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REGULAR RESEARCH ARTICLE

Form and function of the strangest crinoid stem: Devonian of Morocco

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Abstract

Trombonicrinus (col.) *hanshessi* gen. et sp. nov. is a crinoid species of unusual morphology and is based solely on the stem. It comes from the (probably Lower) Devonian of Tafraoute, Anti Atlas Mountains, Morocco. It is a long crinoid stem of circular section, tapering distally throughout, with a tight curvature through 180° between the mesistele and proxistele; attachment is distally by short, pointed, unsegmented pseudoradices. The overall appearance is reminiscent of the slide of a trombone. The dististele is essentially straight, the mesistele is more or less convoluted, and the proxistele is straight and parallels the more distal stem. The dististele was attached to an upright object around which the pseudoradices formed a close attachment. The crinoid's stem was growing down towards the substrate. The mesistele was free of the attachment surface and grew in a more convoluted manner. The proxistele was adapted to elevate the crown, growing upwards and in the opposite direction of the rest of the crinoid. This is a form unique to *T.* (col.) *hanshessi* and not recognised hitherto in the Crinoidea. The conical, most proximal part of this stem in the holotype may suggest that it was immediately beneath the cup; the specimen is considered complete apart from the crown. The loss of the crown was most likely the result of autotomy. Although the proxistele of the paratype is relatively longer, it is probably incomplete. This crinoid was either a cladid or a camerate.

Keywords *Trombonicrinus* (col.) · Tafraoute · Functional morphology · Life orientation · Attachment · Pseudoradices

Introduction

The simple, plant-like structure of a stalked crinoid is an outline well known to most palaeontologists. Although crinoids may be reconstructed in books and museums in the nineteenth century 'tulip flower' form even today (Donovan 2011a, b), since the pioneering observations of Macurda and Meyer (1974) we have accumulated abundant data that at least most extant stalked taxa are rheophilic, not rheophobic. That is, modern stalked crinoids actively harvest feeding water currents on the sea floor; they do not wait for food particles to drop through a column of still water.

However, applying this knowledge back into the Palaeozoic is problematic. Diversity of crinoid form in the Ordovician to Permian was far greater than in the entire post-Palaeozoic. These ancient crinoids included taxa that cannot be easily squeezed into the upright stem, rheophilic feeding model. Well-known examples include the recumbent calceocrinids, with a hinged cup which enabled them to feed like a crinoid 'brachiopod' (Ager 1963, Fig. 5.3A; Brower 1966, 1985; Ausich 1986), and the coiled myelodactylids, that look more like a pin-wheel firework than a fossil (Donovan and Sevastopulo 1989). Within taxa that are otherwise not unusual, there may be modifications of particular structures that are extraordinary and unique, such as the contrasting arms of the mid-Palaeozoic cladids *Crotalocrinites* Austin and Austin, 1843, and *Petalocrinus* Weller and Davidson, 1896 (Donovan et al. 2012, pl. 16, fig. 1, and pls 19, 20, respectively). And at least as extraordinary are the many bizarre forms of the stem (Donovan 2016).

