OLDEST RECORD OF PEDUNCULAR ATTACHMENT OF BRACHIOPODS TO CRINOID STEMS, UPPER ORDOVICIAN, OHIO, U.S.A.
(BRACHIOPODA; ATRYPIDA; ECHINODERMATA; CRINOIDEA)

MICHAEL R. SANDY
Department of Geology, University of Dayton, 300 College Park, Dayton, Ohio 45469-2364, U.S.A.

A HAND-SPECIMEN, bedding-plane sample of limestone (wackestone) from the Upper Ordovician Waynesville Formation has numerous brachiopod specimens (at least 60) exposed on its surface (Figure 1). The brachiopods have been identified as members of the atrypid species *Zygospira modesta* (Say in Hall) 1847 (the type species of the genus *Zygospira* Hall, 1862) and are concentrated in an area measuring approximately 9 cm x 2 cm. A wide range of specimen sizes from juvenile to adult are present and are believed to represent a brachiopod life-assemblage (Figure 2).

The slab was collected by I. H. Harris from the vicinity of Waynesville, Warren County, southwestern Ohio, a town located approximately 27 km SSE of Dayton, Ohio. The exact locality from which the slab was collected is not specified on the specimen label, but fine specimens of marine invertebrate fossils, including crinoids and brachiopods of the species *Zygospira modesta*, can be found along both U.S. Routes 42 and 73 near Waynesville. It is highly likely that the slab is from the Waynesville Formation, the type locality being in the vicinity of Waynesville, Ohio. Excavations during the 1970s for the dam and emergency spillway of Caesar Creek Reservoir, approximately 5 km SE of Waynesville, yielded some well-preserved crinoids from laterally equivalent Upper Ordovician sediments (Schumacher and Ausich, 1983; Schumacher, 1986).

**Environmental setting.**—Storm-sedimentation has been identified as a significant component in the environmental history and sedimentology of the Upper Ordovician (Cincinnatian) rocks of southwestern Ohio, southeastern Indiana, and northern Kentucky (e.g., Tobin, 1982). The Waynesville Formation recently was interpreted by Holland (1993) as an offshore, shale-dominated lithofacies with uncommon distal storm beds. This lithofacies contains a body-fossil assemblage of small, thin-shelled brachiopods (characterized by *Onniella*, an orthid), ramose bryo-ozoans, trilobites, crinoids, and graptolites. The presence of multi-element skeletons of trilobites and crinoids that commonly are articulated was taken as an indication of a quiet, deep-water environment (Brett and Baird, 1986; Brett and Speyer, 1990; Holland, 1993). It is likely that storm-generated distal turbidites and subsequent rapid sedimentation were crucial to the preservation of the juxtaposed brachiopods and crinoid stem discussed herein. Alternatively, quiet-water sedimentation could account for the phenomenon observed, but the brachiopods probably would be more dispersed about the crinoid stem as the brachiopod pedicles rotted; the ossicles of the crinoid stem would also be expected to show more signs of disarticulation.

**Brachiopod attachment surface.**—Attachment of brachiopods to hard substrates by the use of a pedicle is extremely common in the 500-million-year-plus history of the articulate brachiopods (e.g., Rudwick, 1970). This is the inferred mode of attachment for *Zygospira* to the crinoid stem discussed herein. *Zygospira* has a small pedicle opening (foramen). However, a pedicle foramen does not necessarily indicate that a brachiopod is attached to a hard substrate throughout life by a functional pedicle (see Richardson, 1981).

A portion of an articulated crinoid stem, referred to the monobathrid camerate *Pycnocrinus* sp., is exposed in the center of and parallel to the long axis of this *Zygospira* concentration (Figures 1 and 2). These brachiopods circumscribe the crinoid column, being present in the rock both below, above, and at the sides of the column. No evidence of the brachiopod pedicle-attachment scar *Podichnus* Bromley and Surlyk, 1973, was seen on the crinoid ossicles, but not all brachiopod pedicles had the ability to etch calcareous substrates.

**Paleoecological significance.**—This slab records the paleoecological phenomenon of brachiopods attached by pedicles in high density to a crinoid stem. This is perhaps no surprise—several species of brachiopods, including dense clusters of specimens of *Zygospira modesta*, have been recorded attached to bryozoans in the Upper Ordovician of southwestern Ohio (Richards, 1972). However, direct evidence of attachment of articulate brachiopods to other organisms is rare in the fossil record. Brett and Eckert (1982) recorded the rhychnonellid brachiopod *Steigerhynchus* as attached to the stem and root systems of the crinoid *Eucalyptocrinides* from the Silurian Rochester Shale of Ontario, Canada. However, in contrast to the Ordovician example described herein, the Silurian example apparently had a much lower density of brachiopods.

The *Pycnocrinus* crinoid specimen is believed to have lived as part of the Ordovician benthos, attached to the seafloor. Subsequently *Zygospira* spat settled on the crinoid stem and grew, utilizing it as a hard substrate for peduncular attachment. Successive spawnings of brachiopods probably settled in close proximity to their elders that previously had attached to the crinoid and adjacent hard substrates (e.g., other crinoids based on observations herein; brachiopods and bryozoans in Richards, 1972).

The crinoid stem is largely intact and probably was displaced and buried by a storm-generated current, allowing the crinoid stem and surrounding brachiopods to be preserved close to where they lived. No trace of the crinoid's calyx or holdfast are visible. Either the crinoid was broken into a number of separate pieces during storm-sedimentation, or a more complete specimen was broken into separate pieces before the slab was collected.

