Multi-snail infestation of Devonian crinoids and the nature of platyceratid-crinoid interactions

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The well-known association of platyceratid snails and crinoids typically involves a single snail positioned on the tegmen of the crinoid host; this has led to the inference of coprophagy. Two specimens of the camerate crinoid *Arthroacantha* from the Middle Devonian Silica Formation of Ohio, USA, exhibit numerous snails on their tegmens. On one of these, 6 platyceratid juveniles of approximately equal size are found on the tegmen. On the second crinoid, the largest of 7 infesting platyceratids occupies the typical position over the anal vent while others are either superposed (tiered) upon it or are positioned elsewhere on the tegmen. These specimens illustrate that platyceratids (1) settled on crinoids as spat, (2) were not strictly coprophagous during life yet (3) benefited from a position over the anal vent.

Key words: Crinoids, Platyceratids, biotic interactions, Middle Devonian, Silica Formation, Ohio, USA.

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Introduction

Direct evidence of biotic interactions among extinct organisms is rarely preserved in the fossil record, and even when clear evidence for some type of an association exists, interpreting its exact nature proves difficult. One of the classic examples of a biotic interaction involves Paleozoic pelmatozoan echinoderms (including crinoids, blastoids, cystoids) and platyceratid snails (Boucot 1990). The occurrence of platyceratid snails preserved attached to the calyxes of crinoids was noted as early as the mid-19th century (Austin and Austin 1843; Yandell and Shumard 1847; Owen 1862; Meek and Worthen 1866). Even then this association was recognized as more than a mere taphonomic artifact: the snails and crinoids were interpreted to have been interacting during life. However, although many examples of platyceratids attached to crinoids are now known, spanning an interval from the Ordovician through the Permian (for a supposed Triassic example see Bandel 1992), not all questions about the nature of this interaction have been answered. In this study, I report two cases of Middle Devonian adult crinoids from the Silica Formation of Ohio (United States) infested by multiple juvenile platyceratids that provide additional clues as to the nature of the interaction. These examples illustrate that platyceratids (1) settled on crinoids as spat, (2) though they were not strictly coprophagous during life they (3) nevertheless benefited from a position over the anal vent.

The specimens described herein are housed in the University of Michigan, Museum of Paleontology (UMMP).

Review of platyceratid-crinoid association

Among the first reports and interpretations of the snail-crinoid fossils was that of Austin and Austin (1843: 73) who noted that: "Though the *Poteriocrinus* is chiefly met with in company with the *Productas*, other crinoids have been found with univalves inclosed [*sic*] within their rays in such a position as to leave but little doubt that a sudden death had overtaken them in the midst of their repast." The notion that the specimens represented crinoids caught in the act of feeding on snails persisted through the 1850s. It was not until Meek and Worthen (1866; 1868) noted the irregular shape of the snail margin forming a tight fit to the crinoid calyx and thus more than a brief interaction, that the idea of snails relying for food on crinoids was considered. By the 1880s (Wachsmuth and Springer 1881; Hinde 1885; Keyes 1888a, b), the fact that snails occupy a position over the crinoids' anal aperture led to the inference of coprophagy. Although the idea that platyceratids fed on crinoid waste and thus benefited from the association has persisted through the 20th century (e.g., Clarke 1921; Bowsher 1955; Lane 1978; Meyer and Ausich 1983; Boucot 1990), the question whether it was neutral, or detrimental to the crinoid has been debated; claims that it was beneficial have generally not been made, with the exception of Wood's (1980: 110) statement that "The host benefitted [*sic*] by receiving a competent elimination system . . .". Commensalism, which

