Teratology and pathology of some Paleozoic conulariids

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Conulariids exhibiting various pathologies and teratological conditions have been examined from Paleozoic rocks of North America, South America, Europe, and Africa. Published examples of teratological conditions in conulariids have been reviewed. To these cases we add a specimen of *Paraconularia missouriensis* (Swallow) from the Mississippian of Ohio which possesses six faces. The supposed three-sided conulariid species *Conularina triangulata* (Raymond) is based upon a specimen which is not a conulariid. This genus is removed from the phylum Conulariida and is considered *incertae sedis.* Pathologies include injuries to the exoskeleton which are grouped into patterns termed scalloped, cleft, and embayed. Scalloped injuries represent minor chipping at the aperture of the conulariid exoskeleton, and may have occurred accidentally or through predation. Cleft and embayed injuries, found only on post-Silurian taxa, indicate that conulariids suffered severe sublethal attacks more frequently after the rise of several types of durophagous predators in the middle Paleozoic. Some middle and late Paleozoic conulariid species strengthened the exoskeleton, perhaps to resist predation. Regeneration of injured integument or rods has occurred in conulariids exhibiting damaged exoskeletons. □ *Conulariid, teratology, pathology, predation, Ordovician, Devonian, Mississippian, Bolivia, New York, Ohio.*

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The Conulariida is a phylum (Babcock & Feldmann 1986a) of marine invertebrates known from Ordovician through Triassic rocks mostly through remains of elongate, pyramidal exoskeletons of calcium phosphatic composition. The conulariid exoskeleton comprises a four-sided, flexible calcium phosphate and protein integument supported by more rigid, articulated calcium phosphate rods (Babcock & Feldmann 1986a; Feldmann & Babcock 1986). Although there may be a wide range of preservational styles resulting from post-mortem events, few conulariids have been described which exhibit structural abnormalities attributable to genetic or life history events.

The purpose of this paper is to review published examples of teratological conditions in conulariids from Paleozoic rocks, to describe a remarkable six-sided conulariid interpreted as teratological, and to describe and classify examples of healed injuries in conulariids. Our examples have been drawn from an examination of over 5000 conulariids from Ordovician through Permian rocks of North America, South America, Europe, and Africa. Study of one teratological specimen indicates that, although conulariids possessed a weakly bilaterally symmetrical exoskeleton, they may have functioned as radially symmetrical organisms in life. Examination of specimens exhibiting repaired injuries indicates that conulariids had the ability to repair damaged exoskeletal material. From about the Middle Devonian on, shell-crushing and shell-chipping predators may have exerted considerable control on the morphology of conulariids. Exoskeletal strengthening devices are common among middle and late Paleozoic forms and they may have aided in deterring predation.

Specimens which are either figured or referred to in this paper are deposited in the following institutions: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM), Cleveland Museum of Natural History, Cleveland, Ohio (CMNH), Field Museum of Natural History, Chicago, Illinois (FMNH UC, FMNH PE), Geological Survey of Canada, Ottawa, Ontario (GSC), McGregor Museum, Kimberley, Republic of South Africa (MGM), U.S. National Museum of Natural History, Washington, D.C. (USNM), and Yacimientos Petroliferos Fiscales Bolivianos, Centro de Tecnología Petrolera, Santa Cruz, Bolivia (YPFB).

Teratological conulariids

Previous studies. – Few examples of presumed teratological conulariids have been recorded. Most can be demonstrated to be the result of preservational accidents, life history accidents, or to be organisms other than conulariids. The first published example of a specimen that differed from the normal four-sided condition was a misshapen individual of *Anaconularia anomala* (Barrande) from the Ordovician of Bohemia that was described as having four faces apically and three faces aperturally (Barrande 1867, Pl. 8:23–25; redrawn in Kiderlen 1937, Fig. 25). Later, Kiderlen (1937, Figs. 26–27) figured cross sections of some specimens referred to *Paraconularia africana* (Sharpe) from the Devonian of Bolivia which were interpreted as having two or three faces. The supposed conulariid species *Conularina triangulata* (Raymond) from the Ordovician of New York and Quebec has been interpreted to be either three-sided (Sinclair 1942:221–222) or six-sided (Raymond 1905:379, 1908:216). Finally, Sinclair (1942:222), in remarks on the three-sided morphology of *C. triangulata*, indicated that he knew of three-sided conulariids other than those referable to *C. triangulata*, but he did not describe or figure any, nor did he indicate in which collections they were deposited.

The holotype of *C. triangulata* (Raymond) (CM 2099), the type species of *Conularina*, has been reexamined in the course of this work. The specimen (Fig. 1A–C) was collected from the Trenton Group (Middle Ordovician) at Cystid Point, Valcour Island, New York. Additional specimens referable to this species have also been reported from Middle Ordovician carbonate strata of Quebec (Sinclair 1942:221). The holotype is similar in appearance to some specimens of *Conularia trentonensis* Hall from the same formation in that the skeleton is thin (0.2 mm or less in thickness), multilayered and black and shiny in appearance. The composition of the *C. triangulata* skeleton is judged to be calcium phosphate. The black color may have been imparted to some fossils of *Conularia* and *Conularina* from the Trenton Group by the carbonization of protein within the skeletons. There is no indication of rods supporting the integument in *C. triangulata*. Because it lacks rods, the type species of *Conularina* differs markedly from the characteristic morphology of the conulariids, and for this reason, it is here excluded from the Conulariida.

