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泥盆纪锥石类 *Changshaconus* Zhu，1985 和 *Reticulaconularia* Babcock *et* Feldmann，1986 两属的解剖学和系统学

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中文提要　重新描述了湖南中泥盆世的锥石 *Changshaconus carinata* Zhu，1985。通过比较，笔者认为 *Changshaconus* 与产自南非泥盆系和南、北美洲下泥盆统中的 *Reticulaconularia* Babcock *et* Feldmann，1986 非常相似。*Changshaconus* 和 *Reticulaconularia* 两属由于锥管表面横肋间具有纵向脊状构造，与横肋构造一起构成了网状的表面装饰，从而区别于其它所有锥石类化石。两属的其它特征还包括：(1)在角沟处，横肋成交错状排列；(2)横肋在角沟的肩部向口端明显弯曲；(3)面中线呈明显的脊状隆起。以上 3 个特征在 *Climacoconus* Sinclair，1952 属中存在，因此 *Changshaconus*、*Reticulaconularia* 和 *Climacoconus* 构成了一个单系类群，而不同于其它锥石类。这 3 属又与 *Notoconularia* Thomas，1969 和 *Paraconularia* Sinclair，1952 两属相似，横肋都在角沟处呈交错状排列。

关键词　锥石类　解剖学　系统学　中泥盆世　湖南

ANATOMY AND SYSTEMATICS OF THE DEVONIAN CONULARIIDS *CHANGSHACONUS* ZHU，1985 AND *RETICULACONULARIA* BABCOCK *ET* FELDMANN，1986

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Abstract　*Changshaconus carinata* Zhu，1985，a Middle Devonian conulariid from Hunan Province，southeastern China，is redescribed and refigured. *Changshaconus* probably was most closely related to *Reticulaconularia* Babcock *et* Feldmann，1986，which occurs in the Devonian of South Africa and the Lower Devonian of Bolivia，New Jersey，and Quebec. *Changshaconus* and *Reticulaconularia* differ from all other conulariids in having transverse ribs and interspace ridges that are arranged in such a way as to form a reticulate facial ornament. Additional characteristics of *Changshaconus* and *Reticulaconularia* include (1) interruption plus alternate arrangement and interlocking of the transverse ribs in the corner sulcus；(2) sharp bending of the transverse ribs toward the aperture on the shoulders (edges) of the corner sulcus；(3) midline of the four faces marked by an external ridge. Together，these three additional similarities are uniquely shared with *Climacoconus* Sinclair，1952，and can be interpreted as evidence that *Changshaconus*，*Reticulaconularia*，and *Climacoconus* were members of a single，monophyletic taxon that excluded all other conulariids. This group，in turn，may have been most closely related to *Notoconularia* Thomas，1969 and *Paraconularia* Sinclair，1952，both of which exhibit interruption plus alternation and interlocking of the transverse ribs in the corner sulcus.

Key words　conulariids，anatomy and systematic，Middle Devonian，Hunan Province

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INTRODUCTION

Conulariids are a rare and little studied component of the Paleozoic marine fauna of China. Although a number of papers have been published on conulariid-like fossils (carinachitiids and hexangulaconulariids) of the basal Cambrian Small Shelly Fauna (e.g., Qian and Bengtson, 1989; Conway Morris and Chen, 1992; Qian *et al.*, 1997; see also references cited in these papers), only a handful of articles, all relatively short, have dealt with conulariids from post-Cambrian strata of China (Yin, 1933; Zhang, 1977; Xu and Li, 1979; Liu, 1981; Zhu, 1985; Zhu and Xu, 1988). In one of the most recent articles, Zhu (1985) described nine new conulariids from Devonian and Permian rocks of four regions (Guizhou, Hunan, and Jiangxi provinces; Ningxia Autonomous Region). One of these conulariids, represented by a single specimen from the late Middle Devonian Qiziqiao Formation of Hunan Province, was named *Changshaconus carinata*, a new, monospecific genus and species. Reexamination of this specimen, reposited in the type collections of the Nanjing Institute of Geology and Palaeontology, shows that it is most similar to *Reticulaconularia* Babcock *et* Feldmann, 1986. According to Babcock *et al.* (1987), *Reticulaconularia* consists of three species, two [*R. penouili* (Clarke, 1907) and *R. sussexensis* (Herpers, 1949)] from the Lower Devonian of eastern North America (Quebec and New Jersey), and one [*R. baini* (Ulrich, 1892)] from the Lower Devonian of Bolivia and the Devonian of South Africa.