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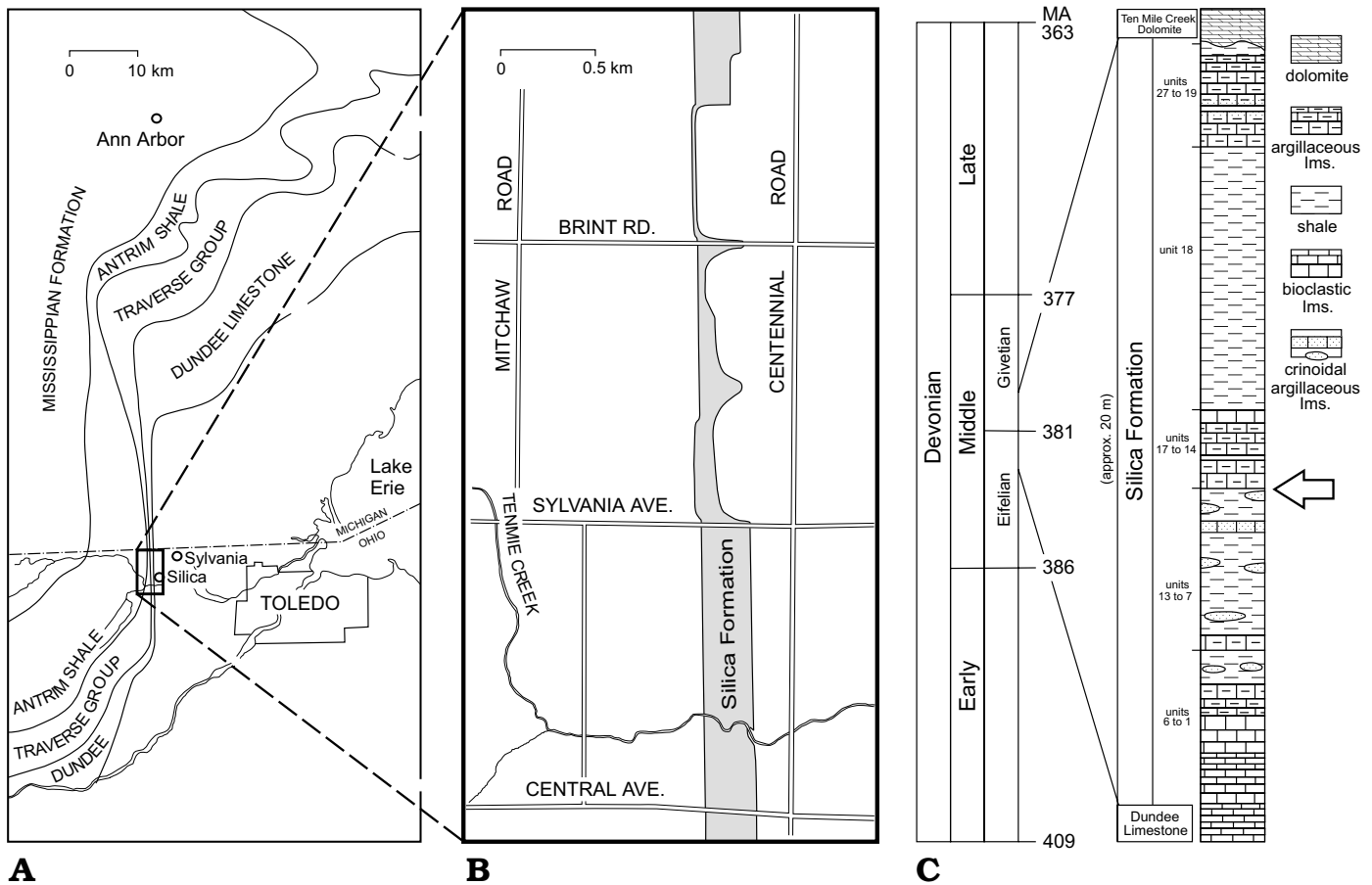http://www.paleo.pan.pl/acta/acta47/app47-133.pdf

Fig. 1. Middle Devonian Silica Formation of northcentral USA. **A**. Geologic map of southeastern Michigan and northcentral Ohio, showing some of the Devonian formations. **B**. Location of quarried Silica Formation exposures that are the source of most Silica Formation fossils. **C**. A summary stratigraphic section of the Silica Formation. Arrow points to Unit 13 from which the crinoid-platyceratid specimens were collected. Modified from Kesling and Chilman 1975 and Brett 1999.

assumes that the presence of the snail was neutral to the host because "there does not seem to be the slightest indication that the crinoid was in any manner inconvenienced by the attachment of the gastropod" (Keyes 1888a: 240), has generally been treated as the "null hypothesis", and is the interpretation most commonly invoked (Bowsher 1955; Lane 1978; Meyer and Ausich 1983). However, a detrimental effect of the snail on the crinoid, often described as parasitism, has been favored by several authors. For example, Clarke (1921: 64) viewed the presence of the elongate anal tube among some crinoids as an escape strategy from the "parasitic gastropod which must have been obnoxious to it as it interfered with the normal alimentary function". Others have suggested that the presence of the snail was detrimental to the host because (1) being "weighty" it affected its balance (Thomas 1919); (2) being gametophagous it affected its reproduction (Lane 1984); and (3) by drilling into the gut of its host, it may have fed on its food and gametes, in addition to its waste (Baumiller 1990). All these represent plausible hypotheses, but none have been tested explicitly; to date only one study (Rollins and Brezinski 1988), showing that snail-infested crinoids were smaller than uninfested ones, has directly addressed the issue of parasitism.

In addition to the problem of determining the exact nature of the relationship between the infesting snails and host crinoids, other aspects of the biology of these organisms remain elusive. For example, it is still unclear whether the snails were permanently affixed to the crinoid tegmen, whether they were capable of migrating from host to host, and whether they were obligate coprophages. The obligate nature of the snail-crinoid relationship and strict coprophagy were favored by Bowsher (1955). Meyer and Ausich (1983: 402), in a similar vein, argued that at least the Devonian individuals of *Platyceras* "were undoubtedly permanently affixed to the crinoid tegmen throughout their postlarval life".

