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SUBLETHAL AND LETHAL INJURIES OF PENNSYLVANIAN CONULARIIDS FROM OKLAHOMA

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ABSTRACT—Many specimens of the conulariid *Paraconularia magna* (Ries) from the Tackett Formation (Upper Pennsylvanian, Missourian) of Oklahoma exhibit repaired or unrepaired injured exoskeletons. Scalloped, cleft, and embayed patterns are interpreted to be repaired sublethal damages produced by unknown events or organisms. Punctures, which are the first reported in conulariids, were not followed by exoskeletal repair and were probably lethal. Cladodont sharks are implicated as possible predators of *P. magna* because of a close correspondence in size and pattern between the dentition of some sharks and the punctures preserved in conulariid exoskeletons.

INTRODUCTION

DURING RECENT years, much new information on conulariid paleobiology has been published. Notable papers include those by Babcock and Feldmann (1986a, 1986b) and Babcock et al. (1987a, 1987b). Conulariid remains are associated with those of various organisms indicative of normal marine conditions (Moore et al., 1952; Babcock and Feldmann, 1986a). Although not typically a major component of fossil assemblages, some conulariids are abundant, or even dominant, in a few special settings. Examples include the Ordovician iron-ore beds of Czechoslovakia (Barrande, 1867; Bouček, 1928), the Devonian "*Conularia* shales" of Bolivia (Steinmann *in* Ulrich, 1892; Babcock et al., 1987b, 1987c), and some Pennsylvanian dark-gray or black shales of the North American Midcontinent (Sinclair, 1948; this paper).

The purpose of this study is to document injuries in individuals of *Paraconularia magna* (Ries, 1949) from two Pennsylvanian-age dark-gray shales of Oklahoma. The injuries fall into two categories: 1) healed injuries similar to those described by Babcock et al. (1987a); and 2) injuries that were not healed and are considered to have been fatal to the conulariids.

LOCALITIES AND MATERIAL

The conulariids were collected from two localities in the Tackett Formation of the Coffeeville Subgroup of the Skiatook Group (Bennison, 1985) in east-central Oklahoma. All specimens are identified as *Paraconularia magna* (Ries, 1949; see also Branson, 1965), and those from locality 1 are topotypes.

Locality 1 is in the Lower Tackett Shale Member (Bennison, 1985) exposed in the bed of an abandoned road approximately 2.1 km east of Oklahoma State Highway 56 in Okfuskee County (north section line of sec. 3, T12N, R10E, Okfuskee 7½′ quadrangle). Previous to the work of Bennison (1985), Pennsylvanian strata at this locality were correlated with the Seminole Formation (Ries, 1949, 1954a, 1954b; Branson, 1965). Specimens from this locality that were provisionally identified as *Calloconularia strimplei* Sinclair, 1952, by Hemish (1986) were examined by the authors and are here reassigned to *P. magna*. These specimens were not, however, included in counts of specimens from this locality. Surface collecting yielded 427 conulariids, as well as some bivalves, brachiopods, and ammonoid cephalopods, notably *Pennoceras* sp., *Paraschistoceras* sp., and *Glaphyrites* sp.

Locality 2 is in the Upper Tackett Shale Member (Bennison, 1985) exposed in a glade, probably an abandoned oil well pad, about 1.8 km south and 1.0 km west of Haydenville in Okfuskee County (NE¼, NE¼, NW¼, sec. 29, T13N, R10E, Mason 7½′ quadrangle). At this locality, 327 conulariids were found loose at the surface and 105 were extracted by organic-solvent techniques (see Mapes and Mapes, 1982) from a 29.5-kg in situ shale sample. This sample was taken from a 10-cm-thick interval above which numerous conulariids were found lying loose on the surface. The shale was virtually lacking in other fossils.

Of the 859 examined conulariids, most were not significantly disarticulated or crushed except by inferred predation. The great abundance of nearly intact, inflated specimens suggests that these gregarious organisms lived in dense local clusters (see Babcock and Feldmann, 1986a, 1986b) that were rapidly buried by sediments before much disarticulation of the exoskeleton could take place.

Figured specimens are deposited in the U.S. National Museum of Natural History (USNM), Washington, D.C.