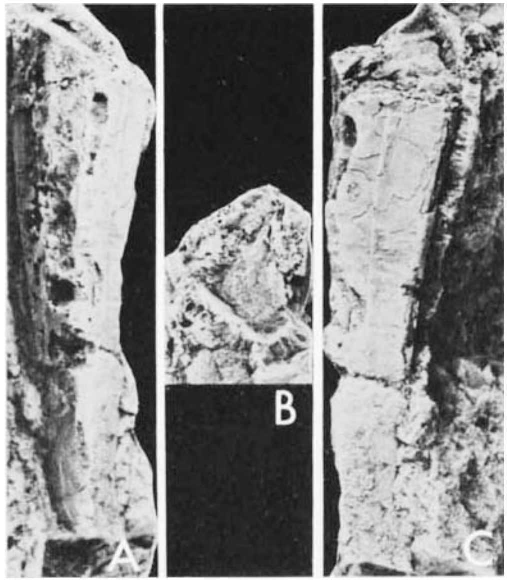


Fig. 1. Holotype of *Conularina triangulata* (Raymond) from the Chazy Group (Middle Ordovician) of Valcour Island, New York (CM 2099). □ A. Lateral view. □ B. Natural cross sectional view. □ C. Facial view. The specimen does not possess rods typical of conulariid architecture. All figures ×3.0.

Conularina triangulata has longitudinal thickenings at the corners of its faces and probably has a calcium phosphatic composition. In these respects, it is similar to *Sphenothallus*, a Paleozoic worm (Mason & Yochelson 1985). However, *Conularina triangulata* differs from *Sphenothallus* in many respects, including the possession of three faces, each with a raised midline. For the present, it is best to classify it as *incertae sedis*.

The whereabouts of Barrande's (1867) specimen of a presumed teratological *Anaconularia anomala* (Barrande) from Bohemia is not known. Barrande's figures of the specimen, including two cross sections, have been reproduced herein (Fig. 2A–C). This specimen preserves four faces in the apical one-third (Fig. 2B) and three faces in the apertural region (Fig. 2C). Judging from Fig. 2A, it does not seem as though post-mortem compression of the conulariid exoskeleton is responsible for the loss of one face in the apertural two-thirds, as the specimen does not appear to be much twisted or compressed. Although it is difficult to supplement Barrande's interpretation without examining the specimen, the nature of the condition indicates a repaired damage rather than a structural malformation. There is a notice-

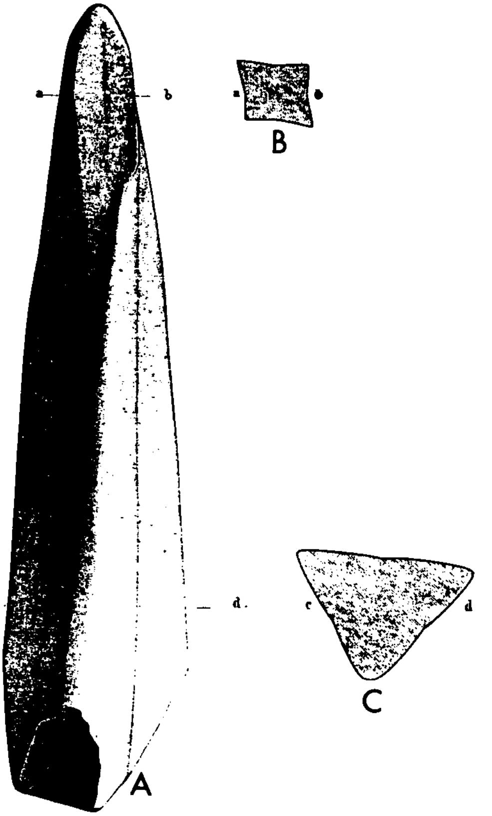


Fig. 2. Deformed *Anaconularia anomala* (Barrande) from the Drabov Quartzite (Ordovician) of Mt. Drabov, Czechoslovakia. Reproduced from Barrande (1867, Pl. 8:23–25). ×0.75. □ A. Corner view. Note that the specimen is shown here as it was oriented by Barrande, with the aperture pointing down. □ B. Cross section a–b. □ C. Cross section c–d.

Fig. 3. Cross sectional outlines of supposed teratological specimens of *Paraconularia africana* (Sharpe) from the Icla Formation (Devonian) of Bolivia. □ A. A possible two-sided individual. Reproduced from Kiderlen (1937, Fig. 26). ×0.75. □ B. A possible three-sided individual. Reproduced from Kiderlen (1937, Fig. 27). ×0.67.

able change in the trend of the midline on the face oriented to the left in Fig. 2A. This change occurs at the most aperturad position of the fourth, or shortest, face. Furthermore, the fourth face appears to have been truncated by the face oriented to the right in the same figure. We tentatively regard this specimen as an individual exhibiting a healed injury, probably an embayed injury (see below under the heading 'Pathologies of conulariids').

Kiderlen (1937:140, Figs. 26–27) indicated the presence of teratological conulariids in the Devonian '*Conularia* shales' of Bolivia. One specimen, referred to *Paraconularia africana* (Sharpe), was illustrated by a cross section (Fig. 3A herein) and an incomplete view of one face. Another specimen, supposedly three-sided, was illustrated by a cross section only (Fig. 3B herein).

Upon the examination of nearly 160 Bolivian conulariids referable to *P. africana* housed in the collections of the U.S. National Museum of Natural History and the Yacimientos Petroliferos Fiscales Bolivianos, Centro de Tecnología Petrolera, we have not found a single specimen exhibiting only two or three faces. Moreover, the examination of more than 1100 other conulariids from the Devonian of Bolivia, assignable to other taxa, has not yielded a single teratological individual.

Two taxa of conulariids from the Devonian of Bolivia are particularly susceptible to post-mortem distortion, *Conularia quichua* Ulrich and *P. africana* (Sharpe). Individuals of *C. quichua*, which are occasionally misidentified as *P. africana*, are often markedly collapsed or compressed, yielding variations on an elongate ovoid cross section (Fig. 4F–M). Specimens are often compressed so that they could be easily mistaken for two-sided (Fig. 4F–J, M) or three-sided (Fig. 4K–L) fossils. Individuals of *P. africana* tend to exhibit infoldings or outfoldings at one or more midlines, as well as collapse features, and also can yield a variety of cross sectional forms (Fig. 4B–D). It is possible, but by no means certain, that the deformed conulariids from Bolivia which Kiderlen figured were ones which were affected by post-mortem distortion. If, however, the specimens figured by Kiderlen were genuine examples of teratological cases, our studies of the Bolivian material indicate that occurrences of preserved teratological specimens are exceedingly rare.

