

# Fusion or hypertrophy?: the unusual arms of the Petalocrinidae (Ordovician-Devonian: Crinoidea)

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**Abstract.**—Using polarized light microscopy, the large, triangular or cylindrical second brachial plate of the Petalocrinidae is demonstrated to be a compound brachial formed through fusion of brachial plates along the distal margin of the growing arms. Based on the number of ambulacral bifurcations, brachials from the primibrachitaxis through at least the quintibrachitaxis may have been fused to form this large plate. In *Petalocrinus*, fused brachials form a second brachial that assumed the same crystallographic orientation, but in *Spirocrinus*, multidirectional extinctions preserve some of the original multiplate arrangement.

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## Introduction

Arms of the Petalocrinidae are composed of only two functional brachial plates and have multiple ambulacral bifurcations on the second brachial plate. The first brachial plate is normal in appearance, but the second brachial plate is a compound plate that is either subtriangular or cylindrical. *Eopetalocrinus* Li, 1993 is the oldest crinoid with this unique arm morphology, and it originated during the Ordovician (Darriwilian; Dawan Formation) on the South China Block. During the early Silurian (Llandovery, Aeronian), the Petalocrinidae diversified, yielding three genera: *Petalocrinus* Weller and Davidson, 1896; *Sinopetalocrinus* Mu and Lin, 1987; and *Spirocrinus* Mu and Wu, 1974 (Mao et al., 2015, 2017). *Petalocrinus* has ambulacra confined to the oral side of the second brachial plate (Fig. 1.1, 1.3), and ambulacra grow over the edges of the second brachial in *Sinopetalocrinus* so that ambulacra are present on both the oral and aboral side of this arm plate (Mao et al., 2017, fig. 4). In *Spirocrinus*, ambulacra are either approximately straight or spiral around the cylindrical second brachial (Fig. 1.2). During the Silurian, only *Petalocrinus* dispersed beyond the South China Block, and this genus became a distinctive crinoid in reef-associated habitats in Laurentia, Avalonia, and Baltica. The final known occurrence of the Petalocrinidae is *Vadarocrinus* Prokop, 1983, which is from the Pragian of the Czech Republic.

The fundamental question surrounding the petalocrinids is the origin of their unique second brachial plate. Was this plate derived from a single, hypertrophied brachial plate exhibiting excessive growth, or did this plate form through fusion of multiple brachial plates? If they are composed of fused plates, how was this accomplished? In this paper, we use polarized light microscopy to address this question.