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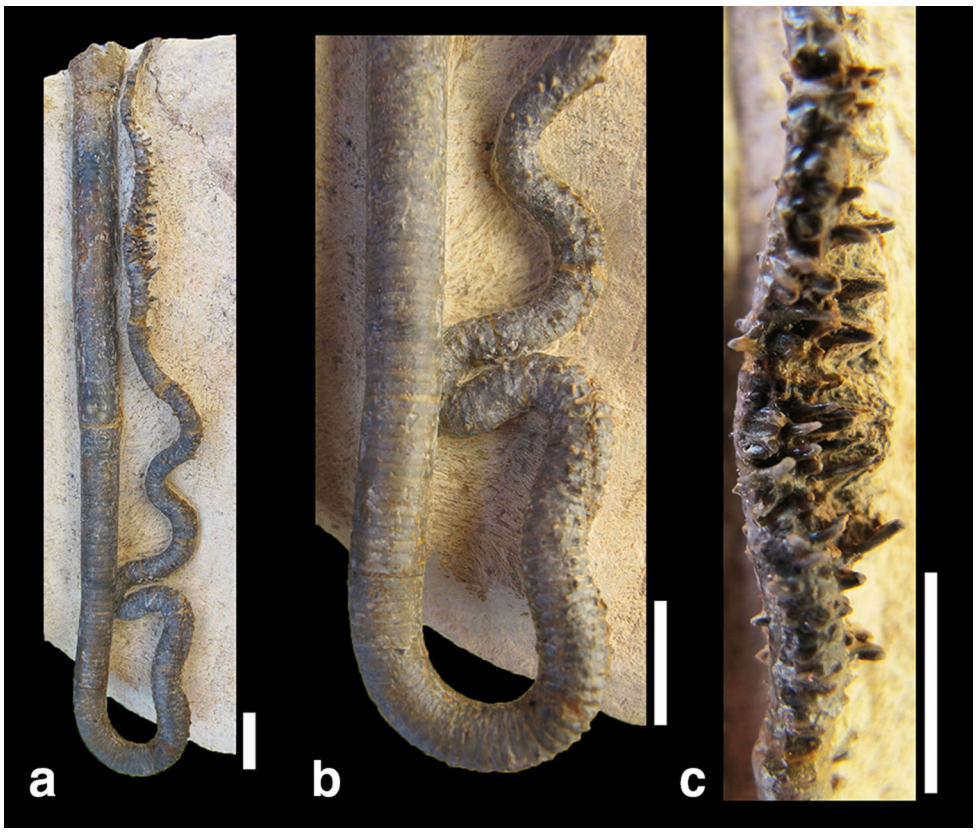

Fig. 1 *Trombonicrinus* (col.) *hanshessi* gen. et sp. nov., holotype, RGM.1350539, from Tafraoute, Anti Atlas Mountains, Devonian of Morocco. **a** Complete specimen in life position; pseudoradices (upper right) were presumably formerly attached to an upright substrate. **b** The prominent 180° bend in the stem that folds it back parallel with itself. Note that there are other strong folds in the stem on the right of the image (mesistele), but none on the left (proxistele). **c** Numerous, pointed pseudoradices in the dististele. All scale bars represent 10 mm

Herein, we describe a fossil crinoid stem of unique form and, as interpreted, function. The title of the paper is rather sweeping, 'the strangest crinoid stem', but we are at least confident that there are none stranger. The combination of a series of unusual adaptations recognised in this specimen makes it worthy of detailed study, even though the crown remains unknown.

The terminology of the crinoid stem follows Moore et al. (1968, 1978), Webster (1974) and Donovan (1986). The holotype and paratype specimens are deposited in the Naturalis Biodiversity Center, Leiden, The Netherlands (prefix RGM).

Locality and horizon

An ideal account of a new fossil species should be accompanied by a precise grid reference(s) and/or GPS data, an accurate locality map, a measured section and images of the exposure. But there are circumstances when this is not possible, such as when a specimen is collected from float, when it forms part of an old collection in a museum or when it is purchased from a professional dealer. The holotype described herein (Fig. 1) was saved from obscurity by M.S.P., who recognised its unique attributes and purchased it from a fossil dealer in Morocco to deposit it in a museum collection for posterity. The paratype (Fig. 2) was similarly found in a rock shop in Morocco during the Subcommission on Devonian Stratigraphy fieldtrip in 2011 by J.A.W.

The best locality data for the holotype contributed from the dealer were summarised in an e-mail to M.S.P. in 2014, where an earlier error was corrected that the specimen came from Jebel Ofaten (Feist and Chatterton 2015, fig. 1). In fact, the correct locality is Tafraoute, which is relatively less well known. *Paleontica Fossiel.Net* (https://english.fossiel.net/sites/fossil_site.php?plaats=547) provides a locality map and noted that this site is north of the village of Tafraoute. It is Devonian, presumably Lower Devonian (Pragian) on the basis of the (unpublished) identifications of the included trilobites. Locality data for the paratype are lacking.