New material. – We have examined more than 5000 conulariids from North America, South America, Europe, and Africa and ranging in age from Ordovician to Permian. Among these, only one indisputable teratological specimen has been examined. This specimen (USNM 409811; Figs. 5–6) is a six-sided individual from the Cuyahoga Formation (Middle Mississippian) at Dixon's Mill, on the Little Scioto River, approximately

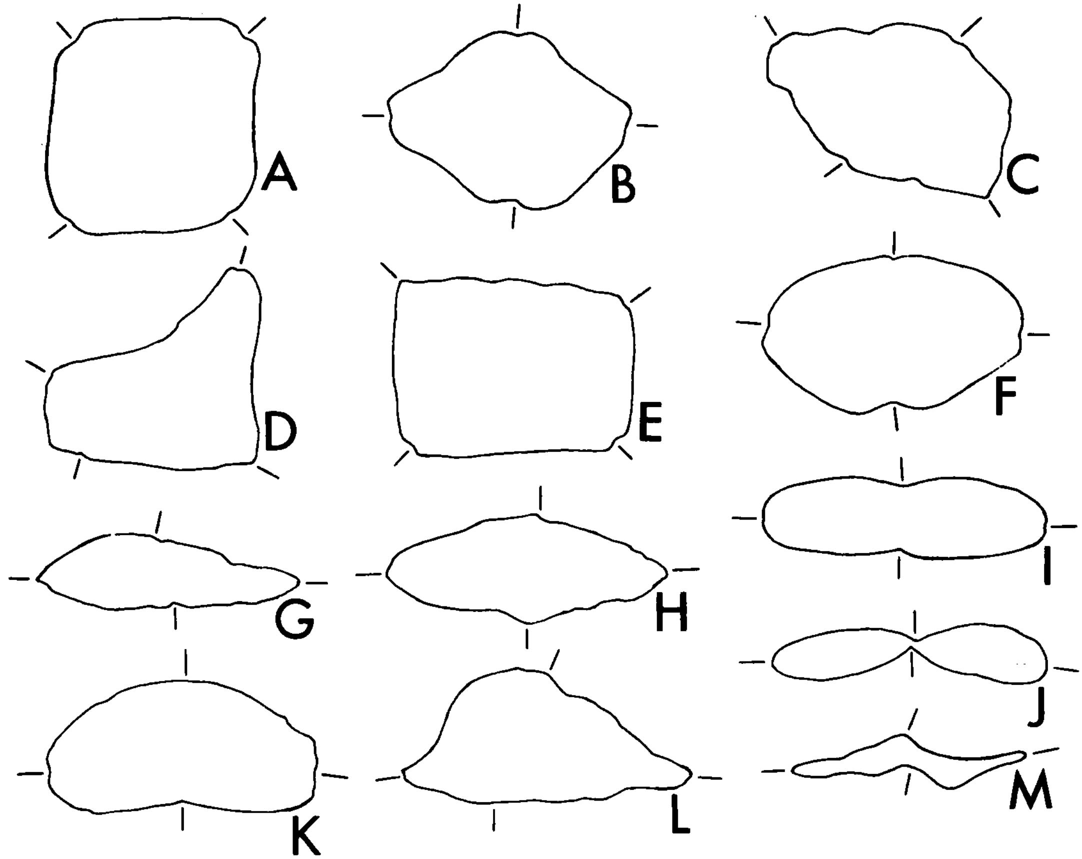


Fig. 4. Representative natural cross sectional outlines of four specimens of *Paraconularia africana* (Sharpe) (A–D) and nine specimens of *Conulària quichua* Ulrich (E–M) from the Devonian '*Conularia* shales' (Belén, Icla and Sicasica formations) of Bolivia. Two specimens (A, E) are essentially uncompressed, but the others have been affected, in varying degrees, by post-mortem deformation. Such specimens could be interpreted as individuals that possessed two (F–J, M), three (K, L), five (C), or six (D) faces. Registration marks indicate positions of corner grooves and indicate that all specimens figured here were four-sided. □ A. YPFB 751, ×1.2. □ B. YPFB 459, ×0.9. □ C. YPFB 1531, ×1.1. □ D. USNM 409481, ×1.1. □ E. USNM 409482, ×3.0. □ F. USNM 409483, ×1.2. □ G. YPFB 459, ×1.8. □ H. USNM 409484, ×1.2. □ I. YPFB 4523, ×1.2. □ J. USNM 409485, ×3.5. □ K. USNM 409486, ×1.5. □ L. USNM 409487, ×2.0. □ M. USNM 409488, ×0.8.

5 km northeast of Sciotoville, Scioto County, Ohio. The specimen was collected in 1897 by George H. Girty and Wilber Stout, and is referable to *Paraconularia missouriensis* (Swallow). It was noted by T. Gary Gautier in a collection of fossils from Dixon's Mill in the U.S. Geological Survey collection, housed in the U.S. National Museum of Natural History.

This *P. missouriensis* specimen is preserved in three dimensions in a siderite concretion but was completely freed of matrix in the process of preparation. It is almost entirely replaced by siderite. Very few of the rods show remains of their original calcium phosphatic composition. Relatively little distortion of the skeleton has occurred except at the aperture, indicating that siderite precipitation occurred soon after the organism died and settled to the ocean bottom. The fossil now lacks the apex, probably because it extended outside the limits of the concretion. The specimen clearly possesses six faces, as is demonstrated in Fig. 5, a photograph made from a thin latex mold of the exterior of the specimen. The mold has been cut along one of the corner grooves and laid out flat. Because several faces are inturned sharply near the aperture, a small amount of each face, near the aperture, has been cut from the mold. As preserved on the fossil, each angle of juncture formed where two faces meet is approximately 60°. In uncompressed, four-sided, examples of