Both *Changshaconus* and *Reticulaconularia* exhibit the following anatomical features: (1) midline of the four faces marked by an external ridge; (2) interspaces spanned by short ridges (interspace ridges; Van Iten *et al.*, 1996) that line up across the transverse ribs and parallel the corner of their respective half-face; (3) transverse ribs with nodes that occur on lines that parallel the interspace ridges; (4) transverse ribs terminate in the corner sulcus, where the ends of the transverse ribs of one face alternate and interlock with the ends of the transverse ribs of the adjacent face; (5) transverse ribs bent sharply toward the aperture on the shoulders (edges) of the corner sulcus. *Changshaconus* differs from *Reticulaconularia* in having the nodes located at the ends of the interspace *ridges* [as opposed to having them located at the ends of the interspace *furrows* (Van Iten *et al.*, 1996), the condition in *Reticulaconularia*]. The collinear alignment of the widely spaced interspace ridges gives *Changshaconus* and *Reticulaconularia* a distinctive, reticulate facial ornament that is uniquely exhibited by these two taxa.

Previous descriptions of *C. carinata* and the three species of *Reticulaconularia* differ greatly in the amount of anatomical information they contain. Most of the anatomical characteristics (items 2, 4, and 5; location of the nodes) listed in the paragraph above are absent in Zhu's (1985) diagnosis and description of *C. carinata*. These same data (and item 1) also are absent in Babcock and Feldmann's (1986b) and Babcock *et al.*'s (1987) diagnoses and descriptions of *Reticulaconularia*. Except for the location of the nodes, all these characteristics are contained in Sinclair's (1942) description of *Conularia gaspesia* Sinclair, 1942, a species later incorporated by Babcock and Feldmann(1986b) into *R. penouili*. Similarly, much of the anatomical information presented above also is contained in Herper's (1949) description of a single specimen of *Conularia sussexensis* Herpers, 1949 (= *R. sussexensis*; Babcock and Feldmann, 1986b).

The authors of the present paper seek to rectify deficiencies in the most recent literature on conulariid anatomy by providing more complete descriptions of *Changshaconus* and *Reticulaconularia*. Our descriptions of these two taxa are in closest agreement with Sinclair's (1942) description of *Conularia gaspesia* (= *R. penouili*). In addition, we argue that *Changshaconus* and *Reticulaconularia* probably are best interpreted as members of a single, monophyletic group that excluded all other conulariids, and was most closely related to *Climacoconus* Sinclair, 1952, *Notoconularia* Thomas, 1969, and *Paraconularia* Sinclair, 1952.

ANATOMICAL TERMINOLOGY AND GENUS-LEVEL TAXONOMY

Use of anatomical terminology in this paper is

generally consistent with precedents to be found in Sinclair (1940, 1942, 1952), Moore and Harrington (1956), Van Iten (1991, 1992a, b), and Van Iten *et al*. (1996). We compared *Changshaconus* and *Reticulaconularia* with actual specimens and/or photographic illustrations of all previously published conulariid genera ($N \approx 40$). However, there has been no comprehensive review of conulariid systematics and taxonomy since the work of Moore and Harrington (1956), and we suspect that many currently recognized conulariid genera are paraphyletic. Indeed, some genera, including for example *Changshaconus*, are monospecific, and all genera erected thus far were established without the use of cladistic methodology (i.e., without an attempt to distinguish between homologies that are derived and homologies that are primitive). We agree with Babcock and Feldmann (1986a) in regarding the following taxa as paraphyletic: *Adesmoconularia* Driscoll, 1963 [interpreted by Babcock and Feldmann (1986a) as a junior synonym of *Paraconularia*]; *Diconularia* Sinclair, 1952 and *Mesoconularia* Bouček, 1939 [interpreted by Babcock and Feldmann (1986a) as junior synonyms of *Conularia* Miller in Sowerby, 1821]. In addition, we also think that *Beijingoconularia* Xu and Li, 1979, *Calloconularia* Sinclair, 1952, *Cathayconularia* Xu *et* Li, 1979, *Holoconularia* Hergarten, 1985, *Hunanoconularia* Xu *et* Li, 1979, *Pustuloconularia* Zhu, 1985, and *Yinoconularia* Zhu, 1985 probably are members of a single, genus-level clade that includes *Paraconularia*.

MATERIALS AND METHODS

This study is based on anatomical data previously published (e.g., Sinclair, 1942; Herpers, 1949; Zhu, 1985; Babcock and Feldmann, 1986b; Babcock *et al*., 1987) and on direct examination of reposited specimens of *Changshaconus carinata*, *Reticulaconularia baini*, *R. penouili*, and *R. sussexensis*. *C. carinata* was examined and photographed using reflected light and scanning electron microscopy (SEM). For SEM work, uncoated *C. carinata* specimens were attached to a metal stub, and a band of carbon paint was drawn connecting the edge of the fossil to the stub. Abbreviations of repositories housing specimens referred to in this paper are as follows: GSC, Geological Survey of Canada, Ottawa, Ontario; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, PRC; NJSM, New Jersey State Museum, Trenton, New Jersey, USA; USNM, United States National Museum of Natural History, Washington, D. C.