The two crinoid specimens were collected as a by-product of commercial mining of the Devonian strata of Anti Atlas Mountains for trilobites, which are world famous and often exquisitely preserved. In contrast, Devonian crinoids from Morocco remain poorly known, and are often preserved as fragments, stem sections and thecal cups, rather than crowns. Waters and Klug (research in progress), Klug et al. (2014), Webster et al. (2005) and Webster and Becker (2009) have recently discussed the history of crinoid studies from Morocco, and described Devonian crinoids from various localities. None of these papers discussed

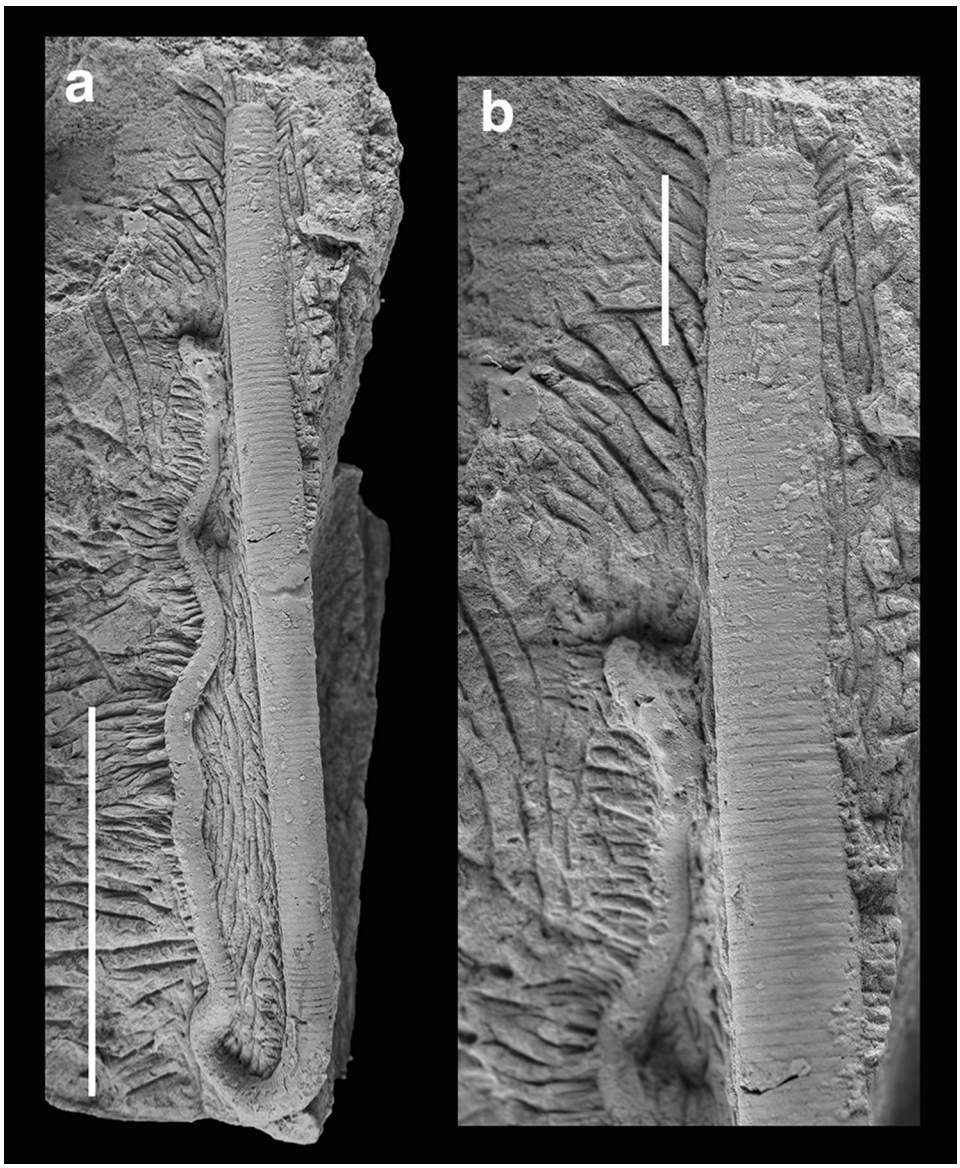

Fig. 2 *Trombonicrinus* (col.) *hanshessi* gen. et sp. nov., paratype, RGM.1350540, from the Devonian of Morocco. **a** Complete specimen in life position; note that the proxistele is longer than the proxistele + mesistele combined, in contrast to the holotype. Scale bar represents 50 mm. **b** Enlargement of proximal proxistele and dististele. Note proxistele is homeomorphic. Scale bar represents 10 mm

crinoids from Tafraoute nor described taxa that are likely suspects for the theca of the new genus described herein. The paucity of Devonian crinoid studies from Morocco plus the unique morphology of the stem led us to describe this new genus even though stratigraphic and locality data are limited.

Systematic palaeontology

Class Crinoidea J.S. MILLER, 1821

Incertae sedis
Morphogenus *Trombonicrinus* (col.) gen. nov.

Etymology: From the French *trombone* (earlier, *trombon*), a brass wind instrument with a slide bent in a tight U-shape (Little et al. 1983, p. 2368). The overall appearance of this crinoid stem is reminiscent of the slide of a trombone.

Type species: *Trombonicrinus* (col.) *hanshessi* gen. et sp. nov. The only species known.

Diagnosis: A long crinoid stem of circular section, tapering distally throughout, with a tight curvature through 180° between the mesistele and proxistele; attached distally by short, pointed, unsegmented pseudoradices.