SUBLETHAL AND LETHAL INJURIES

Sublethal injuries.—Healed injuries among conulariids were largely unstudied previous to the work of Babcock et al. (1987a). Those authors recognized three types of healed injuries on conulariid exoskeletons and classified them as scalloped, cleft, and embayed, following a scheme developed by Alexander (1986) for brachiopod shells. Exoskeletons healed subsequent to breakage indicate that the injuries were not lethal. Scalloped patterns are small, truncating one or a few rods, and probably resulted from minor chipping or crushing of the exoskeleton at the aperture. Rods added later are arranged normally, although some may show a small change in angle (Figure 1.2, 1.7). Some such injuries may have been caused by crowding of individuals or by durophagous predators. Cleft patterns are subtriangular, generally on two adjacent faces, and formed when incisions were closed by the secretion of integument or integument and rods (Figure 1.4). Embayed patterns have smooth or jagged outlines and formed after large portions of exoskeleton were lost. Many rods are truncated and repairs to the exoskeleton were made using integument with or without rods (see Babcock et al., 1987a, fig. 9). Both cleft and embayed injuries are probably the result of sublethal predation in most known examples.

Among the 859 specimens of *Paraconularia magna* from the two localities, 160 (18.6%) have identifiable scalloped injuries, eight (0.9%) have cleft injuries, and two (0.2%) have embayed injuries (Table 1). Many specimens have more than one scalloped injury and some show multiple types of injuries. Because injured conulariids with weakened exoskeletal structures are not as likely to be preserved as uninjured ones, these figures are regarded as minimum numbers of injured specimens. Rare specimens have incomplete rods that were added after scalloped breaks were inflicted (Figure 1.7). Similar malformations in other organisms, which partially resulted from infection of secretory

FIGURE *1*—Topotype specimens of *Paraconularia magna* (Ries) from the Tackett Formation (Pennsylvanian, Missourian) of Okfuskee County, Oklahoma, showing punctures. *1*, corner view, *2*, major face of specimen showing zig-zag trend of punctures; puncture on major face is superimposed over pre-existing scalloped injury (arrow), both ×3; *3*, detail of puncture on major face, ×4.5, USNM 430569. *4*, specimen showing puncture at corner superimposed on pre-existing cleft injury (arrow), ×3; *5*, detail of puncture, ×4.5, USNM 430570. *6*, *7*, corner view and major face of irregularly crushed specimen showing multiple punctures; pre-existing scalloped injuries (arrows) in apertural region show unusual repair, USNM 430571, ×3. *8*, *9*, corner view and minor face of specimen showing zig-zag trend of punctures, ×3, USNM 430572.

tissues, were described as neoplasms by Šnajdr (1978). Previously, neoplasms were observed in only one conulariid, a specimen of *Paraconularia margaritae* Babcock, 1988, from the Permian of Devon Island, Canada (Babcock, 1988).

Lethal injuries.—Sixty-eight specimens (7.9%) of *Paraconularia magna* have injuries that do not fall into any of the categories recognized by Babcock et al. (1987a). These injuries are here termed punctures and closely resemble punctures in a nautiloid body chamber described by Mapes and Hansen (1984). Punctures are conical depressions having circular to nearly elliptical outlines (Figure 1.1–1.9). Fracturing of the exoskeleton is nearly annular (Figure 1.3) to irregular (Figure 1.5), and seems to be controlled partly by the thickness of the exoskeleton and the positions of the rods. Punctures are usually less than 3 mm in maximum dimension (Figure 1.3), but can be larger, especially if present in the corner region (Figure 1.5). The largest observed individual injury, which is centered in a corner groove, has maximum and minimum dimensions of 5.5 and 3.5 mm, respectively. In addition to the 68 conulariids that have punctures, one body chamber of an orthoconic nautiloid from locality 2 also shows similar punctures.

Punctures in conulariids were most likely formed by inward crushing of the exoskeleton. The depressions vary in depth and have remains of fragmented exoskeleton at their bases (Figure 1.1–1.9). Because exoskeletal repair was not observed in any specimen having punctures, it is inferred that punctures represent lethal injuries. If several punctures are present on one specimen, the injuries may have a roughly zig-zag pattern when traced across the four faces of the conulariid exoskeleton (Figure 1.1, 1.2, 1.8, 1.9). The regular shape and pattern of these exo-