## Background

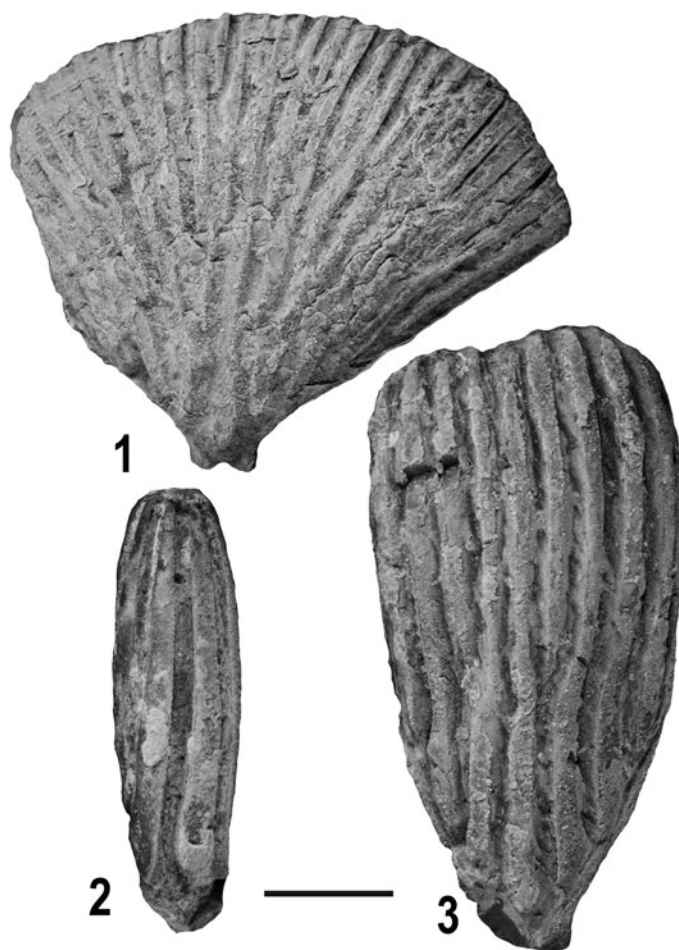
Echinoderms have a modular skeleton composed of multiple plates. When formed, plates are high-magnesium calcite with a porous stereom microstructure that consists of a meshwork of calcite trabeculae surrounded by soft tissue in the living animal (Macurda and Meyer, 1975). Each plate is the product of intracellular biomineralization (Okazaki, 1960; Märkel, 1986; Gorzelack et al., 2011, 2017), and is a single calcite crystal in optical continuity (e.g., Jackson, 1912; Raup, 1959; Towe, 1967). During diagenesis, the original crystallinity of the plate is the seed for syntaxial cement, which occludes the pore spaces of the stereom. The result is one relatively large calcite crystal representing each plate, and the crystallinity of individual plates is typically maintained in fossil specimens. This unique skeletal construction has formed the basis by which to ask a variety of questions (e.g., Raup, 1959, 1960, 1962, 1965, 1966; Emlet, 1985, 1989; Bodenbender, 1996, 1997; Bodenbender and Hiemstra, 1998; Bodenbender and Ausich, 2000; O'Malley et al., 2013, 2016).

In virtually all crinoids other than the Petalocrinidae, arms are composed of multiple plates (brachials). Ambulacra typically are located within a groove on the oral side of the brachials, and ambulacra commonly bifurcate on a specialized, pentagonal axillary brachial. New arm plates are added distally and grow through ontogeny. Juvenile brachials are typically much higher than wide and grow anisometrically to produce an adult brachial that is commonly as high as wide or wider than high (Brower, 1973, 1974, 1978; Ausich and Wood, 2012).

When Weller and Davidson (1896, p. 169) first described *Petalocrinus*, they referred to the second brachial plates as the following: “The plates composing them closely ankylosed, no sutures visible.” Subsequently, Thomas (1916, p. 289) said the brachials above the first primibrachial were “...united into a solid fan-shaped piece.” Lane and Moore (1978, p. T594) indicated that the “... brachials of each ray completely fused into single, large, fan-shaped arm plate...”

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**Figure 1.** Oral view of petalocrinid second brachial plates. (1) *Petalocrinus inferior* Bather, 1898; OSU 54648; (2) *Spirocrinus circularis* Mao et al., 2017; OSU 54650; (3) *Petalocrinus stenopetalus* Mao et al., 2017; OSU 64649. Scale bar 5.0 mm.

Terminology for naming crinoid arm plates is based on the divisions within the arms. Brachials from the radial plate to and including the first arm bifurcation (if present) are termed primibrachials and compose the primibrachitaxis; brachials after the first arm bifurcation to and including the second arm bifurcation (if present) are secundibrachials and compose the secundibrachitaxis; etc. In a simple view, arms of petalocrinids are atomous (nonbranching) and are composed of a first and second primibrachial. However, as discussed below, the large arm plate in petalocrinids is a compound plate and was formed by the fusion of numerous brachitaxes. Thus, the typical arm terminology is in some ways inaccurate. For the purposes of this paper, the first, small brachial in petalocrinids will be referred to as the first primibrachial; but the second, large arm plate will be referred to as the second brachial rather than the second primibrachial.