Remarks: A new term, pseudoradice, is used herein, in the morphogeneric diagnosis and elsewhere, in preference to the widely used pseudocirrus. Moore et al. (1978, p. T240) defined pseudocirrus as an "Unsegmented sideward projection from columnal resembling cirrus in having axial canal but very irregular in form and distribution." But cirri sensu stricto are flexible appendages with contractile

tissues capable of grasping, and are known almost exclusively from post-Palaeozoic isocrinines and comatulids (Donovan 1993). Palaeozoic and certain post-Palaeozoic crinoids, such as bourgueticrinines, have jointed, but inflexible radices (also called radicles or roots) without contractile tissues. As pseudoradices are known mainly (entirely?) from Palaeozoic crinoids and, in their inflexibility, are closer to radices in function than cirri, we consider the term pseudocirrus to be a misnomer that we correct herein.

Range: Lower(?) Devonian of Morocco.

Trombonicrinus (col.) *hanshessi* gen. et sp. nov.

Figures 1, 2

Etymology: In honour of the late Hans Hess.

Type material: Holotype, RGM.1350539 (Fig. 1); paratype, RGM.1350540 (Fig. 2).

Other material: A third specimen was on sale from the Middle Devonian of Alnif, Morocco [(www.bigfossil.com/undescribed-crinoid—morocco-4707-p.asp) (accessed 17 April 2018)].

Locality and horizon: Lower(?) Devonian of Tafraoute, Anti Atlas Mountains, Morocco.

Diagnosis: As for the morphogenus (see above).

Description of holotype: Total length of stem *c*. 270 + mm; crown not preserved, but stem may be complete. The stem is divided into the dististele (Fig. 1a, c), mesistele (Fig. 1a, b) and proxistele (Fig. 1a, b), with a transition through 180° between the mesistele and proxistele.

Dististele gently sinuous, slender, circular in section, about 50 mm long, tapering to a point. Pseudoradices common in the more proximal 35 mm of dististele. Pseudoradices pointed, conical, tooth-like, unsegmented, concentrated mainly on the side of the dististele away from the more proximal proxistele (Fig. 1a). Order of columnals not apparent, perhaps obscured by cleaning.