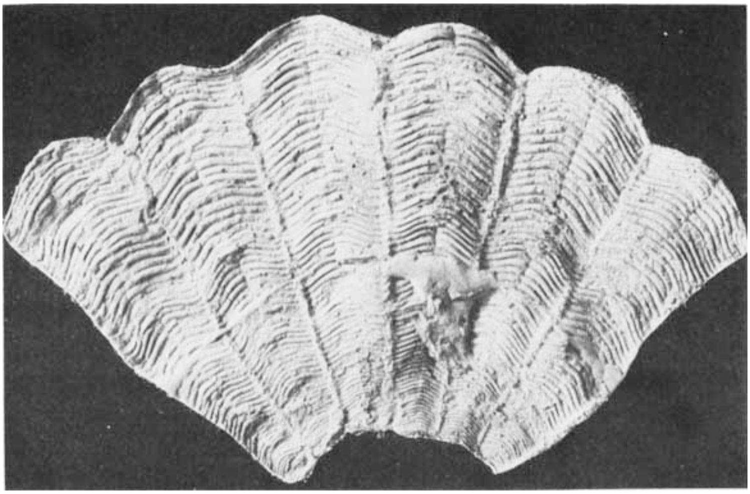


Fig. 5. Latex mold of teratological *Paraconularia missouriensis* (Swallow) from the Cuyahoga Formation (Early Mississippian) at Dixon's Mill, on the Little Scioto River, near Sciotoville, Scioto County, Ohio. The mold has been cut along a corner groove and laid out flat. USNM 409812, ×1.0.

the same species, each angle of juncture is approximately 90°.

Each of the apical angles on USNM 409811 is equal to 17°. Major apical angles of other specimens referable to *Paraconularia missouriensis* are commonly in the range of 14–21° and minor angles are usually in the range of 11–15° (Babcock & Feldmann 1986c). Thus, it seems that this teratological specimen lacked the definite bilateral symmetry reflected in conulariids as paired major and minor faces subtending larger and smaller apical angles, respectively (Babcock & Feldmann 1986a). Furthermore, it seems that the minor faces may have been genetically suppressed in favor of the major faces. The six-sided condition, exhibited on a large specimen of this taxon, permits speculation on one aspect of the lifestyle of the conulariids. They may have functioned as radially symmetrical organisms and not as bilaterally symmetrical ones. If the reverse were the case, the radially symmetrical design of the exoskeleton of USNM 409811 would have been deleterious to the organism and it would not have likely survived to achieve full size. There is not enough evidence at present to speculate on the nature of symmetry in the ancestors of conulariids. Radial symmetry is not suggested to be a neotenous condition.

Four of the six faces exhibit infoldings at their apertural ends (Fig. 6). Such infoldings of the apertural terminations ('apertural lappets' or 'apertural lobes' of older literature) represent geopetal structures in 23 specimens of *Conularia, Paraconularia,* and *Reticulaconularia* collected in

Fig. 6. Stereopair of *Paraconularia missouriensis* (Swallow) from which mold in Fig. 5 was made. Note that four faces are inturned aperturally; two faces, at the back of the specimen in this view, are fully extended. USNM 409811, ×1.0.

place by Babcock and Wilson in rocks of the Belén and Sicasica formations (Devonian) in Bolivia and of the Cuyahoga Formation (Early Mississippian) in Ohio. These infoldings have been interpreted by Babcock & Feldmann (1986a) as taphonomic structures resulting from collapse near the aperture of some of the faces after the conulariids came to rest at the sediment surface. The faces of the conulariid skeleton which show the infoldings, or the most pronounced infoldings if more than two faces exhibit them, indicate the direction which was 'stratigraphically up' when the conulariids settled, as determined from other sedimentary structures including oscillation ripple marks and Bouma sequences.

Pathologies of conulariids

General. – Occurrences of pathological specimens of conulariids are known (e.g. Richardson 1942; Babcock & Feldmann 1986b, c), but are poorly documented. Healed injuries are potentially useful in understanding the development of the conulariid exoskeleton, and in reconstructing some life history events, as well as for lending clues to the configuration of some of the internal soft parts.

Pathologies in conulariids that are reviewed herein include only sublethal damages to the conulariid exoskeleton. Presumably, internal soft parts were also affected by some of the events which caused damage to the exoskeleton, but our limited knowledge of conulariid soft parts (Steul 1984; Babcock & Feldmann 1986a; Babcock & Feldmann 1986b, c) does not permit description of the injury to living tissues. All disfigurations of conulariid exoskeletons described were healed by the living animals. Those individuals that sustained lethal injuries would not be readily preserved as fossils and, if they were preserved, the injuries would be difficult to distinguish from post-mortem breakage.

Classification of pathologies. – Observed injuries to conulariid exoskeletons are classified below according to terminology introduced by Alex-