### Materials and methods

Three petalocrinid second brachial plates were embedded in bioplastic, and thin sections were prepared along the long axis of the arm plate. Specimens studied include *Petalocrinus inferior* Bather, 1898, Leijiatun Formation (Aeronian), Baisha Section, South China Block, China; *Petalocrinus stenopetalus* Mao

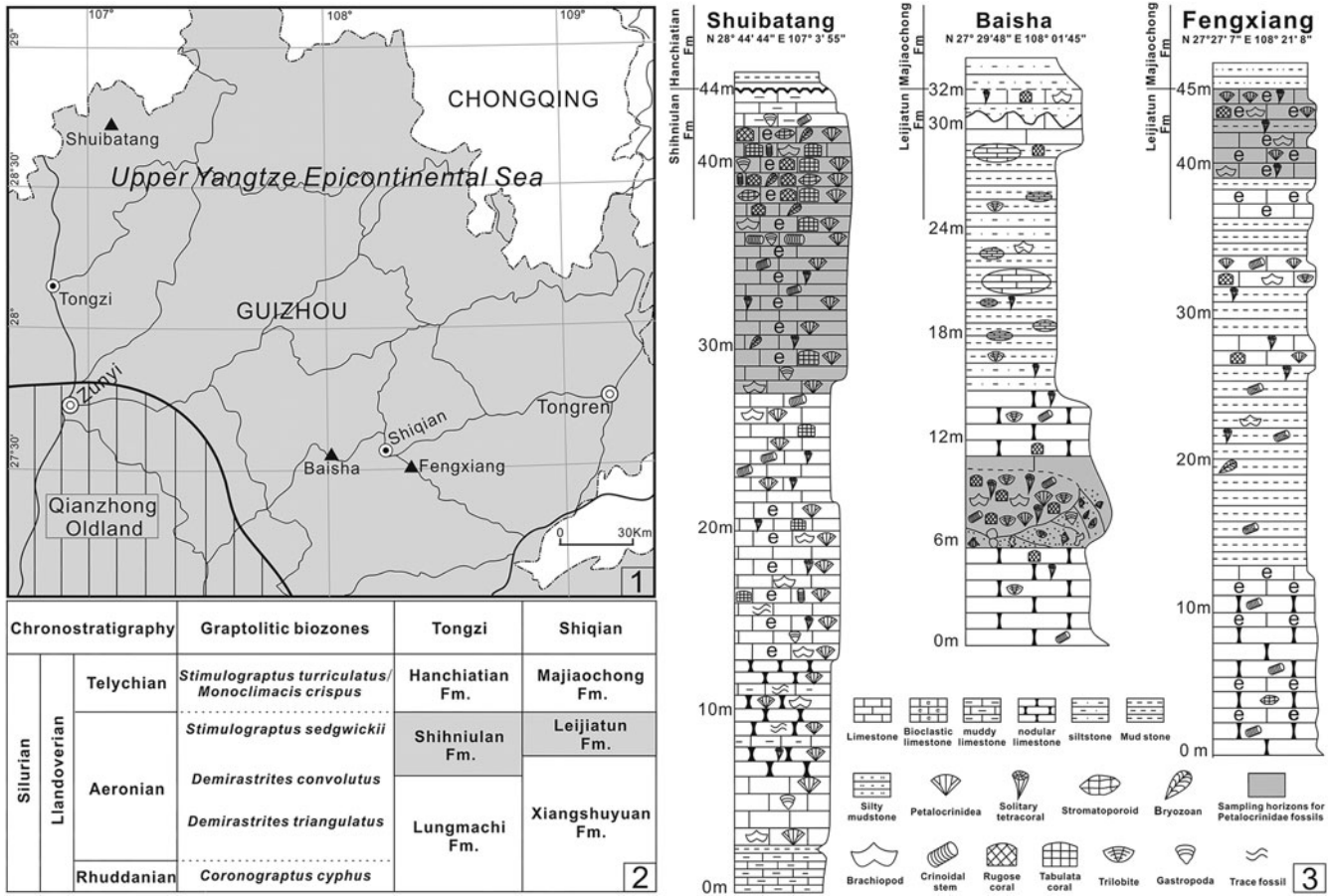
et al., 2017, Leijiatun Formation (Aeronian), Fengxiang Section, South China Block, China; and *Spirocrinus circularis* Mao et al., 2017, Shihniulan Formation (Aeronian), Shuibatang Section, South China Block, China (Fig. 2; see Mao et al., 2017 for stratigraphic and biogeographic details). These encompass most of the range of second brachial shapes present among Silurian petalocrinids, including the typical widely diverging, subtriangular second brachial of *Petalocrinus inferior* (Fig. 1.1), the narrow subtriangular second brachial of *Petalocrinus stenopetalus* (Fig. 1.3), and the cylindrical second brachial of *Spirocrinus circularis* (Fig. 1.2).