However, the presence of numerous unattached platycertids has led several authors to favor a non-obligate relationship between snails and crinoids. Of course, such an interpretation also implies that the snails were not strictly coprophagous, being able to acquire their nutrients through other means. Thus Clarke (1908), noting the presence of many unattached Devonian and Carboniferous platyceratids, concluded that the relationship was non-obligate and that an individual was not committed to it throughout its life. Using similar logic, Thompson (1970: 224) concluded that the platyceratid *Cyclonema*, in addition to being coprophagous, could have been "an
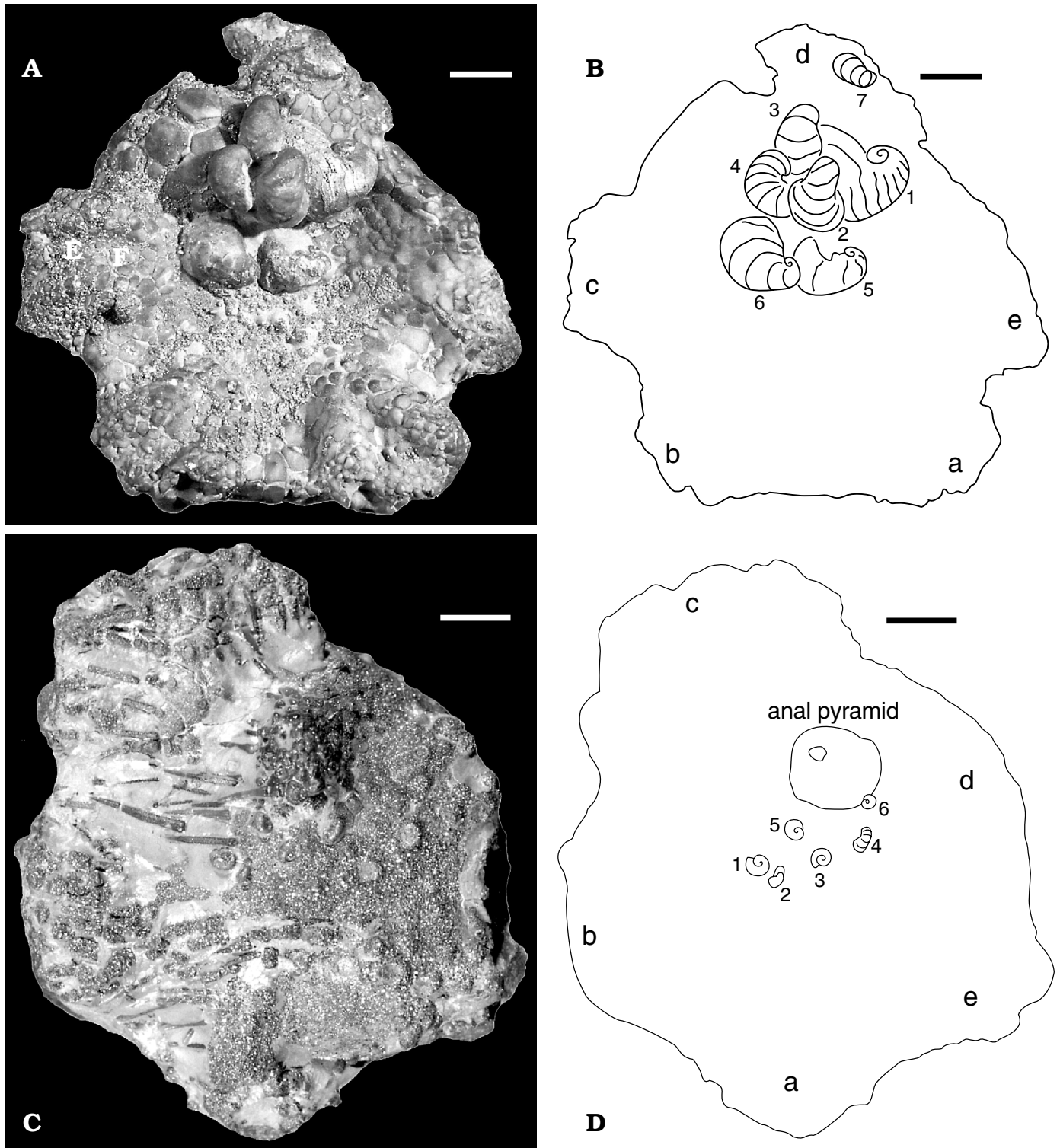
Fig. 2. Two specimens of *Arthroacantha* with platyceratid snails. **A**. A view of the tegmen of the larger of the two specimens (UMMP 68703) with 7 platyceratids. **B**. A sketch of A showing the orientation of the snails relative to the crinoid rays. **C**. A view of the tegmen of the smaller of the two *Arthroacantha* specimens (UMMP 68704*)* with six platyceratids. **D**. A sketch of C showing the orientation of the snails relative to the crinoid rays. Ray nomenclature following Ubaghs (1978). Scale bars 0.5 mm.