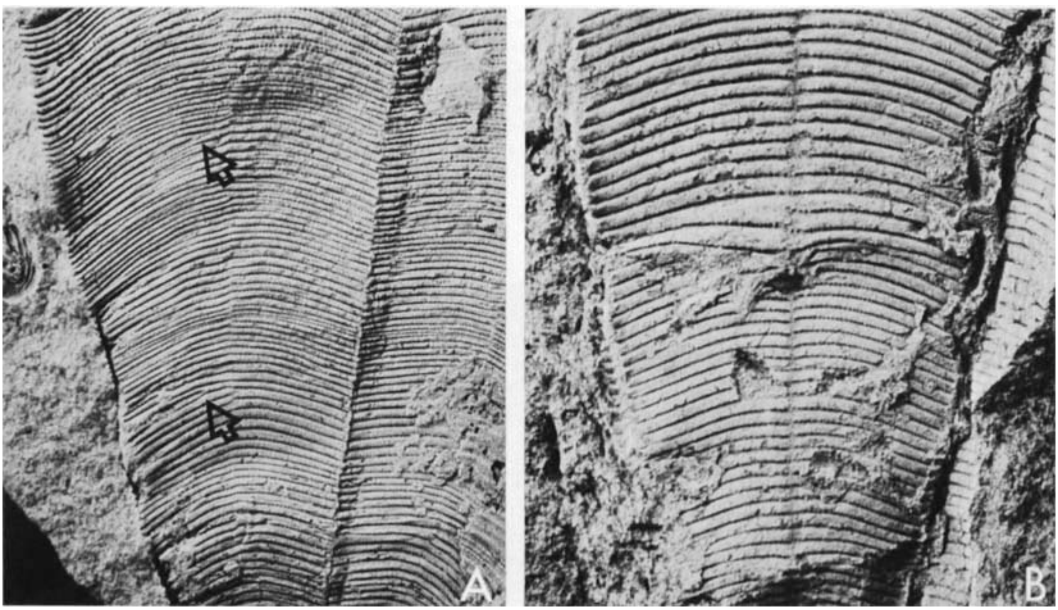


Fig. 7. Scalloped type of damage in conulariids. □ A. *Conularia quichua* Ulrich from the Icla Formation (Devonian) of Icla, Bolivia, YPFB 456, ×2.5. Two examples of scalloping are indicated by arrows. □ B. *Paraconularia hollebeni* (Geinitz) from the Zechstein Formation (Permian), Ilmenau, Thüringen, East Germany, GSC 85059, ×2.5.

ander (1986) for injuries to the shells of some Ordovician brachiopods. Three of the four types of shell breakage patterns identified by Alexander are here recognized in the exoskeletons of conulariids. They are scalloped, cleft, and embayed. Divoted breakages have not been observed in conulariids.

Breakage patterns categorized as *scalloped* (Fig. 7A–B) are ones which represent minor damage at the apertural margin and are usually found at exoskeletal constrictions. Scalloped patterns can be readily identified by the truncation of one or a few rods. Rods which have been added to the exoskeleton subsequent to the injury are arranged normally, though a small change in rod angle may occur (Fig. 7B). The contact between the truncated rods and those immediately aperturad of them commonly resembles an angular unconformity, especially if the injury has occurred near the midline of a face. Scalloped breakage patterns are easiest to identify in conulariids that have closely-spaced rods, including many species of *Conularia*.

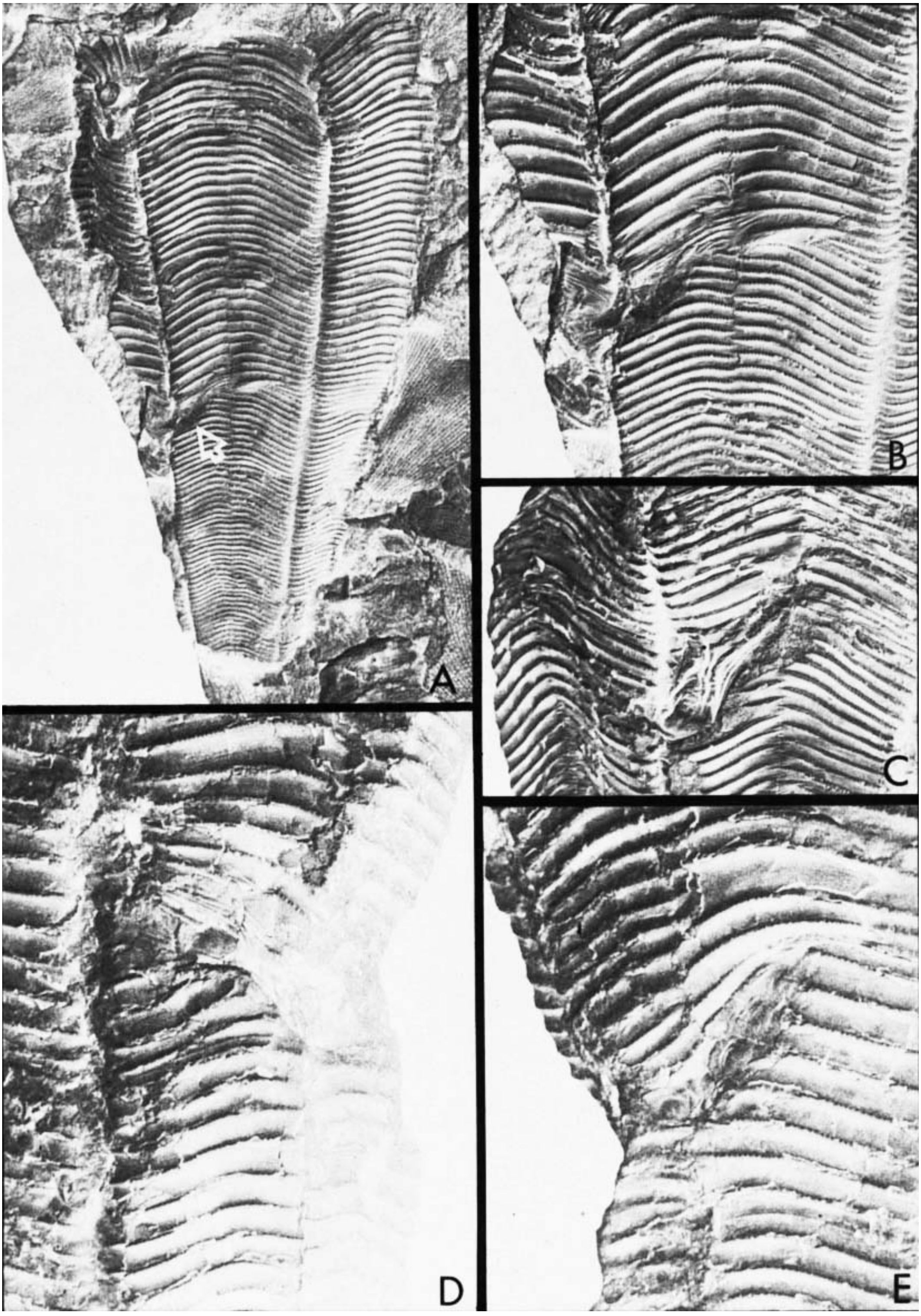
In brachiopods, Alexander (1986:275) observed a change in elevation of the shell at the site of a scalloped breakage. This condition does not usually occur in conulariids, probably as a result of the thin exoskeleton. Breakage of this type in conulariids probably occurred by minor chipping or crushing of the exoskeleton at the aperture. Later secretion of exoskeleton at the apertural end seems to have been virtually uninhibited in most cases.