*Repository and institutional abbreviation.*—Specimens are deposited in the Orton Geological Museum, Ohio State University (OSU).

### Crystallinity of petalocrinid second brachial plates

In all three specimens studied, most of the second brachial plates are composed of one crystal of calcite with unit extinction in crossed polarized light. This region includes multiple ambulacral bifurcations.

The *Petalocrinus inferior* second brachial plate was 18.0 mm in height (Fig. 1.1), and the prepared thin section



**Figure 2.** Geographic and stratigraphic occurrences of Llandovery petalocrinids in Guizhou Province, China. (1) Location of stratigraphic sections in Guizhou Province; (2) positions of the Shihniulan and Leijiatuan formations relative to graptolite biozones; (3) stratigraphic columns with petalocrinid-yielding beds indicated (from Mao et al., 2017).

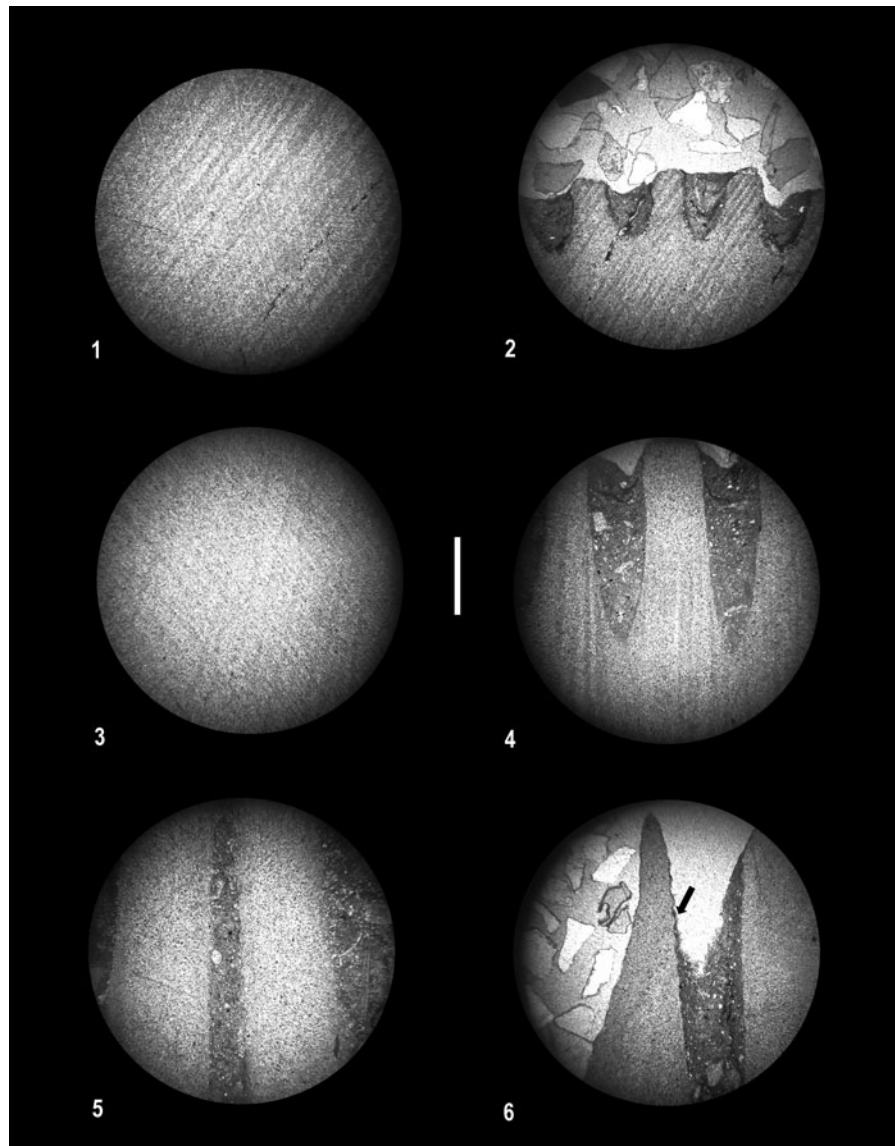
was 17.5 mm in height and 20 mm in maximum width. As noted above, nearly the entire plate had unit extinction, indicating construction by a single crystal (Fig. 3.1; Supplemental Figs. 1.1, 2). In contrast, the distal 0.5 mm of this specimen is a thin zone with subtle, wavy extinction, indicating a crystallinity that contrasts with the majority of the plate (Fig. 3.2; Supplemental Figs. 1.2, 3). Prior to preparation, the *Petalocrinus stenopetalus* second brachial plate was 22.0 mm in height with a maximum width of 10.5 mm (Fig. 1.3), and the prepared thin section remained 22.0 mm in height. Similar to *P. inferior*, the majority of the plate was a single crystal (Fig. 3.3; Supplemental Figs. 1.3, 4), and the distal 0.5 mm of the *P. stenopetalus* second brachial plate has subtle, wavy extinction (Fig. 3.4; Supplemental Figs. 1.4, 5).