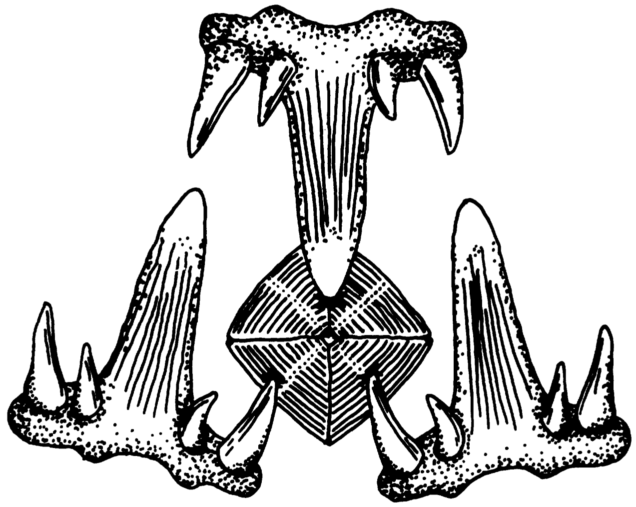

FIGURE 2—Speculative diagram showing the inferred positions of cladodont shark teeth as they may have bitten a small specimen of *Paraconularia magna* (Ries), based upon punctures preserved on USNM 430569.

skeletal breaks rules out the possibility that they are the result of postmortem breakage. Also, no described form of skeletal boring shows crushed skeletal material from the prey within the hole.

The punctures on specimens of *Paraconularia magna* were probably inflicted by the teeth of cladodont sharks (Figure 2). The morphology, pattern, and size of the punctures closely resemble those shown on a Pennsylvanian nautiloid described by Mapes and Hansen (1984). Based on the size and pattern of punctures, those authors argued that the cladodont *Symmorium reniforme* Cope, 1893, was the most likely predator. *Symmorium* has also been implicated in lethal attacks on other Pennsylvanian nautiloids (Boston et al., 1987) and on Pennsylvanian ammonoids (Sims et al., 1987). Evidence of predation on Paleozoic invertebrates by other chondrichthyans is described by Brunton (1966), Moy-Thomas and Miles (1971), and Alexander (1981, 1986). The morphology of the punctures, the relatively close spacing between some of them, and their variable depths on conulariids from the Tackett Formation are consistent with an interpretation involving crushing between the teeth of a cladodont, possibly *Symmorium* (see for examples Zangerl, 1981; Williams, 1985). Variable depths of punctures in *P. magna* may be due to wounds inflicted by cusps of different heights and teeth having various positions in the tooth families. The zig-zag trend of punctures is attributed to the positions of individual teeth as well as to lateral cusps that are directed at angles different from those of the central cusps.

The number of punctures present on specimens is variable from one to at least 18. All of the specimens are incomplete, however, so more punctures may have originally been present. The distances between the centers of the punctures are also quite variable, ranging from about 2 mm to more than 10 mm. Often, several closely spaced punctures resulted in irregular skeletal crushing (Figure 1.6, 1.7). Some punctures are superimposed upon fractured areas left by preceding bites (Figure 1.6). Ordinarily in conulariids, exoskeletal collapse involves lengthwise breakage at or near the corner grooves or midlines (see for examples Babcock and Feldmann, 1986a, 1986b; Babcock et al., 1987b, 1987c), but specimens of *Paraconularia magna* that are interpreted to have been attacked by sharks show breakage patterns that have no relation to the positions of the corner grooves or midlines. Some of these fractures may have been enhanced during compaction.

Cladodont sharks were the dominant identifiable predators on *Paraconularia magna.* Of course, most lethal attacks probably resulted in fragmented or consumed exoskeletons, thus rendering the identification of other predators impossible. It is speculated that, under the depositional conditions of the Tackett Formation, conulariids lived clustered in locally dense thickets. Sharks that preyed upon these conulariids could have scooped up large mouthfuls of prey. The flexible stalks (Babcock and Feldmann, 1986a, 1986b; Babcock et al., 1987b, 1987c) of the conulariids readily gave way and piercing of the exoskeleton probably ruptured membranes or muscle tissues by which the internal organs were held in place. Specimens of *P. magna* showing evidence of multiple bites are common, and many such specimens are irregularly crushed.

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TABLE 1—Frequency of injury among specimens of *Paraconularia magna* (Ries) from the Tackett Formation (Pennsylvanian, Missourian), Okfuskee County, Oklahoma.

	Locality 1, surface sample	Locality 2, surface sample	Locality 2, in situ sample	Total
Number of specimens	427	105	327	859
Number scalloped only	51	51	30	132
Number cleft only	2	3	1	6
Number embayed only	0	1	1	2
Number punctured only	32	5	1	38
Number cleft and punctured	2	0	0	2
Number scalloped and punctured	24	4	0	28
Total damaged	111	64	33	208

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