herbivore scraping the surface layer of mud or algae for detritus, or a filter feeder on plankton" and that its diet could have varied through ontogeny. Likewise, Rollins and Brezinski (1988: 216) suggested that "in some cases at least, platyceratids fed upon organic detritus of the incoming stream, either with or without coprophagy".
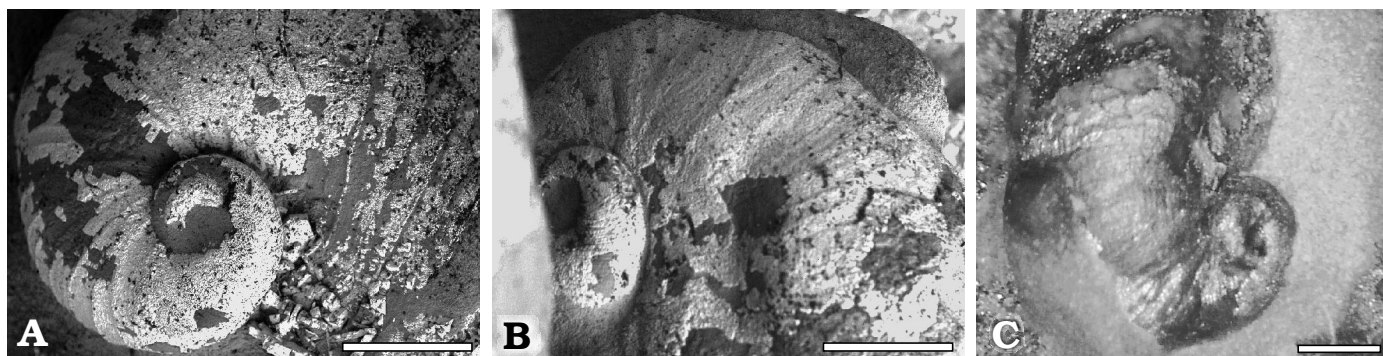
Fig.3.Examples of platyceratid specimens from the larger of the two *Arthroacantha* (UMMP68703).**A**. Early whorls of the largest specimen of *Platyceras (Platyceras) buccelentum* Hall found on the two crinoids and the one situated over the anal vent; it is snail 1 of Fig. 2B (SEM micrograph). **B**, **C**. Early whorls of specimen of *Platyceras* (*Platyceras*) *buccelentum* Hall from the larger of the two crinoids; it is snail 5 of Fig. 2B (B, SEM micrograph, note the closely spaced growth lines on the first whorl). Scale bar 1.0 mm.

The specimens described in this study provide new evidence that has a bearing on these issues.

Crinoids and platyceratids of the Silica Formation

Geologic and geographic setting.—The Silica Formation of Middle Devonian age is exposed in several active and abandoned quarries in northwestern Ohio and southeastern Michigan, along the southeastern margin of the Michigan Basin (Fig. 1A). Since the early part of the 20th century, the Silica Formation quarries, especially those just southwest of Sylvania, Lucas County, Ohio, have been favorite collecting localities for professionals and amateurs, and their rich faunas have been extensively studied (see Kesling and Chilman 1975 for review). The exposures of the Silica Formation in the vicinity of Sylvania strike approximately north-south being controlled by the trend of the Lucas County monocline. Nussmann (1975), who did a detailed study of the lithostratigraphy of the Silica Formation, recognized 27 units representing approximately 20 m of thick mudstones, thinner argillaceous limestones, and thin lenses consisting of crinoid and bryozoan debris (Fig. 1B). The Silica Formation, part of the Traverse Group, is overlain by the Ten Mile Creek Dolomite and underlain by the Dundee Limestone. It is of Late Eifelian–Early Givetian age (Cooper et al. 1942).

Crinoid occurrences.—The Silica Formation, known for its diverse fauna of bryozoans, brachiopods, corals, trilobites, and phyllocarid crustaceans, is also rich in echinoderms, including 2 blastoid, 17 crinoid, 1 starfish, 2 brittle star, and 1 edrioasteroid species (Kesling and Chilman 1975). Spectacular preservation of crinoids is associated with Nussmann's (1975) unit 13, which he describes as a "shale break" between crinoidal, argillaceous limestones of unit 12 and basal unit 14. In these units, often extensive lenses of skeletal

debris of bryozoans, crinoids, and brachiopods are intercalated within sparsely fossiliferous light gray calcareous shales. Most of the delicately preserved crinoid specimens, including the two specimens reported here, are found on "smothered bottoms" at the interface of unit 12 and the mudstones of unit 13. Kier (1952) interpreted this to mean rapid burial by mud. Likewise, Brett (1999) suggested burial by "mud-rich slurries . . . transported . . . by storm generated gradient currents" (p. 134). He argued that although the pelmatozoans were adapted for living in muddy substrates in relatively deep water and below normal wave-base, their occurrence in and around lenses of skeletal debris implies processes of taphonomic feedback.

