disk of the ophiuroid, width 3.2 mm, slight tilt shows also a partial view of the upper surface: the raised articulation surfaces are surrounded in the background by a peripheral region that is the “wing” of the vertebra. The zygotreme pit (receives the zygosphene) is between the paired epanapophyses. The epanapophyses are separated from the zygapophyses by dorsolateral sockets that receive the zycondyles. The zygapophyses border a very large basin-like hollow that is the insertion area for the ventral longitudinal muscles. The opening of the auluroid canal for the rwc is not visible beneath the zygotreme due to downward tilt of the vertebra (but see Figs. 5–6). Scale bar equals 1.2 mm.

Schöndorf (1909) was a misinterpretation, corrected by Spencer (1927). The undersurface placement of the laterals (Figs. 2A–C) was depicted correctly by Sollas (1913: Fig. 2A); other drawings have the laterals incorrectly placed laterally (Spencer 1927: Fig. 217C; Moore *et al.* 1952: Fig. 20–4.12; Ubaghs 1953: Fig. 48B; Spencer & Wright 1966: Fig. 80.2e). Although Spencer (1927: 334) mentions an open ambulacral groove, it has no depth. We assume that a madreporic pore is present but hidden [*cf.* Ferguson 1995 on small hidden madreporic pores in *Ophioderma appressa* (Say, 1825)]. The arm tip to arm tip breadth of a mature *O. flexilis*, if the rays were straightened out, would be about 130 mm to 150 mm; the rays usually increase in thickness for a short distance from the body, being about 5.6 mm in breadth at the widest part (WW), then tapering gradually to their extremities (specimen described by Meek & Worthen 1868). In YPM.227927, $r=7.4$ mm, $R=60$ mm, $R:r=8.1$. A smaller balled-up specimen is YPM.227919 in which $BD=13.2$ mm, estimated $R=26.4$ mm; $DD=6.7$ mm; $r=3.35$ mm; $R:r=7.9$; $W=2.8$ mm; and estimated extent of disk interbrachium is 24° .

Isolated vertebrae (Figs. 3–8). The halves of vertebrae (ambulacral ossicles) are firmly fused; the line of suture is only sometimes visible (Fig. 7). The complex shape and the general proportions of the vertebrae are best understood by examining the SEM stereo-pair images of the vertebrae (Figs. 3–8). Labeling of features is based on the following benchmark understanding (Spencer 1927; Haude & Thomas 1983): Exceptional enlargement of the ventral longitudinal muscle fields has pushed the zygosphene from its plesiomorphic ventral position (ventral nose of a vertical hinge structure) well into the dorsal region (Fig. 6); this was accompanied by individuation and separation of the usually fused ontogenetic left and right halves of the epanapophysis into paired epanapophyses located lateral to the immigrant socket for the zygosphene (Fig. 3); the combined result was the transformation of a vertical hinge into a horizontal hinge, such that up-and-down nodding movements were more readily