Mesistele longer than dististele, diameter gradually increasing more proximally. Mesistele more convoluted than either proxistele or dististele (Fig. 1a, b), albeit less so in the paratype. Latera spiny, spines shaped like short pseudoradices; latera otherwise planar. Spines are concentrated on the side away from the proxistele. Column appears homeomorphic, latera gently convex.

The mesistele–proxistele transition curves through 180° (Fig. 1a, b). The column is homeomorphic or only weakly heteromorphic, composed of numerous low columnals that are each slightly wedge shaped. Articulation symplectial. Latera gently convex, unsculptured apart from sparse low tubercles only on the outside of the curve and not extending to the proxistele.

Proxistele straight, long, expanding in diameter proximally. Latus unsculptured, planar, lacking pseudoradices and spines. Column appears heteromorphic more proximally in the holotype, perhaps N212, nodals highest *et seq*., but it is certainly homeomorphic in the paratype (Fig. 2b). A slight flaring of the column at the proximal-most (broken) end may indicate that this was immediately beneath the cup.

Remarks: The type specimens have been cleaned and appear polished. This has the effect of obscuring the fine details of some parts of the stem, so details of the arrangements of columnals (homeomorphic, heteromorphic) are obscure in places.

Discussion

Our interpretation of the life orientation of *T*. (col.) *hanshessi* is shown in Figs. 1 and 2. A runner-type attachment would commonly be interpreted as lying flat on the sea floor, with the crown being elevated by the more proximal column (Macurda and Meyer 1974; Hess 1999). Such crinoids have an essentially straight, recumbent part of the column with cirri, radices or pseudoradices arrayed gently or sharply downwards into the sediment surface. But *T*. (col.) *hanshessi* is somewhat different in form. The part of the dististele bearing pseudoradices is sinuous, but essentially straight overall (Figs. 1a, c, 2a); the mesistele is more or less convoluted (contrast Figs. 1a, b with 2a); and the proxistele is straight and parallels the more distal stem. Any sinuosity in the part of the dististele considered to have been attached is thought to be a reflection of the inherent form of the substrate; that of the mesistele (Fig. 1a, b) may be a growth strategy of the column 'hunting' for an attachment surface. If the distal stem was a conventional runner attachment, this would mean that the proximal column and crown were only elevated above the sea floor by a matter of a few millimeters. This is nonsensical; the crown would have been forced to feed only just above the sediment surface.

Rather, we consider that the dististele was attached to an upright object around which the pseudoradices formed a close attachment; analogous attachments are not unknown in, for example, brachiopods (Ager 1963, fig. 15.6). The upright object is not preserved and is presumed to have been algae or some other marine plant which has rotted away. Probable attachment to a plant indicates that this association most likely occurred in shallow water. The crinoid's stem was thus growing, at least initially, towards the sediment substrate, that is, down. The mesistele was

free of the attachment surface and grew in a more convoluted manner, perhaps seeking a substrate for attachment; the spines on the latera of this part of the stem are incipient pseudoradices which would have attached if a suitable substrate was available. The proxistele lacked pseudoradices and spines; it was adapted to elevate the crown, growing upwards and in the opposite direction of the rest of the crinoid.

Most crinoids insert new columnals immediately beneath the cup. Exceptions include, for example, not only members of the flexible crinoid genus *Taxocrinus* Phillips *in* Morris, 1843 (Wulff and Ausich 1989; Donovan and Fearnhead, in press) but also certain other taxa. There is no evidence of a *Taxocrinus*-like generating columnal in the proxistele of *Trombonicrinus* (col.) *hanshessi*, so columnals are considered to have been inserted immediately beneath the cup. The conical, most proximal part of this stem in the holotype suggests that it was immediately beneath the cup by comparison with many other crinoid taxa; that is, the specimen is considered complete apart from the crown. The loss of the crown was most likely the result of autotomy (Donovan 2012). In contrast, the proxistele of the paratype is relatively longer (Fig. 2) and, lacking a most proximal conical section, was presumably immature at death.