The most common crinoid found in the Silica Formation is the monocyclic camerate *Arthroacantha carpenteri* (Hinde 1885). Typically the cups of these crinoids are found intact, preserved in three dimensions, with no or little distortion. The stalk is generally missing entirely and only the most proximal portions of the arms remain attached to the cup (Kesling and Chilman 1975: pls. 61, 62). *A. carpenteri* is characterized by the presence of articulating spines on the cup, tegmen, and arms and, although these are rarely preserved, ornamentation of pitted tubercles attests to their presence.

Crinoids and platyceratids.—In many instances *A. carpenteri* is found in association with platyceratid snails: in the Silica Formation the frequency of this association is high, 20 to over 30 percent of *A. carpenteri* were reported by Stewart (1927) to have attached snails. In most examples of this association the snail is found attached to the crinoid tegmen and it covers the anal vent that is elevated on an eccentrically placed conical pyramid composed of numerous plates. The margin of the snail aperture conforms exactly to tegmenal irregularities of *A. carpenteri* (Bowsher 1955: pl. 2).

Stewart (1927) described three species of platyceratids from the Silica Formation of Ohio, all members of the subgenus *Platyceras (Platyceras)*. These are *P. (Platyceras) buccelentum* Hall, 1879, *P. (Platyceras) carinatum* Hall, 1879, and *P. (Platyceras) rarispinum* Hall, 1879. Like other members of the subgenus, they are characterized by being irregularly
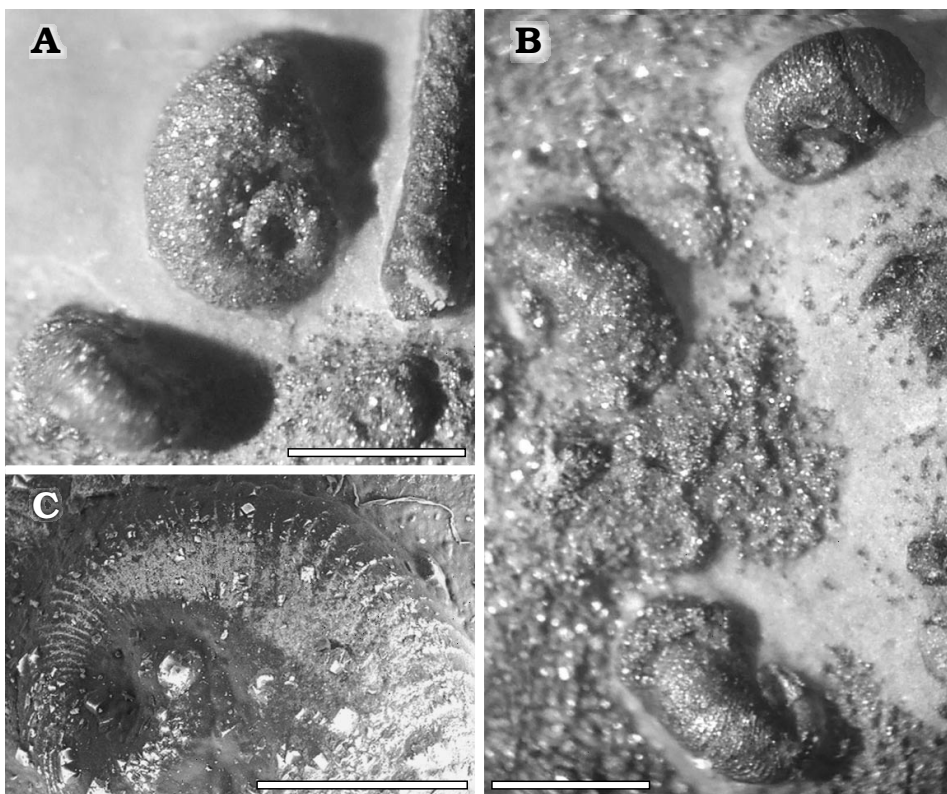
Fig. 4. Juvenile specimens of platyceratids from the smaller of the two *Arthroacantha* (UMMP 68704). **A**. Two juveniles of *Platyceras* (*Platyceras*) sp. At center of figure is snail 3 of Fig. 2D; lower left hand corner is snail 2 of Fig. 2D. Scale bar 1.0 mm. **B**. Three juveniles of *Platyceras* (*Platyceras*) sp. Upper right hand corner is snail 5 of Fig. 2D; center left is snail 3 of Fig. 2D; at bottom is snail 4 of Fig. 2D. Note the growth lines, especially clear on the bottom specimen. Scale bar 1.0 mm. **C**. SEM micrograph of the early whorl of the juvenile *Platyceras* (*Platyceras*) sp. Note the fine growth lines. It is snail 2 of Fig. 2D. Scale bar 0.5 mm.

capuliform, with the initial first and second whorls coiled. All three species have been found associated with crinoids (Kesling and Chilman 1975).