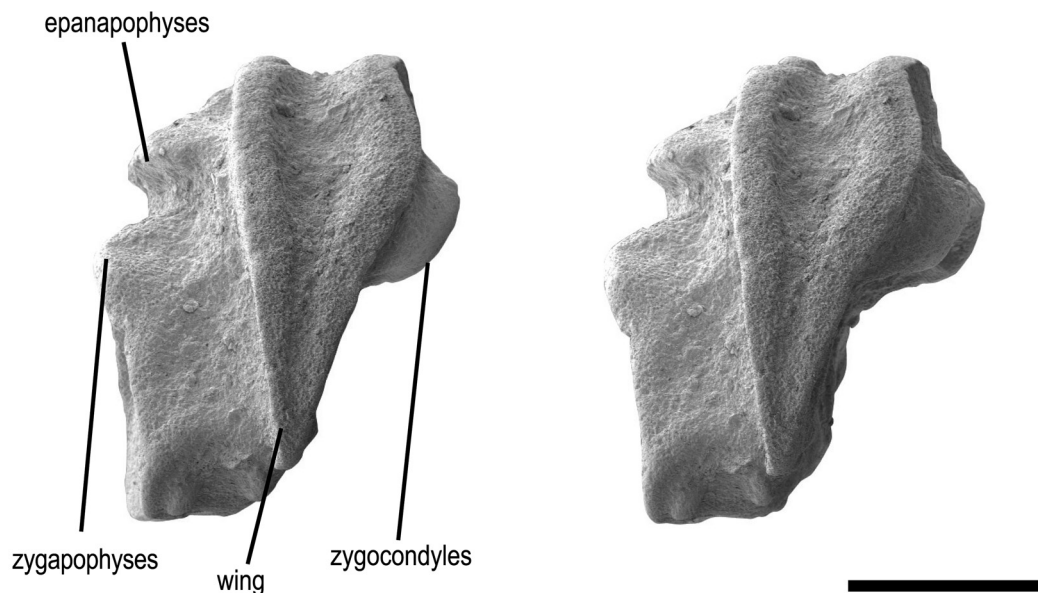


FIGURE 4. *Onychaster* sp. (YPM.227928) vertebra, left lateral view, height 2.4 mm, with upper surface at top, proximal at left, distal at right. The “wing” of the vertebra is wide at the upper surface and narrows downward to a point. The ventral narrowing of the wing, permits the telescoping of the adjacent articular surfaces into each other, and thus the observed extreme ventral arm coiling. The reentrant between the epanapophysis and the zygapophysis is the dorsolateral socket for the zygocondyle. Scale bar equals 1 mm.

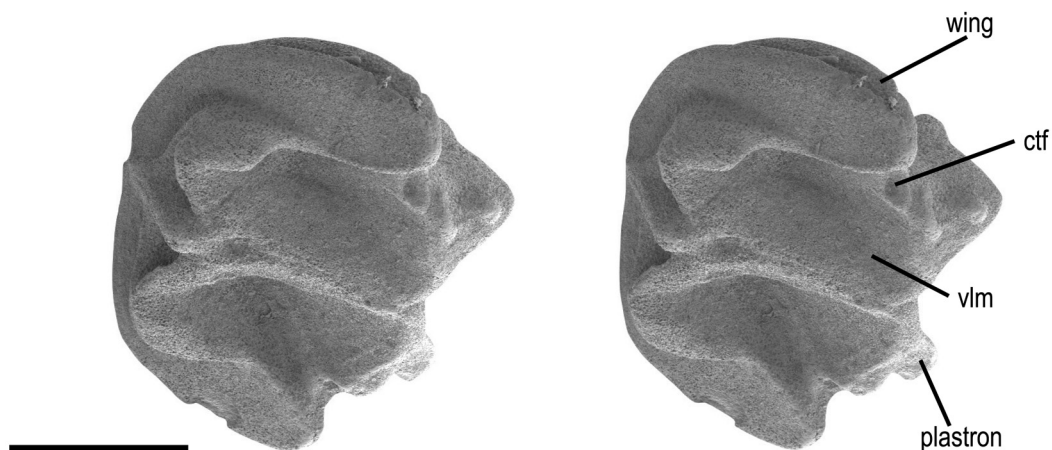


FIGURE 5. *Onychaster* sp. (YPM.227929) vertebra, oblique rotated view of distal articulation surface, image height 2.7 mm, underside is to the right. The bird-shaped articulation knobs are the paired zygocondyles and unpaired zygosphene; the large fossae comprise articular socket (upper part of fossae) and insertion field for the ventral longitudinal muscles (lower part of fossae). The opening of the auluroid canal for the rwc is below the zygosphene knob. A cup for a tube foot (ctf) is beside the ventral tip of the vertebral wing. The short extent of the plastron is evident. Scale bar equals 1.2 mm.

carried out than lateral movements. Hinging and telescoping of the articular surfaces permits ventral enrollment and obstructs twisting or lateral bending (Fig. 4). The zygapophyses function like the cardinal teeth of a pelecypod hinge: they are self-guiding in their deep sockets, resistant to torsion, and capable of opening widely. The auluroid canal for the radial water vessel also migrated into the upper region and retained its adjacency/proximity to the zygosphene (Fig. 6). Other distinctive features include: a median dorsal cleft or circular pit on the upper surface (Fig. 8 hollow), and a diminished undersurface plastron (Fig. 7). The ventral longitudinal muscles (vlm) of *Onychaster* inserted onto the end surfaces of the plastron (confirming Sollas 1913; Schöndorf 1913), not onto the wings of the vertebrae. The cups for the tube feet (ctf) are in an abradial undersurface position (Figs. 5–6). Traces of the