The larval crinoid, attaching to the elevated substrate, would have oriented growth upwards, away from the substrate, if that was the preferred direction of growth of this species. It must be assumed that the preferred initial direction of growth was down, like that of a pseudoplanktic crinoid attached to a floating log or a Silurian *Scyphocrinites* Zenker, 1833, hanging down from its lobolith (Simms 1986; Haude 1972, 1992). This is an adaptation unique to *T.* (col.) *hanshessi* and not recognised hitherto in the Crinoidea.

The 180° bend between the mesistele and proxistele invites speculation. Did the dististele and mesistele grow downwards, and only then did the stem bend to enable the proxistele to grow upwards? Or was the transition between the mesistele and proxistele fluid, reorienting and becoming more distal as the stem grew longer? Although uncertain, the latter explanation is suggested by the preservation of these specimens. In both type specimens, the tip of the dististele is either at the same level as the most proximal proxistele or higher (Figs. 1a, 2a). This may be coincidence, but it at least suggests that there may be a correlation between the two, perhaps of some optimal height for feeding above the initial level of attachment.

The question of classification is unresolved. Such a robust column is certainly not a disparid, a group of gracile crinoids that were in decline after the Early Palaeozoic. *Trombonicrinus* (col.) *hanshessi* is, therefore, either a cladid or a camerate (either monobathrid or diplobathrid; the former were more common at this time; Donovan and Fearnhead 2014), but we are unaware of any crinoid belonging to either group with such a stem geometry.

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References

Ager, D. V. (1963). *Principles of Paleoecology*. New York: McGraw-Hill.

Ausich, W. I. (1986). Palaeoecology and history of the Calceocrinidae (Palaeozoic Crinoidea). *Palaeontology, 29,* 85–99.

Austin, T., & Austin, T., Jr. (1843). Description of several new genera and species of Crinoidea. *Annals and Magazine of Natural History (series 1), 11,* 195–207.

Brower, J. C. (1966). Functional morphology of Calceocrinidae with description of some new species. *Journal of Paleontology, 40,* 613–634.

Brower, J. C. (1985). Ontogeny and functional morphology of two Ordovician calceocrinids. In B. F. Keegan, & B. D. S. O'Connor (Eds.), *Echinodermata: Proceedings of the Fifth International Echinoderm Conference, Galway, 24–29 September, 1984* (pp. 13–18). Rotterdam: A. A. Balkema.

Donovan, S. K. (1986). Pelmatozoan columnals from the Ordovician of the British Isles. Part 1. *Monographs of the Palaeontographical Society, London, 138*(568), 1–68.

Donovan, S. K. (1993). Contractile tissues in the cirri of ancient crinoids: criteria for recognition. *Lethaia, 26,* 163–169.

Donovan, S. K. (2011a). Spineless displays or why inaccurate restorations of fossil invertebrates discredit our museums. *Geological Curator, 9,* 279–284.

Donovan, S. K. (2011b). The poorly illustrated crinoid. *Lethaia, 44,* 125–135.

Donovan, S. K. (2012). Was autotomy a pervasive adaptation of the crinoid stalk during the Palaeozoic? *Geology, 40,* 867–870.

Donovan, S. K. (2016). Problematic aspects of the form and function of the stem in Palaeozoic crinoids. *Earth-Science Reviews, 154,* 174–182.

Donovan, S. K., & Fearnhead, F. E. (2014). A dearth of diplobathrids (Crinoidea) from the type Devonian System, south-west England. *Proceedings of the Yorkshire Geological Society, 60,* 91–97.

Donovan, S. K., & Fearnhead, F. E. (in press). The British Devonian Crinoidea. Part 2, addendum to Part 1, Cladida, Disparida and columnals. *Monograph of the Palaeontographical Society, London*.

Donovan, S. K., & Sevastopulo, G. D. (1989). Myelodactylid crinoids from the Silurian of the British Isles. *Palaeontology, 32,* 689–710.

Donovan, S. K., Widdison, R. E., Lewis, D. N., & Fearnhead, F. E. (2012). The British Silurian Crinoidea. Part 3, addendum to parts 1 and 2, Camerata and columnals. *Monograph of the Palaeontographical Society, London, 166*(638), 135–259.