Cleft injuries (Fig. 8A–E) are V-shaped incisions into the conulariid exoskeleton which have been subsequently closed by the secretion of integument or integument and rods. Such damage generally takes a subtriangular shape on each of two adjacent faces (Fig. 8D–E). On all specimens observed, the profile of the exoskeleton appears to be modified in the vicinity of the cleft injury. This modification is undoubtedly owing to a closure of the exoskeleton around the gap. The position of a cleft injury bears no apparent relation to the position of the aperture. Healed wounds of this type indicate that conulariids could probably repair damaged exoskeletal material anywhere within the portion of the skeleton occupied by the living organism. Repair of cleft injuries in brachiopods probably occurred by secretions of calcium carbonate from the mantle (Alexander 1986:277) and it is reasonable to conclude that conulariids likewise possessed a sheath of soft tissue with a secretory function which lined the inner portion of the exoskeleton.

Embayed breakage patterns (Fig. 9A–B) involve the truncation of many rods and the loss of a large portion of the exoskeleton. The removed area may be jaggedly or smoothly outlined. Such injuries may be located at the aperture (Fig. 9B), but this is not necessarily so (Fig. 9A). Healing which has occurred is obvious and, in all observed examples, incomplete. Repaired areas are completely covered over by integument, but rods do not typically cover the entire damaged area (Fig. 9B). They may even be missing altogether (Fig. 9A). When rods are present, they tend to be arranged at a high angle to the truncated rods (Fig. 9B). Repair of embayed breaks, like clefts, implies the presence of a sheath of soft tissue which could secrete calcium phosphate.

Table 1. Frequency of injury among selected conulariid taxa.

	Number of specimens	Number scalloped	Number cleft	Number embayed	Total damaged
ORDOVICIAN TAXA					
Climacoconus quadrata	24	0	0	0	0
Conularia trentonensis	97	47	0	0	47
DEVONIAN TAXA					
Conularia albertensis	6	2	0	1	3
Conularia quichua	33	19	0	0	19
Paraconularia africana	52	6	2	1	9
Paraconularia ulrichana	95	5	0	1	6
Reticulaconularia baini	24	3	0	0	3


A
B
C
D
E

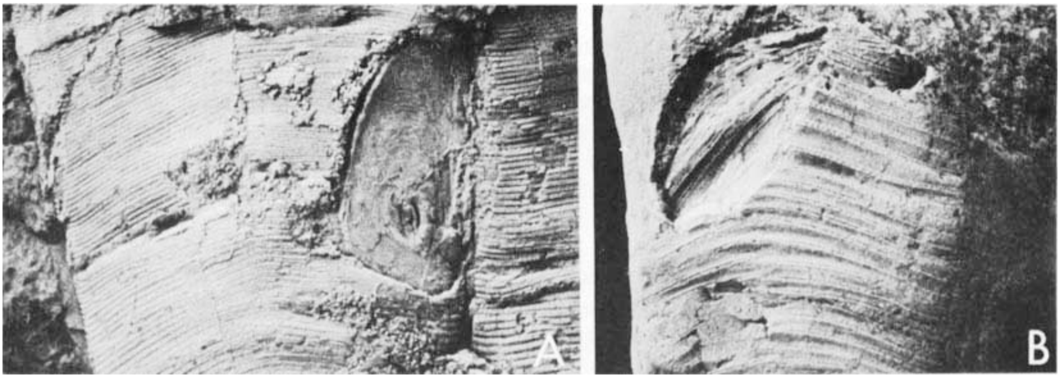


Fig. 9. Embayed type of damage in conulariids. □ A. *Conularia multicostata* Meek & Worthen, probably from the Cuyahoga Formation (Early Mississippian) of southern Ohio. Note incremental 'rings' of tissue repair and lack of rods in repaired area. CM 34533, ×1.5. □ B. *Paraconularia chagrinensis* Babcock and Feldmann from the Chagrin Shale (Late Devonian) of Mill Creek, Lake County, Ohio, CMNH 6717, ×1.5.

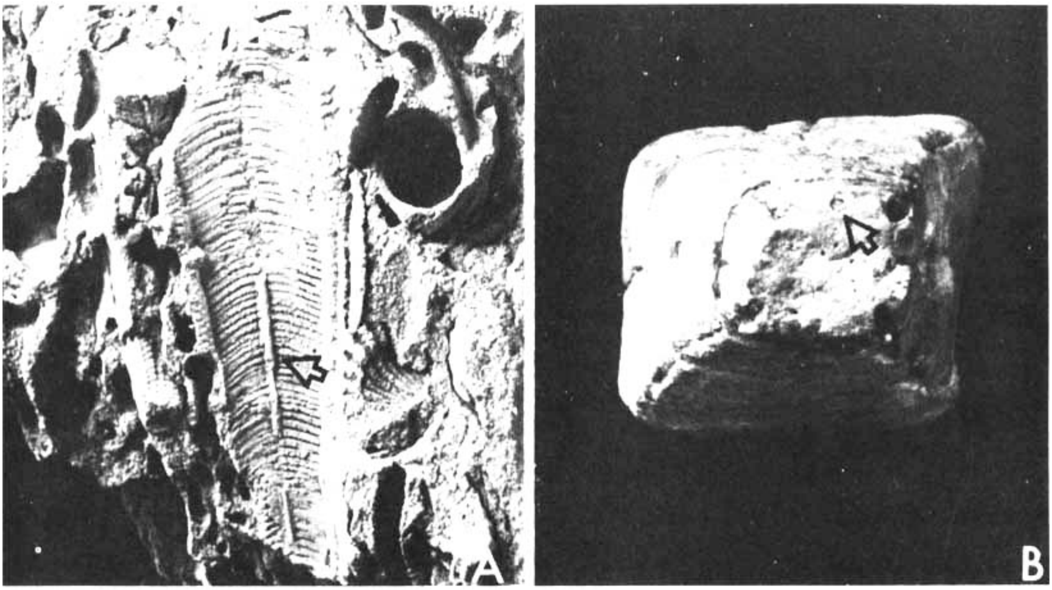


Fig. 10. □ A. *Paraconularia ulrichana* (Clarke) from the Devonian of Bolivia showing a longitudinal thickening of integument at a midline (arrow). View is of the interior of the exoskeleton. This specimen and four others of the same species on the slab have been preserved in a crinoid packstone, but are uncrushed. YPFB 3981, ×2.5. □ B. Holotype of *Conularia albertensis* Reed from the Devonian of South Africa, natural cross section, viewed from apical end. Arrow indicates a thickening of integument at a midline. Specimen not coated with ammonium chloride. MGM 2017, ×1.5.