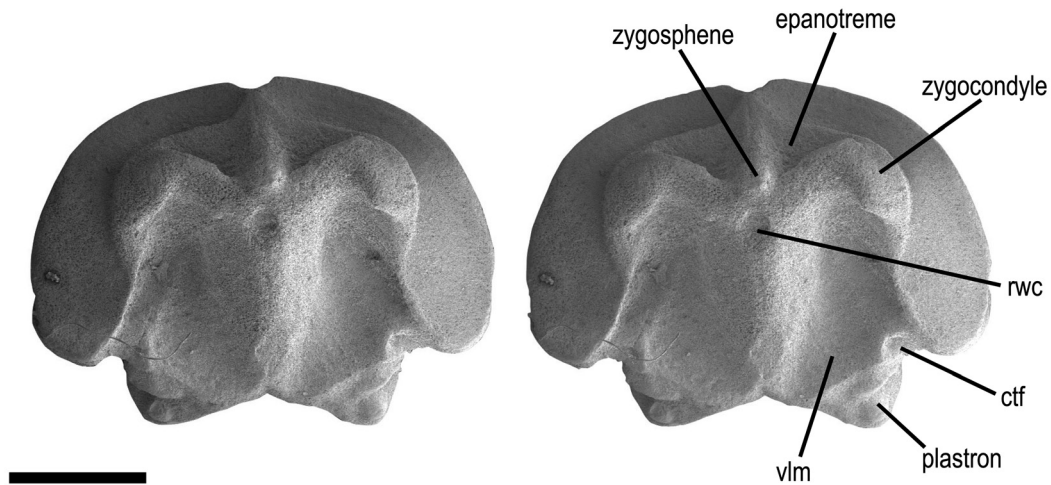


FIGURE 6. *Onychaster* sp. (YPM.227929) vertebra, width 3.3 mm, view of distal surface that faces toward the arm tip, with upper surface at top. The articulation processes of the distal surface present the general impression of raised bird wings with substantial vertical droop toward the wing-tip. The wing-like ridges are the zygocondyles (paired dorsal knobs of distal surface), and the bird's head is the zygosphene. The zygosphene and the zygocondyles are separated by V-shaped articular hollows (paired epanotremes) that receive the paired epanapophyses. The most conspicuous feature of the distal surface is the very large cavity beneath the zygocondyles. The cavity has left and right basins separated by a low median ridge. The under surface of the zygocondyles forms the upper portion of each deep basin and is an articular facet; the upper portion of each basin is an articular socket that receives the zygapophysis. There is no detectable boundary that demarcates the articular socket-area from the vlm fossa-area. The opening of the auluroid canal for the radial water vessel (rwc) is plainly seen at the upper end of the median ridge, below the zygosphene, and between the zygocondyles. The very small cups for the tube feet are located at the outer lower corners of the vlm fossae, in a notch between the ventral tip of the "wing" and the under surface plastron. The muscle fields for the dorsal longitudinal muscles are deduced to be on the wings of the vertebra, toward the upper edges, small and inconspicuous compared with the ventral muscle fields, but the exact location and boundaries have not been discerned. The central profile of the underside of the vertebra resembles a roof-top with a very small roof angle; the undersurface-lateral plates attached to this underside of the vertebra. Scale bar equals 1 mm.