Whereas the *Arthroacantha*-platyceratid association is generally characterized by a single snail positioned on the crinoid tegmen, the two crinoid specimens described here are unusual in having multiple snails (Fig. 2). The larger of the two specimens of *Arthroacantha* (UMMP 68703), measuring 22 mm in cup height (base to first primibrach) and 35 mm in cup width (at the level of first primibrachs), has seven platyceratids attached to its tegmen (Fig. 2A, B). These capuliform snails have 2.5 to 3 whorls and range in maximum dimension from 5.3 to 8.7 mm (Fig. 3). The first two whorls remain in contact and expand at a uniform rate; beyond these, expansion rate increases and leads to open coiling. The outer lip, where visible, is smooth and lacks reentrants. The surface is marked by growth lines that change from straight to sinuous through ontogeny. In the first whorl, spacing between parallel growth lines increases to ca 50 microns. All seven specimens most likely belong to *P.* (*Platyceras*) *bucculentum* Hall; the lack of spines and of a pronounced dorsal ridge distinguish them from *P.* (*Platyceras*) *rarispinum* and *P.* (*Platyceras*) *carinatum*, the other platyceratids commonly found in the Silica Formation.

The snails are positioned either on or in close proximity to the anal pyramid. The largest snail is situated with its aperture over the anal vent. Its aperture, were it not obscured by other snails, shows no reentrants and conforms tightly to the crinoid tegmen. Three slightly smaller individuals are superimposed over the largest snail with their apertures partially overlapping its last whorl and partially the plates of the anal pyramid. Two other snails occupy a position near the center of the tegmen. The smallest snail (5.3 mm in maximum dimension) is found on the c-ray side (nomenclature following Ubaghs 1978), on the tegmen, and at the level of the arm base of the c-ray. The mode of attachment of the snails to the tegmen implies they are preserved in life position, while the articulated proximal brachials and cup of the crinoid indicate that the snails had been infesting a live host at the time of burial.

The smaller of the two specimens of *Arthroacantha* (UMMP 68704), measuring 16 mm in cup height and 25 mm in cup width, has six minute snails attached to its tegmen (Fig. 2C, D). It has an even greater amount of detail preserved than the larger specimen, including many of the ca. 5 mm long spines that characterize this taxon. The spines, though no longer articulated to the cup and tegmen, are in place, lying flat with their articular facets immediately adjacent to tubercles of the cup and tegmen where they originally attached. The six capuliform snails range in size from 1.1 to 1.7 mm in maximum dimension, and consist of 1 to 1.5 whorls (Fig. 4). Whorls are in contact and expand at a uniform rate. The outer lip is simple and smooth, showing no reentrants. Growth lines are straight and spacing between growth lines increases to ca. 50 µm in the first whorl. All features are consistent with the assignment of these snails to *Platyceras* (*Platyceras*), but SEM analysis of the early whorls of adult specimens of the Silica Formation platyceratids housed in UMMP revealed that all three species, *P.* (*Platyceras*) *bucculentum*, *P.* (*Platyceras*)

rarispinum and *P.* (*Platyceras*) *carinatum*, share similar shape and ornamentation; no distinguishing characteristics of juveniles could be identified. Therefore at present these specimens are not assigned to a species.

The mode of preservation of this specimen, especially the presence of the delicate spines and the exceedingly fine muddy matrix, indicate that the minute snails and their host were buried alive by a smothering event and that relative to each other virtually no post-mortem displacement has occurred.

Discussion

The Silica Formation specimens of platyceratids and crinoids allow us to re-examine some of the claims about the nature of this association and about the mode of life of platyceratids. The presence of 6 small, juvenile platyceratids on the smaller specimen of *Arthroacantha* confirms the notion (e.g., Kluessendorf 1983) that snails could settle on crinoids as spat and need not have searched for a host by crawling. Moreover, these specimens are of approximately the same size, indicating that they settled onto the tegmen as plankton/nekton at the same time and thus represent a single spat fall.

One can draw several conclusions about the mode of feeding of these snails. First, given that none of the juvenile platyceratids found on the smaller crinoid are associated with the anal vent, these snails were either not coprophagous as juveniles or were knocked off the vent prior to burial, which appears to be an unlikely scenario. Furthermore, of the seven snails on the larger crinoid, only one is positioned over the anal vent to take full advantage of access to the crinoid's digestive/excretory system. This suggests that adult platyceratids had a broader feeding repertoire than strict coprophagy and that an association with the anal vent was not obligatory for adults.

This represents a case of trophic polymorphism that finds a modern analogy in the capulid *Trichotropis cancellata*. Pernet and Kohn (1998) reported that this snail can function both as a suspension feeder and a kleptoparasite. The latter mode of feeding involves inserting the pseudoproboscis into the mouth of a suspension-feeding polychaete and intercepting particles captured by the host. Whether platyceratids also stole captured nutrients, fed on crinoid gametes, or excreta is unknown at present, but the multi-snail examples indicate they must have been capable of modes of feeding independent of the crinoid.