Prior to preparation, the second brachial plate of *Spirocrinus circularis* was 18.0 mm in height and 5.0 mm in diameter (Fig. 1.2), and the prepared thin section was 15.0 mm in height. As in *Petalocrinus*, the majority of the *S. circularis* second brachial plate is a single crystal in optical continuity (Fig. 3.5; Supplemental Figs. 1.5, 6), but the distal, narrow zone of wavy extinction is absent. In contrast, one small (3.4 mm in height and 0.5 mm in width) individual crystal is incorporated at the distal end of the second brachial plate (Fig. 3.6; Supplemental Figs. 1.6, 7). The crystallinity of this crystal is different from that of the remainder of the plate.

**Interpretation**

The large second brachial plate of petalocrinids was not formed by hypertrophy of a single, normal-sized, second primibrachial. Rather, this large brachial plate is interpreted to have been formed by the fusion of multiple plates, with or without merging of the crystal orientations of individual plates. This confirms the interpretations of previous workers (Weller and Davidson, 1896; Thomas, 1916; Lane and Moore, 1978). The wavy extinction of the distal portion of the *Petalocrinus* specimens is interpreted as fused plates that have incompletely merged their crystallographic orientations to that of the remainder of the second brachial plate. This implies that the second compound brachial plate was formed through progressive fusion of ever more distal brachial plates. Distal brachial plates fused to more proximal plates, and these plates also fused with laterally adjacent plates. Thus, this large plate is referred to as the second brachial plate because it is a combination of multiple brachitaxes. The plate illustrated in Figure 1.1 was formed through the fusion of the second primibrachial through several tertibrachitaxis plates.