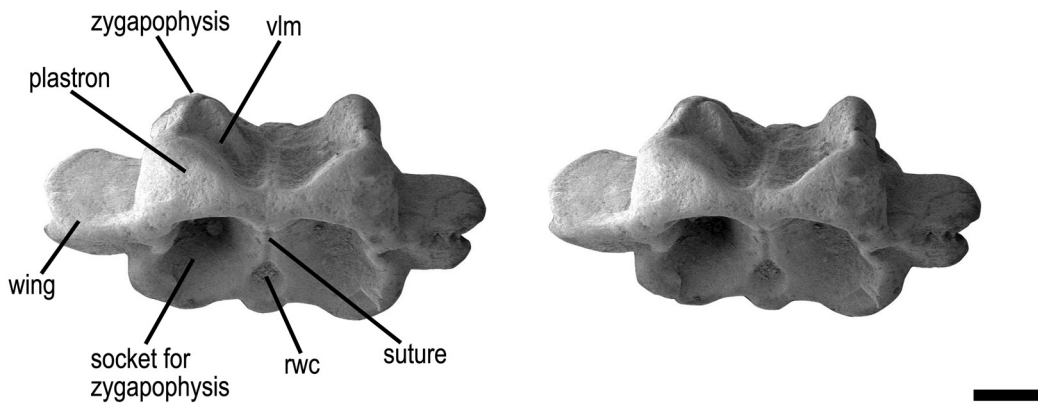


FIGURE 7. *Onychaster* sp. (YPM.227930) vertebra, under surface view, width 5.7 mm, proximal direction at top. The underside is so excavated by the large left and right basin-like cavities of the distal surface that the undersurface plastron is shortened to a transverse bar, more like a waist belt than a plastron (shorter than in *O. velbertensis*). It is divided into left-right wedge-shaped areas (bow-tie shape) by its V-shaped proximal border; the distal border is adjacent to the cups for the tube feet. Prominent cavities for the attachment of the ventral longitudinal muscles are at the distal and proximal ends of the vertebra; adjacency with the undersurface plastron is a reliable landmark for identifying these muscle fossae. Traces of the suture between the firmly joined vertebral halves are evident in the oblique views of the ends of the vertebra. The ability of the surround of the proximal articulation surface to telescope into the cavity of the distal articulation surface is reflected in the widths of the proximal and distal profiles: narrower proximal profile, wider distal profile. The close fit of the telescoping parts resisted both torsional and horizontal bending of the arm joints. Lateral to the undersurface plastron are the alar wings of the vertebra which narrow ventrally to a tip. The plastron is the articulation surface for the undersurface-laterals. Scale bar equals 1 mm.