Since relying on the host for nutrients allows the snail to reduce its own metabolic costs, a snail that can employ such a feeding strategy should be at a metabolic advantage relative to its conspecifics that are excluded from the host. The distribution of snails on the larger crinoid allows us to test for such an advantage. The seven specimens found on the tegmen of this crinoid belong to the same species *P.* (*Platyceras*) *bucculentum* and show a small size range (Fig. 5A). However, the
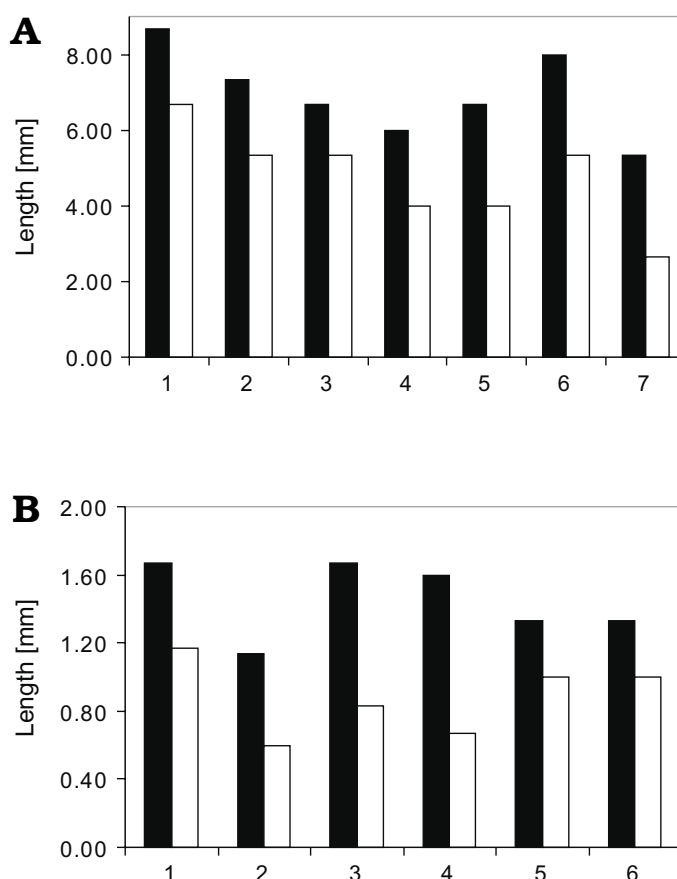

Fig. 5. Sizes of platyceratids found associated with *Arthroacantha*. **A**. Sizes of the 7 platyceratids found on the larger of two *Arthroacantha* specimens. Maximum length (solid bars) and length orthogonal to maximum length (open bars). Specimens numbered as in Fig. 2B. Note the narrow range of sizes and the greatest size of platyceratid that occupies the anal vent (1 of Fig. 2B). **B**. Sizes of the 6 juvenile platyceratids found on the smaller of two *Arthroacantha* specimens. Maximum length (solid bars) and length orthogonal to maximum length (open bars). Specimens numbered as in Fig. 2.

largest specimen is the one positioned directly over the anal vent and thus the one with direct access to the host. This snail may simply have been the first one to reach the host, and may be largest by virtue of its age. However, this would imply at least two spat falls, one of which would be represented by only the single, largest individual, and the other that occurred just subsequent to the first, by the six remaining snails, a less parsimonious alternative. It is more likely that all seven snails represent a single spat fall and are thus of the same age. If this inference is correct, the larger size is a reflection of greater rate of growth and is likely to be a direct consequence of access to crinoid waste, gut, gametes, or any combination of these, and shows the advantage of using the crinoid host as a nutrient source.

Finally, we can ask whether the multi-snail infestations of a host were a rarity, or whether the general absence of specimens illustrating this phenomenon is a taphonomic artifact. In the multi-snail examples of this study, snails occupy different parts of the tegmen and their simple apertures lack

reentrants, suggesting that they need not have been fully sedentary nor attached as firmly to their host as snails found directly over the anal vent. Therefore, they would have been more susceptible to dislodgment, and the rarity of multiple infestation examples (for two additional examples see pl. 63 in Kesling and Chilman 1975, and figs. 5–7 in Kluessendorf 1983) is likely a case of taphonomic bias.

Acknowledgments

References

Austin, T. and Austin, T. 1843–1846. *Monograph on Recent and Fossil Crinoidea*. 128 pp. Bristol.

Bandel, K. 1992. Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritomorpha (Gastropoda). *Palaontologisches Zeitschrift* 66: 231–240.

Baumiller, T.K. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontology* 33: 743–748.

Boucot, A.J. 1990. *Evolutionary paleobiology of behavior and coevolution*. xxiii+725 pp. Elsevier, Amsterdam.

Bowsher, A.L. 1955. Origin and adaptation of platyceratid gastropods. *University of Kansas, Paleontological Contributions, Mollusca* 5: 1–11.

Brett, C.E. 1999. Middle Devonian Arkona Shale of Ontario, Canada, and Silica Shale of Ohio, USA. *In*: H. Hess, W.I. Ausich, C.E. Brett, and M.J. Simms (eds.), *Fossil Crinoids*, 129–134. Cambridge University Press, Cambridge.