An attempt to trace the crinoid stem using X-Rays was not successful; the bottom surface of the slab is irregular and this did not help the resolution of the technique.

**Other examples of Ordovician brachiopods on crinoid stems.**—Specimens of *Zygospira modesta* apparently attached in sporadic clusters to the stems of crinoids, *Locrinus subcrassus*, are known from the Corryville Formation (Upper Ordovician), Cincinnati area, Ohio and Florence, Kentucky (University of Cincinnati Geology Museum specimen numbers 46014, 46015, and D. L. Meyer Collection). Brachiopods are known on crinoid stems from the Upper Kope Formation (Upper Ordovician) of the Cincinnati area (Sharon Diekmeyer, personal commun.).

In addition, crinoid stems with attached inarticulate brachiopods representing the genera *Petrocrania* and *Trematis* are known in the Fairview Formation (Upper Ordovician) of the Cincinnati region (Jack Kallmeyer, personal commun.).

**Brachiopods and crinoids.**—There appear to be at least three
methods by which different articulate brachiopods attached themselves to crinoids, representing the development of secondary tiering in this group (see Bottjer and Ausich, 1986, p. 409):

1) Direct cementation of the pedicle valve (Unklesbay and Niewoechner, 1959, and references therein; observed in juvenile stage, Grant, 1963).

2) Curved spines along the hingeline that wrap around crinoid stems (and other objects) as in some Late Paleozoic productid brachiopods (e.g., Etheridge, 1876; Unklesbay and Niewoechner, 1959; Muir-Wood and Cooper, 1960; Grant, 1963, 1968, 1981; Brunton, 1966; Meyer and Ausich, 1983; Boucot, 1990). Meyer and Ausich (1983) considered this an interaction between crinoids and brachiopods within a Devonian to Permian time frame.

3) By pedicle attachment (Brett and Eckert, 1982; also herein). It is likely that specimens of Zygospira lived in a variety of orientations with respect to a given crinoid stem. Grant (1963) concluded that some individuals of Linoproductus attached by spines to crinoids had lived with their pedicle valve uppermost and some with their pedicle valve lowermost.

Figure 1—Bedding-plane view of limestone containing specimens of Zygospira modesta (Say in Hall) concentrated in an aligned group. Articulated crinoid ossicles, referred to Pycnocrinus sp., are visible in the bottom half of the figure. Waynesville Formation, Upper Ordovician, from Waynesville, Warren County, Ohio. Disarticulated crinoid ossicles, isolated specimens of Zygospira, and fragmented bryozoans are scattered on the bedding plane, but are not obviously part of the crinoid-brachio pod cluster described herein. I. H. Harris Collection. USNM 40485, ×1 (scale in upper left corner is in mm.)

Figure 2—Detail of Figure 1 showing more clearly the clustering of specimens showing a range of growth sizes of Zygospira modesta (Say in Hall) in an elongate-aligned group, presumably around an articulated crinoid stem, referred to Pycnocrinus sp. Locality and horizon as for Figure 1. USNM 40485, ×2.4 (scale in upper left corner is in mm.)
On a single slab of rock from the Rochester Shale (Silurian), Ontario, Canada, Brett and Eckert (1982) recorded corals, brachiopods, and crinoids as utilizing crinoid columnals as attachment substrates. The rhynchonellid brachiopod Stegerhynchus appears to have attached pedically to the stems and root systems of the crinoid Escalypocrinites (Brett and Eckert, 1982, p. 7, 10). It would appear from the block of Rochester Shale, however, that the density of rhynchonellids attached to crinoids was very low and probably did not rival the high density for the specimens of Zygospira from the Ordovician (Brett and Eckert, 1982, figs. 3, 4C; Figures 1, 2 herein). Brett (1991, p. 320, fig. 12C) also recorded specimens of the rhynchonellid Stegerhynchus from the Silurian Waldron Shale of Indiana that had attached to Cornellites worm tubes encrusting on a gastropod, Natococemia, which in turn may have been communal on a crinoid.

Concluding remarks. — Brett and Eckert (1982, p. 16) considered that the Silurian rhynchonellid Stegerhynchus probably attached near the base of crinoid stems at the sediment–water interface, maintaining, in effect, their “normal” living position, anchored by a pedicle to a hard substrate on the sea floor. The Ordovician examples of specimens of Zygospira pedically attached to crinoid stems are the oldest record of this phenomenon. This elevated the brachiopods above the sea bottom and the specimens of Zygospira became part of the suspension-feeders raised above the seafloor, developing tiering (“secondary tierers” of Bottjer and Ausich, 1986). This also would be a consequence of attachment of brachiopods, including Zygospira, to bryozoan colonies, as reported by Richards (1972) from contemporaneous Late Ordovician sediments (there are other examples of this phenomenon, e.g., Early Ordovician, David Harper, personal commun.; Silurian, Wright, 1968).

In the case of brachiopods attached to crinoids in the Ordovician, this would have the possibility of elevating brachiopods a few–to several-tens of centimeters above the sea floor (see Bottjer and Ausich, 1986, fig. 1).

Material. — A single slab of limestone (wackestone) containing at least 60 specimens of the atypid brachiopod Zygospira modesta (Say in Hall), and an articulated crinoid stem, referred to Pycnoocrinus sp., Wayneville Formation, Upper Ordovician, from Wayneville, Warren County, Ohio. I. H. Harris Collection, National Museum of Natural History, Smithsonian Institution, Washington, D.C., catalog number USNM 40485.

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REFERENCES


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