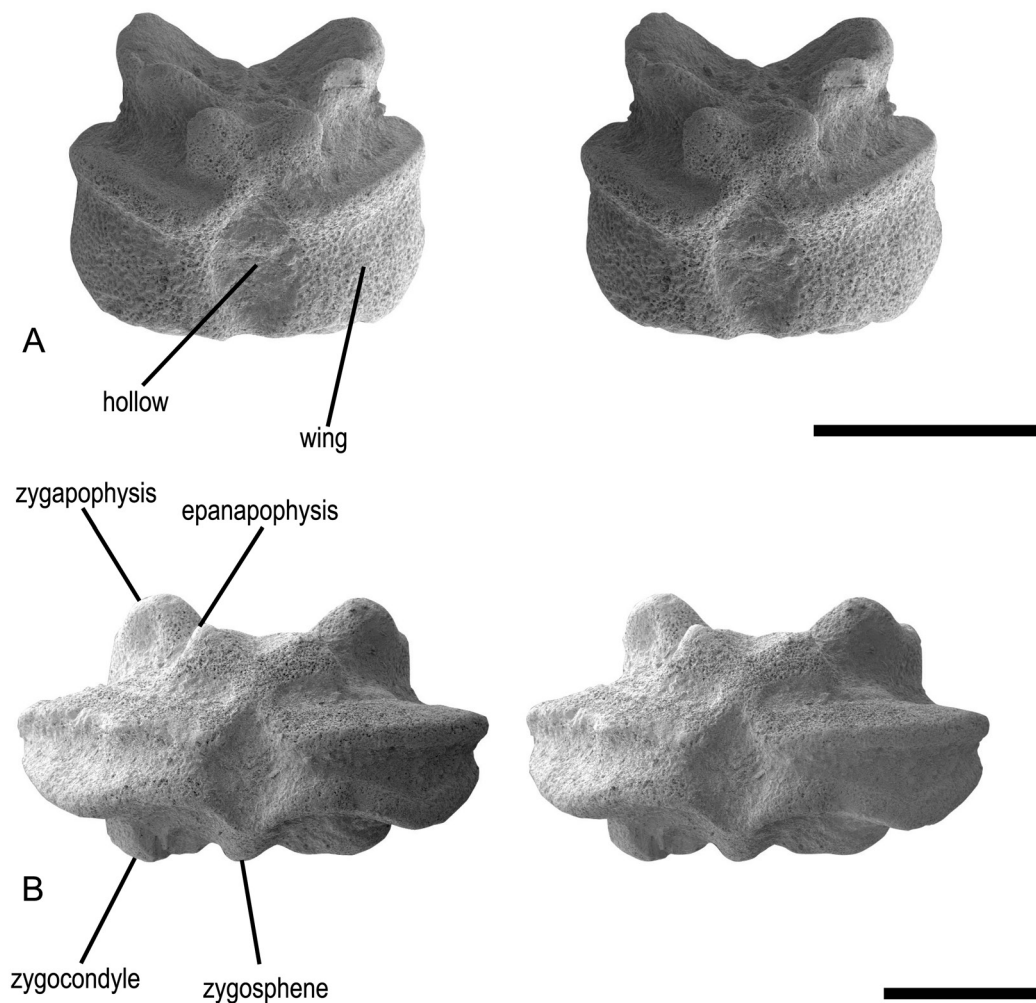


FIGURE 8. A–B: *Onychaster* sp. vertebrae, upper surface views, proximal direction at top. In both images, the “wing” forms the widest and highest periphery of the vertebrae; centrally there is a deep hollow or pit; laterally the wings have raised edges that create a furrow. The articulating knobs of the proximal surface are the upper paired epanapophyses and the lower paired zygapophyses. A: YPM.227931, width 1.5 mm, is a small vertebra from a distal region of an arm, slight tilt shows a partial view of the proximal surface. B: YPM.227932, width 2.9 mm, is from a proximal region of an arm: the articulating knobs of the distal profile are the central zygosphene and the paired zygocondyles. Scale bars equal 1 mm.

branch canal from the radial water vessel to the pores representing the cups for the tube feet are sometimes evident in the deep fossae for the vlm (discoloration traces, thickening traces, erosional traces).

Analysis

The morphology of *Onychaster* vertebrae as described by Spencer (1927) and Haude & Thomas (1983) (the benchmark understanding) is confirmed. In particular, *Onychaster* does not have euryalid-type hourglass-shape vertebral articulations. The significant question becomes: Are *Onychaster* vertebrae transitional toward euryalid-type streptospondylous vertebrae (hourglass articulation and loss of zygophiurid peg), as proposed by Spencer (1927)? Spencer (1925, 1927) demonstrated homologous relations between the vertebral articulations and muscle insertions of *Onychaster*, Ordovician *Hallaster*, and Recent *Ophiura* Lamarck, 1801, and *Gorgonocephalus*. He showed that the differences in layout are only transformations of a ground plan, and according to his analysis *Onychaster* verte-

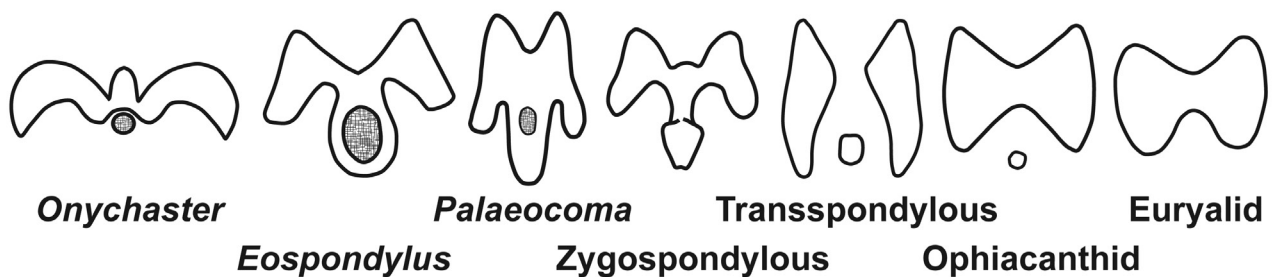


FIGURE 9. Morphospace analysis of vertebral types based on pairwise comparisons of schematic layouts of the zygosphenes and the zygocondyles: the opening of the auluroid canal for the radial water vessel is shaded grey. *Onychaster* and euryalids are at opposite ends of the morphospace axis; classification of *Onychaster* as a euryalid is not supported. Sources: *Onychaster* schematic based on Fig. 6, herein; *Eospondylus* based on Hotchkiss *et al.* (2007: Fig. 11); *Palaeocoma* d’Orbigny, 1850, based on Hess (1962: Fig. 7); zygospondylous schematic based on Bray (1985: Fig. 1, *Ophiocoma echinata* [Lamarck, 1816]); transspondylous based on Štorc (2004: Figure 5, *Ophiosmilax? alternatus*); ophiacanthid based on Litvinova (1989, Fig. 3E, *Ophiolebes vivipara*); euryalid based on Mortensen (1933: Fig. 1, *Trichaster palmiferus* [Lamarck, 1816]).

brae conform with a morphological trajectory toward streptospondylous vertebrae. We will test his conclusion using the same transformational-congruence argument but with a new/expanded data set.