The formation of the *Spirocrinus* second brachial plate is similar to that in *Petalocrinus*, in that the majority of the second brachial is one very large crystal. However, at least one additional large crystal is also present in the *Spirocrinus* second brachial plate (Fig. 3.6; Supplemental Figs. 1.6, 7). On the studied



**Figure 3.** Photomicrographs of thin sections of petalocrinids in crossed-polarized light (scale bar 1.0 mm). (1, 2) *Petalocrinus inferior* Bather, 1898; OSU 54648; (1) central portion of second brachial plate, (2) distal edge of second brachial plate; (3, 4) *Petalocrinus stenopetalus* Mao et al., 2017; OSU 64649; (3) central portion of second brachial plate, (4) distal edge of second brachial plate; (5, 6) *Spirocrinus circularis* Mao et al., 2017; OSU 54650; (5) central portion of second brachial plate, (6) distal edge of second brachial plate, arrow indicates boundary between adjoining crystals (see color images and videos in Supplemental Figures).

specimen, a distal zone of wavy extinction is absent. This second brachial plate was formed by fusion of brachial plates. Most of the fused brachial plates changed their crystallographic orientation to conform to the majority of this plate. However, at least one fused plate retained its original crystallinity. The size of this additional crystal far exceeds the size of a constituent brachial plate. We presume that this additional plate enlarged by fusion of multiple brachials that changed their crystallographic orientations, but we are unable to eliminate the possibility that this extra crystal is the product of a single, hypertrophied brachial plate incorporated into the second brachial plate.

## Discussion

Despite the fact that initial biomineralization of each echinoderm plate occurred within a single mesodermal cell, it is well established

that adjacent plates can merge. This can occur through stereomic interlocking of adjacent plates, as illustrated in clypeasteroid echinoids (e.g., Grun et al., 2018), although in the case of clypeasteroids, most plates maintain their original crystallinity. Similarly, most camerate crinoids are thought to have ankylosed thecal plates that retain individual crystallographic orientations, although the exact mechanism for this fusion has not been documented.

Evolutionary reduction in the number of plates in the proximal circllet of crinoids (either infrabasal or basal circllet) has been demonstrated to be the product of plate fusion. Wilson (1916) developed a rationale for recognizing this fusion, and Peter (2019) provided a modern treatment of plate fusion with the infrabasals of flexible crinoids. Fusion of separate plates also occurred in the transition from pentamerous to holomeric columnals in crinoids (e.g., Warn and Strimple, 1977). Plate fusion is also recognized in other echinoderms. For example, it is widely

recognized as a derived condition in ambulacral plates of crown-group echinoids (Smith, 2005; Gao et al., 2015), and Sprinkle and Sumrall (personal communication, 2018) recognized plate fusion in the formation of the deltoid plate in parablattoids.

Although the plate fusion described here is unusual (if not unique) for crinoid arms, this process of fusion occurs in the crown and column plates of other crinoids, the test of echinoids, and the theca of blastozoan echinoderms. Demonstrating plate fusion in petalocrinids clarifies homology statements for this group and emphasizes the potential of this process for other studies in echinoderm disparity and phylogeny.

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## Accessibility of supplemental data

Color images and videos of the petrographic study of petalocrinid specimens are available from the Dryad Digital Repository: <https://doi:10.5061/dryad.9kj4ms0>.