Clarke, J.M. 1908. The beginnings of dependent life. *Bulletin of the New York State Museum* 121: 1–28.

Clarke, J.M. 1921. *Organic Dependence and Disease: Their Origin and Significance*. 113 pp. Yale University Press, New Haven.

Cooper, G.A., Butts, C., Caster, K.E., Chadwick, G.H., Goldring, W., Kindle, M., Kirk, E., Merriam, C.W., Swartz, F.M., Warren, P.S., Warthin, A.S., and Willard, B. 1942. Correlation of the Devonian sedimentary formation of North America. *Geologic Society of America Bulletin* 53: 1729–1794.

Hall , J. 1879. *Palaeontology of New York (State). Natural History Survey 5, pt. 2, No 1*. 492 pp. C. Van Benthuysen, Albany.

Hinde, G.J. 1885. Description of a new species of crinoids with articulated spines. *The Annals and Magazine of Natural History 5th Series* 15: 157–173.

Kesling, R.V. and Chilman, R.B. 1975. Strata and megafossils of the Middle Devonian Silica Formation. *University of Michigan Museum of Paleontology, Papers on Paleontology* 8: 1–408.

Keyes, C.R. 1888a. On the attachment of *Platyceras* to Paleocrinoids, and its effects in modifying the form of the shell. *American Philosophical Society Proceedings, Transactions* 25: 231–243.

Keyes, C.R. 1888b. The sedentary habits of *Platyceras*. *American Journal of Science* 36: 269–272.

Kier, P.M. 1952. Echinoderms of the Middle Devonian Silica Formation of Ohio. *Contributions from the Museum of Paleontology University of Michigan* 10: 59–81.

Kluessendorf, J. 1983. Observations on the commensalism of Silurian platyceratid gastropods and stalked echinoderms. *Wisconsin Academy Sciences, Arts and Letters* 71: 48–55.

Lane, N.G. 1978. Mutualistic relations of fossil crinoids. *In:* R.C. Moore and C. Teichert (eds.), *Treatise on Invertebrate Paleontology, Part T*, T345–T347. Geological Society of America and University of Kansas, Lawrence.

Lane, N.G. 1984. Predation and survival among inadunate crinoids. *Paleobiology* 10: 453–458.

Meek, F.B. and Worthen, A.H. 1866. Radiata, Echinodermata, Crinoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1866: 251–275.

Meek, F.B. and Worthen, A.H. 1868. Geology and Palaeontology, pt 2, Palaeontology of Illinois. *Illinois Geologic Survey* 3: 289–565.

Meyer, D.L. and Ausich, W.I. 1983. Biotic interactions among Recent and fossil crinoids. *In*: M.F.S. Tevesz and P.L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, 377–427. Plenum, New York.

Nussmann, D.G. 1975. Paleoecology and pyratization. *In*: R.V. Kesling and R.B. Chilman (eds.), Strata and megafossils of the Middle Devonian Silica Formation. *University of Michigan Museum of Paleontology, Papers on Paleontology* 8: 173–220.

Owen, R. 1862. *Report of a Geological Reconnaissance of Indiana Made During the Years 1859 and 1860*. 368 pp. Indianapolis.

Pernet, B. and Kohn, A.J. 1998. Size-related obligate and facultative parasitism in the marine gastropod *Trichotropis cancellata*. *Biological Bulletin* 195: 349–356.

Rollins, H.B. and Brezinski, D.K. 1988. Reinterpretation of crinoid-platyceratid interaction. *Lethaia* 21: 207–217.

Stewart, G.A. 1927. Fauna of the Silica Shale of Lucas County. *Geological Survey of Ohio, Fourth Series, Bulletin* 32: 1–76.

Thomas, A.O. 1919–1920. Echinoderms of the Iowa Devonian. *Iowa Geologic Survey, Annual Reports* 29: 385–552.

Thompson, E.H. 1970. Morphology and taxonomy of *Cyclonema* Hall (Gastropoda), Upper Ordovician, Cincinnatian Province. *Bulletins of American Paleontology* 58: 219–283.

Ubaghs, G. 1978. Skeletal morphology of fossil crinoids. *In:* R.C. Moore and C. Teichert (eds.), *Treatise on Invertebrate Paleontology, Part T*, T58–T216. Geological Society of America and University of Kansas, Lawrence.

Wachsmuth, C. and Springer, F. 1881. Revision of the Paleocrinoidea, pt 2. Family Sphaeroidocrinidae, with the sub-families Platycrinidae, Rhodocrinidae, and Actinocrinidae. *Academy Natural Sciences Philadelphia, Proceedings* 1881: 175–411.

Wood, G.D. 1980. Coprolite, urolite, and "vomite". *Maledicta* 4: 109–115.

Yandell, L.P. and Shumard, B.F. 1847. *Contributions to the Geology of Kentucky*. 36 pp. Prentice and Weissinger, Louisville.