The most current view of the origin of euryaline vertebrae is the evolutionary transformation sequence zygocondylous-type → transspondylous-type → streptospondylous-type (Müller 1950; Litvinova 1989, 1994, but expressed with different terminology; Štorc 2004). The zygocondyles of transspondylous vertebrae (distal surface) are dorso-ventrally elongated and give the impression of euryalid hourglass vertebrae, except that there is a ventral zygospondylous peg and socket. Smith *et al.* (1995: 236, character 8) illustrated vertebrae of *Ophiochondrus* Lyman, 1869, and listed “vertebral articulation with small articulatory peg but large streptospondylous-type facet” as an “intermediate articulation form” between streptospondylous and zygospondylous articulations. Thus the transspondylous vertebrae of *Ophiolebes vivipara* Djakonov, 1949, and *Ophiosmilax? alternatus* Kutscher & Jagt, 2000, are intermediate between the hourglass type and the zygospondylous type (Litvinova 1989; Kutscher & Jagt 2000: 48; Štorc 2004). Only Litvinova (1989: 51) mentioned and included *Onychaster* in this trajectory; so we are also testing this inclusion.

We ask whether the claim of Spencer (1927) and Litvinova (1989) that *Onychaster* vertebrae are on the trajectory to euryalid-type streptospondylous vertebrae (hourglass articulations and loss of zygocondylous peg) is or is not supported when eospondylous and transspondylous vertebrae are included in the analysis. We use schematic layouts of the zygosphenes and the zygocondyles and use pairwise comparisons to arrive at a most reasonable transformational series or morphospace diagram (Fig. 9). We find that *Onychaster* features are transformationally close to eospondylous/furcasterid vertebrae and progressively/increasingly distant from zygospondylous, transspondylous, and streptospondylous vertebrae. Transformational progression from *Eospondylus*-type to *Onychaster*-type involves dorsal movement of the zygosphenes to a location between the zygocondyles, with the auluroid canal retaining its proximity to the zygosphenes. In the transformational progression from zygospondylous to transspondylous to streptospondylous articulations, as deduced by Müller (1950), the zygosphenes (zygocondylous peg) individuates, moves ventrally, and becomes smaller to the point of loss. Whereas joints with hourglass-shaped (saddle-like) articulations can bend in any direction, the *Onychaster*-type joint is totally restricted to downward bending.

Conclusions

The presented analysis of vertebral structure places *Onychaster* and euryalids at opposite ends of a morphospace axis. Accordingly, classification of *Onychaster* as a euryalid is not supported. Based on the present research, and on prior cladistic analysis (Glass 2006), we maintain the family Onychasteridae and align it with the Furcasteridae. The clade Onychasteridae + Furcasteridae contains the genera *Onychaster*, *Furcaster*, *Eospondylus*, *Kentrospondylus*, and possibly *Lumectaster*. A higher taxon name for this clade awaits a more comprehensive reclassification of Palaeozoic Ophiuroidea.

After eliminating *Onychaster*, which does not have streptospondylous vertebrae, the next oldest occurrence of streptospondylous vertebrae is in the Triassic (Anisian) Muschelkalk species *Aspiduriella streichani* (Kutscher, 1987) (see Hess & Meyer 2008: 37, who cite a 2007 personal communication from M. Kutscher). It is important to notice that *A. streichani* is not a euryalid. In fact, ophiuroid groups with streptospondylous vertebrae include Hemieuryalidae, Euryalidae, Gorgonocephalidae, Ophiobyrinae, Asteroschematidae, and others (Kroh 2003). The oldest occurrence of the order Euryalina tabulated by Kroh (2003) and Sepkoski (2002: 276) is *Asteronyx*, family Asteronychidae, in the Late Cretaceous.

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Dedication: This paper is dedicated to the memory of Dr. John H. Dearborn (1933–2010), Professor Emeritus of Marine Sciences, University of Maine. He was a steady and helpful hand to all his students and younger colleagues. He was elected the first Fellow of MPRI. Through his kind heart, generosity, and humorous spirit, he left this world a better place.

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