Fig. 8. Cleft type of damage in conulariids. □ A. *Paraconularia chesterensis* (Worthen) from the Borden Group (Late Mississippian) of Crawfordsville, Indiana, FMNH UC 6813, ×1.25. Arrow indicates healed injury. □ B. Same specimen as in A. Detail of cleft injury, ×2.5. □ C. *Paraconularia africana* (Sharpe) from the Icla Formation (Devonian) of Tarabuco, Bolivia, YPFB 3467, ×1.5. □ D–E. *Paraconularia missouriensis* (Swallow), probably from the Salem Limestone (Late Mississippian) of Indiana. Views of two adjacent faces, FMNH PE 25968, ×1.5.

Discussion of pathologies. – We have tabulated the occurrences of all types of breakage in selected specimens from two collections of conulariids (Table 1). A collection amassed by the late G. Winston Sinclair, housed in the Geological Survey of Canada, contains abundant examples of two Ordovician taxa: (1) *Climacoconus quadrata* (Walcott) from the Chazy Group of New York and Vermont and from the Tetreauville Formation of Quebec; and (2) *Conularia trentonensis* Hall from the Chazy Group of New York and Vermont, the Terrebonne Formation of Quebec, and the Collingwood Formation of Ontario. All well-preserved specimens of these two taxa were included in the count. The collections of the Yacimientos Petroliferos Fiscales Bolivianos, Centro de Tecnología Petrolera were used for estimating the frequency of occurrence of breakages among sample Devonian taxa. The YPFB collections were chosen not only for the large number of specimens represented, but also because the collection has been assembled primarily for the stratigraphic value of specimens. The taxa examined from this suite of specimens are represented in proportions which reflect their true relative abundances. One species, *Conularia albertensis* Reed, however, is represented by only six specimens; conclusions reached herein exclude this form owing to the small sample size. Our reconaissance studies of other collections in the United States, Canada, and Bolivia indicate that the frequencies of exoskeletal damage represented by the samples from the GSC collection are fairly representative of collections made from Ordovician through Silurian rocks, and the YPFB collection mirrors the frequencies of injuries among conulariids from Devonian through Carboniferous rocks.

Among the studied specimens (Table 1), at least one example of a scalloped break occurs on 49% of *Conularia trentonensis* and on 58% of *Conularia quichua*. It was not observed on any specimens of *Climacoconus quadrata,* and was found to be only moderately represented on specimens of *Paraconularia africana* (12%), *P. ulrichana* (5%), and *Reticulaconularia baini* (13%).

Damage to the conulariid exoskeleton resulting from a scalloped break seems to have been minimal and localized at the aperture, usually of a single face. Some scalloped patterns of breakage possibly resulted from the activity of durophagous predators, but others may have been related to the fragile nature of the apertural margin of the conulariid exoskeleton. Also, crowding of individuals, living in clusters (Babcock & Feldmann 1986a), could have been responsible for some injuries of the scalloped pattern. Species of *Conularia* have a much higher rate of scalloping than species referable to all other genera examined in this study and may have had more delicate exoskeletons than the other taxa.

The common occurrence of scalloped breaks at exoskeletal constrictions is intriguing. Exoskeletal constrictions have been interpreted as representing successive positions of the aperture during the life histories of conulariids (Babcock & Feldmann 1986a). It is possible that damage to the exoskeleton at the apertural margin was responsible for a cessation of growth in certain individuals. However, most specimens exhibiting some scalloped breaks exhibit obvious breaks at less than half of the exoskeletal constrictions (e.g. Fig. 7A). Another possibility for the coincidence of scalloped injuries with exoskeletal constrictions is that cessation of growth at the positions of constriction extended the time that certain surfaces acted as the aperture, therefore increasing the probability of damage.

Cleft and embayed injuries are larger in scale than scalloped ones and do not appear to be limited to the apertural region. These probably represent more severe injuries and were likely associated with injury to soft organs. We observed cleft injuries on two specimens of *Paraconularia africana* (Sharpe) (YPFB 3467, a counterpart of same, YPFB 3462; YPFB 3599), and on one specimen each of *P. byblis* (White) (USNM 409489), *P. chesterensis* (Worthen) (FMNH UC 6813), and *P. missouriensis* (Swallow) (FMNH PE 25968). Five specimens have been examined having embayed injuries. The observed frequency of occurrence of this type of injury is: two specimens of *Conularia multicostata* Meek & Worthen (CM 34533, GSC 87204), and one specimen each of *C. albertensis* Reed (YPFB 578), *Paraconularia chagrinensis* Babcock & Feldmann (CMNH 6717), and *P. africana* (Sharpe) (YPFB 416). A specimen of *Anaconularia anomala* (Barrande) which was figured and described by Barrande (1867, Fig. Pl. 8:23–25; figures reproduced herein as Fig. 2A–C) as being teratological is here interpreted as exhibiting four faces apically and three faces aperturally as a result of probable hard part regeneration following a sublethal injury. The injury appears to have been extensive and of the embayed type.