## References

- Ausich, W.I., and Wood, T.E., 2012, Ontogeny in *Hypselocrinus hoveyi*, Mississippian cladid crinoid from Indiana: *Journal of Paleontology*, v. 86, p. 1017–1020.
- Bather, F.A., 1898, *Petalocrinus* (Weller and Davidson): *Quarterly Journal of the Geological Society of London*, v. 54, p. 401–441.
- Bodenbender, B.E., 1996, Patterns of crystallographic axis orientation in blastoid skeletal elements: *Journal of Paleontology*, v. 70, p. 466–484.
- Bodenbender, B.E., 1997, Echinoderm skeletal crystallography and paleobiological applications: *Paleontological Society Papers*, v. 3, p. 191–204.
- Bodenbender, B.E., and Ausich, W.I., 2000, Skeletal crystallography and crinoid calyx architecture: *Journal of Paleontology*, v. 74, p. 52–66.
- Bodenbender, B.E., and Hiemstra, E.J., 1998, Preliminary investigation of cystoid skeletal crystallography: *Geological Society of America Abstracts with Programs*, v. 30, p. 7.
- Brower, J.C., 1973, Crinoids from the Girardeau Limestone (Ordovician): *Palaeontographica Americana*, v. 7, no. 46, p. 263–499.
- Brower, J.C., 1974, Ontogeny of camerate crinoids: *The University of Kansas Paleontological Contributions*, Paper 72, 53 p.
- Brower, J.C., 1978, Camerates, in Moore, R.C., and Teichert, K., eds., *Treatise on Invertebrate Paleontology, Part T, Echinodermata*: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and University of Kansas, v. 2, p. T244–T263.
- Emlet, R.B., 1985, Crystal axes in Recent and fossil echinoids indicate trophic mode in larval development: *Science*, v. 230, p. 937–940.
- Emlet, R.B., 1989, Apical skeletons of sea urchins (Echinodermata: Echinoidea): two methods for inferring mode of larval development: *Paleobiology*, v. 15, p. 223–254.
- Gao, F., Thompson, J.R., Petsios, E., Erkenbrack, E., Moats, R.A., Bottjer, D.J., and Davidson, E.H., 2015, Juvenile skeletogenesis in anciently diverged sea urchin clades: *Developmental Biology*, v. 400, p. 148–158. doi: 10.1016/j.devbio.2015.01.107.
- Gozelack, P., Stolarski, J., Dubois, P., Kopp, C., and Meibom, A., 2011, <sup>26</sup>Mg labeling of the sea urchin regenerating spine: insights into echinoderm biomineralization process: *Journal of Structural Biology*, v. 176, p. 119–126. doi: 10.1016/j.jsb.2011.07.008.
- Gozelack, P., Dery, A., Dubois, P., and Stolarski, J., 2017, Sea urchin growth dynamics at microstructural length scale revealed by Mn-labelling and cathodoluminescence: *Frontiers in Zoology*, v. 14:42, 17 p. doi: 10.1186/s12983-017-0227-8.
- Grun, T.B., Mancosu, A., Belaústegui, Z., and Nebelsick, J.H., 2018, The taphonomy of *Chlypeaster*: a paleontological tool to identify stable structures in natural shell systems: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 289, p. 189–202.
- Jackson, R.T., 1912, Phylogeny of the Echini, with a revision of Paleozoic species: *Memoirs of the Boston Society of Natural History*, v. 7, 491 p.
- Lane, N.G., and Moore, R.C., 1978, Suborder Cyathocrinina, in Moore, R.C., and Teichert, K., eds., *Treatise on Invertebrate Paleontology, Echinodermata, Pt. T(2)*: Geological Society of America and University of Kansas Press, Boulder and Lawrence, p. T578–T607.
- Li, L., 1993, Discovery of *Eopetalocrinus* (gen. nov.) in Lower Ordovician Dawan Formation at Liujiachang, Songzi, Hubei and its significance: *Oil and Gas Geology*, v. 14, p. 272–277. [in Chinese with English summary]
- Mao, Y., Lin, J.-P., and Ausich, W.I., 2015, Chinese origin and radiation of the Palaeozoic crinoid family Petalocrinidae: *Palaeoworld*, v. 24, p. 445–453. doi: j.palwor.2-14.12.007.