Feist, R., & Chatterton, B. D. E. (2015). Kolihapeltine trilobites, the spiniest scutellids from the eastern Anti-Atlas (Morocco, Early Devonian): evolution, environment and classification. *Papers in Palaeontology, 1,* 255–287.

Haude, R. (1972). Bau und Funktion der *Scyphocrinites*-Lobolithen. *Lethaia, 5,* 95–125.

Haude, R. (1992). Scyphocrinoiden, die Bojen-Seelilien im hohen Silur-tiefen Devon. *Paleontographica Abteilung A, Palaeozoologie und Stratigraphie, 222,* 141–187.

Hess, H. (1999). Recent. In H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms (Eds.), *Fossil Crinoids* (pp. 237–244). Cambridge: Cambridge University Press.

Klug, C., De Baets, K., Naglik, C., & Waters, J. (2014). New species of *Tiaracrinus* from the latest Emsian of Morocco. *Acta Palaeontologica Polonica, 59,* 135–145.

Little, W., Fowler, H. W., & Coulson, J. (1983). The Shorter Oxford Dictionary on Historical Principles. In C. T. Onions, G. W. Friedrichsen (Eds.) *Marl-Z and Addenda*. Volume II, 3rd ed. (pp. 1281–2672). Oxford: Oxford University Press.

Macurda, D. B., Jr., & Meyer, D. L. (1974). The feeding posture of modern stalked crinoids (Echinodermata). *Nature, 247,* 394–396.

Miller, J. S. (1821). *A Natural History of the Crinoidea or Lily-Shaped Animals, with Observations on the Genera Asteria, Eurayle, Comatula and Marsupites* (pp. 1–150). Bristol: C. Frost.

Moore, R. C., Jeffords, R. M., & Miller, T. H. (1968). Morphological features of crinoid columns. *University of Kansas Paleontological Contributions, Echinodermata Article, 8,* 1–30.

Moore, R. C., Ubaghs, G., Rasmussen, H. W., Breimer, A. & Lane, N. G. (1978). Glossary of crinoid morphological terms. In Moore, R. C. & Teichert, C. (Eds), *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2(1)*. Geological Society of America and University of Kansas, Boulder and Lawrence, T229, T231, T233—T242.

Morris, J. (1843). *A Catalogue of British Fossils comprising all the Genera and Species hitherto described; With reference to their Geological Distribution and to the Localities in which they have been found*. London: John Van Voorst.

Simms, M. J. (1986). Contrasting lifestyles in Lower Jurassic crinoids: a comparison of benthic and pseudopelagic Isocrinida. *Palaeontology, 29,* 475–493.

Webster, G. D. (1974). Crinoid pluricolumnal noditaxis patterns. *Journal of Paleontology, 48,* 1283–1288.

Webster, G. D., & Becker, R. T. (2009). Devonian (Emsian to Frasnian) crinoids of the Dra Valley, western Anti-Atlas Mountains, Morocco. In P. Königsdorf (Ed.), *Devonian Change: Case Studies in Palaeogeography and Palaeoecology* (vol. 314, pp. 131–148). London: Geological Society London Special Publications.

Webster, G. D., Becker, R. T., & Maples, C. G. (2005). Biostratigraphy, paleoecology and taxonomy of Devonian (Emsian and Famennian) crinoids from southeastern Morocco. *Journal of Paleontology, 79,* 1052–1071.

Weller, S., & Davidson, A. D. (1896). *Petalocrinus mirabilis* (n. sp.) and a new American fauna. *Journal of Geology, 4,* 166–173.

Wulff, J. I., & Ausich, W. I. (1989). Growth of the xenomorphic crinoid column (*Taxocrinus*, Late Mississippian). *Journal of Paleontology, 63,* 657–662.

Zenker, J. C. (1833). Organische Reste (Petrefacten) aus der Altenburger Braunkohlen-Formation etc. *Beiträge zur Naturgeschite Urwelt, Jena*, (pp. 1–67).