No specimens of Ordovician or Silurian conulariids have been observed by us which exhibit cleft or embayed injuries. Among the Devonian forms from Bolivia which were examined (Table 1), these types of injuries were found in 0–4% of specimens, depending upon the taxon. *Conularia albertensis* has been excluded from this calculation because of the small sample size of this form. Cleft and embayed injuries in brachiopods were attributed by Alexander (1986) to sublethal attacks by durophagous predators, and it is reasonable to invoke this mode of origin to most or all such damages in conulariids. Nautiloid cephalopods, which have been widely interpreted to have preyed upon Paleozoic invertebrates (e.g. Berry 1929:178; Henry & Clarkson 1974:94; Alexander 1986:279–280), are common in the Ordovician strata in which *Climacoconus quadrata* and *Conularia trentonensis* are found; they are also common in the Devonian conulariid-bearing beds of Bolivia. Other potential predators that have been reported from rare remains in the Devonian strata of Bolivia are goniatite ammonoids (Hünicken, Kullmann & Suárez-Riglos 1980), chondrichthyan fishes (Janvier 1976), placoderm fishes (Goujet, Janvier & Suárez-Riglos 1985), phyllocarid crustaceans (Hünicken, Kullmann & Suárez-Riglos 1980), eurypterids (Kjellesvig-Waering 1973), and asteroids (Branisa 1965). It is noteworthy that most groups of shell-crushing or shell-chipping Paleozoic marine organisms, except the cephalopods, the trilobites, and some enigmatic animals such as *Anomalocaris*, arose subsequent to the Ordovician (Signor & Brett 1984). Scalloped injuries, which are found in great frequency among some conulariid taxa from the Ordovician on, may have been inflicted, in part, by cephalopods or some arthropods. More severe injuries, known only in Devonian and later species, may have been inflicted largely by attacks from durophagous predators that evolved during the Silurian and Devonian.

The increased number of sublethal injuries in post-Silurian conulariids may have been related to a greater abundance or diversity of predators. Alternatively, conulariids may have developed predation-resistant morphological features, or developed a more diverse set of life history strategies, thereby increasing the number of individuals surviving attacks by durophages. Signor & Brett (1984) indicated that many groups of Paleozoic marine organisms developed predation-resistant features such as spines or shell-strengthening sculpturing or coiling. Conulariids do not seem to have developed any defensive structures, as reflected in their skeletal architecture, in the middle to late Paleozoic. However, some Devonian taxa, such as *Conularia albertensis* Reed and *Paraconularia ulrichana* (Clarke), developed longitudinal thickenings of integument along the interiors of each midline (Fig. 10A–B), thus increasing the rigidity of the exoskeleton. It is possible that these devices aided in reducing lethal attacks by some predators, but this is by no means certain.

Another means of increasing the durability of the skeleton was by increasing the diameter of the rods which form the exoskeletal framework. Rods in species referable to *Paraconularia* seem to be, in general, somewhat stouter than those in *Conularia* (Figs. 7–9). *Conularia* is the dominant conulariid genus present in Early Devonian rocks of North America (Babcock & Feldmann 1986b, c). *Paraconularia* first appeared in the Late Devonian (Famennian) (Babcock 1985), and by the Late Mississippian (Late Visean), was the dominant genus on the continent (data in Babcock & Feldmann 1986c).

In conulariids, exoskeletal breaks that could be classified as divots (*sensu* Alexander 1986) have not been observed. Divots in brachiopods occur where small portions of the shell have been removed; these breaks are unrelated to breakage at the shell margins. It is possible that divots do not occur in conulariids because they possessed a very thin, rather flexible exoskeleton. The same activity that produced a divot on a brachiopod would be more likely to produce an embayed break on a conulariid.

Conclusions

Obvious examples of teratological conulariids seem to be very rare. One undoubted example is a specimen of *Paraconularia missouriensis* from the Mississippian of Ohio (Figs. 5–6). A misshapen specimen of *Anaconularia anomala* from the Ordovician of Bohemia was figured by Barrande (1867, Pl. 8:23–25; herein, Fig. 2A–C), but the malformation was probably pathological, and not teratological, in nature. Kiderlen (1937) figured cross sections of two Devonian conulariids from Bolivia which were interpreted as teratological individuals. It is likely that Kiderlen was misled by post-mortem compression which altered the appearances of normal, four-sided specimens.

Conularina triangulata, a supposed conulariid thought to have either triradial (Sinclair 1942) or hexaradial symmetry (Raymond 1905, 1908), is here removed from the Conulariida because it lacks calcium phosphate rods embedded within a multilayered calcium phosphate and protein exoskeleton.

Observed pathological conditions preserved on conulariid exoskeletons may be arranged into three patterns: scalloped, cleft, and embayed. Scalloped injuries occurred commonly. They were minor and probably had little, if any, effect on internal organs. Predation and accidental events could be implied for the formation of scalloped breakage patterns. Cleft and embayed breakage patterns are rare and represent scars left in the wake of rather severe, though sublethal, attacks by predators. Predators of conulariids may have included cephalopods, fishes, a variety of arthropods, and asteroids. Cleft and embayed injuries occur infrequently in Devonian and Carboniferous conulariids, but they have not yet been observed in pre-Devonian forms. The rise of many durophagous predators during the Silurian and Devonian coincides with the increased incidence of sublethal injuries to conulariids. Exoskeletal strengthening devices may have aided conulariids in reducing the incidence of successful predation by some durophagous organisms.

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Origins and Evolution of the Antarctic Biota

Origins and Evolution of the Antarctic Biota is a discussion meeting sponsored by the Geological Society of London and the Palaeontological Association. It is to be held at the Geological Society of London 24–25 May, 1988.

Organiser: Dr J. A. Crame, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

The broad aim of this meeting is to elucidate the palaeontological history of Antarctica through the Phanerozoic. Particular emphasis will be placed on tracing the origins and evolution of those organisms that have characterized our most southern continent.

Topics for discussion will include:

(1) Faunal and floral distributions in relation to Antarctica's position within the Gondwana supercontinent.

(2) The south polar region as an origination and dispersal centre.

(3) Effects of climatic deterioration on both marine and terrestrial organisms.

Original contributions within this framework are invited from all interested earth and life scientists. It is anticipated that talks will be of approximately 25–30 mins duration and that facilities will be available for poster presentations. The proceedings of the meeting will be published as a *Special Publication of the Geological Society of London.*

Further details may be obtained from Dr J. A. Crame at the above address.