- Mao, Y., Ausich, W.I., Li, Y., Lin, J.-P., and Lin, C., 2017, New taxa and phylogenetic evolution of the Aeronian (Llandovery, Silurian) Petalocrinidae (Echinodermata: Crinoidea) in Guizhou, South China Block: *Journal of Paleontology*, v. 91, p. 477–492. <http://dx.doi.org/10.1017/jpa.2016.156>.
- Macurda, D.B., Jr., and Meyer, D.L., 1975, The microstructure of the crinoid endoskeleton: *University of Kansas Paleontological Contributions*, Paper 74, 22 p.
- Märkel, K., 1986, Ultrastructural investigation of matrix-mediated biomineralization in echinoids (Echinodermata, Echinoidea): *Zoomorphology*, v. 106, p. 232–243.
- Mu, E.-Z., and Lin, C.-H., 1987, Petalocrinidae from the Silurian of Shiqian District, Guizhou: *Bulletin of the Nanjing Institute Geology and Palaeontology, Academica Sinica*, v. 12, p. 1–22. [in Chinese with English summary]
- Mu, E.-Z., and Wu, Y.-R., 1974, Crinoid sections, in *Nanking Institute of Geology and Palaeontology, ed., A Handbook of the Stratigraphy and Paleontology in Southwest China*: Beijing, Academia Sinica, 455 p. [in Chinese]
- O'Malley, C.E., Ausich, W.I., and Chin, Y.-P., 2013, Isolation and characterization of the earliest taxon-specific organic molecules (Mississippian, Crinoidea): *Geology*, v. 41, p. 347–350. doi:10.1130/G33792.1.
- O'Malley, C.E., Ausich, W.I., and Chin, Y.-P., 2016, Deep echinoderm phylogeny preserved in organic molecules from Paleozoic fossils: *Geology*, v. 4, p. 379–382. doi:10.1130/G37761.1.
- Okazaki, K., 1960, Skeleton formation of sea urchin larvae. II. Organic matrix of the spicule: *Embryologia*, v. 5, p. 283–320.
- Peter, M.E., 2019, Aberrations in the infrabasal cirlet of the cladid crinoid *Cupulocrinus* (Echinodermata) and implications for the origin of the flexible crinoids: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 522, p. 52–61.
- Prokop, R.J., 1983, *Vadaroocrinus vassa* gen. et sp. n. (Crinoidea, Petalocrinidae) from the Lower Devonian of Bohemia: *Casopis Národního Muzea, Rada Prirůdovedná*, v. 152, p. 187–188.
- Raup, D.M., 1959, Crystallography of echinoid calcite: *Journal of Geology*, v. 67, p. 661–674.
- Raup, D.M., 1960, Ontogenetic variation in the crystallography of echinoid calcite: *Journal of Paleontology*, v. 34, p. 1041–1050.
- Raup, D.M., 1962, The phylogeny of calcite crystallography in echinoids: *Journal of Paleontology*, v. 36, p. 793–810.
- Raup, D.M., 1965, Crystal orientations in the echinoid apical system: *Journal of Paleontology*, v. 39, p. 934–951.
- Raup, D.M., 1966, Crystallographic data for echinoid coronal plates: *Journal of Paleontology*, v. 40, p. 555–568.
- Smith, A.B., 2005, Growth and form in echinoids: the evolutionary interplay of plate accretion and plate addition, in Briggs, D.E., ed., *Evolving Form and Function: Fossils and Development: Proceedings of a Symposium Honoring Adolf Seilacher for his Contributions to Paleontology*, in Celebration of his 80<sup>th</sup> Birthday: Peabody Museum of Natural History, Yale University, New Haven, p. 181–195.
- Thomas, A.O., 1916, A new crinoid fauna from Monticello, Iowa: *Proceedings of the Iowa Academy of Sciences*, v. 22, p. 289–291.
- Towe, K.M., 1967, Echinoderm calcite: single crystal or polycrystalline aggregate: *Science*, v. 157, p. 1048–1050.
- Warn, J.M., and Strimple, H.L., 1977, The disparid inadunate superfamilies Homocrinacea and Cincinnaticrinacea (Echinodermata, Crinoidea) Ordovician–Silurian, North America: *Bulletins of American Paleontology*, v. 72, p. 1–138.
- Weller, S., and Davidson, A.D., 1896, *Petalocrinus mirabilis* (n. sp.) and a new American fauna: *Journal of Geology*, v. 4, p. 166–173.
- Wilson, H.E., 1916, Evolution of the basal plates in monocyclic Crinoidea Camerata: *Journal of Geology*, v. 24, p. 488–510, 533–553, 665–684.

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