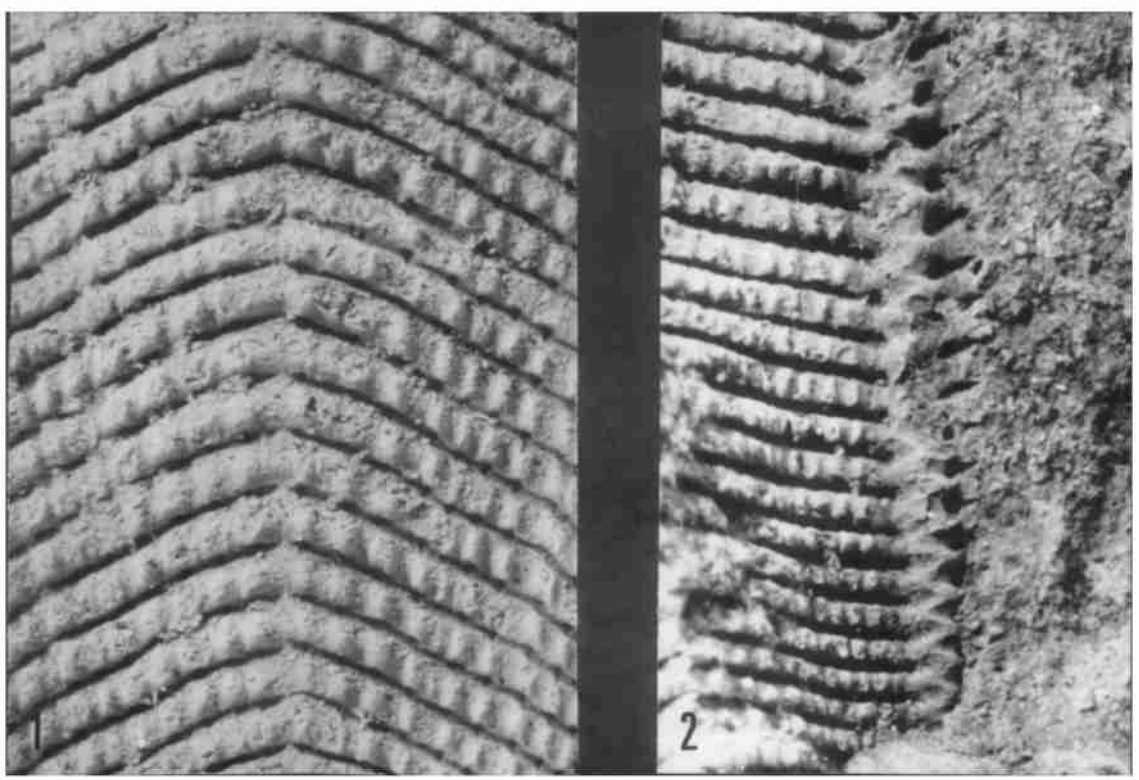
ANATOMY OF RETICULACONULARIA

Babcock and Feldmann's (1986b) diagnosis of the genus *Reticulaconularia* reads as follows: "Conulariids with rods [transverse ribs] that are widely spaced, 12—39/cm. 30%—80% of rods alternate at midline; 20%—70% abut. Apical angles large, 22—59°. Nodes and adapertural spines [interspace ridges; Van Iten *et al*., 1996] present and widely spaced; adapical spines not known". In their discussion of the characteristics of the genus, Babcock and Feldmann (1986b, p. 447) stated that "[s]pecies referable to the genus *Reticulaconularia* differ from all other conulariids in having very large apical angles, 22—59° in the specimens measured in [their study]". Babcock and Feldmann (1986b, p. 447) stated further that "[the] wide spacing between adjacent rods [transverse ribs] and between nodes, as well as between adapertural spines [interspace ridges] is also unique to species of this genus". Finally, Babcock and Feldmann (1986b) noted that the reticulate pattern defined by the collinear alignment of the interspace ridges across the transverse ribs is a characteristic feature of *Reticulaconularia*.

Diagnoses and descriptions of *Reticulaconularia* by Babcock and Feldmann (1986) and Babcock *et al*. (1987) may be supplemented with several additional pieces of information. As noted above in the introduction, most of this information is contained in Sinclair's (1942) detailed description of a single specimen of *Conularia gaspesia*, which is now a type specimen (GSC 87242) of *R. penouili*. In all three species of *Reticulaconularia*, the transverse ribs are interrupted in the corner sulcus (Text-fig. 1.2). More specifically, the transverse ribs of a given face terminate near the midline of the sulcus, and their ends alternate and interlock with the ends of the transverse ribs of the adjacent face. In addition, on

the shoulders (edges) of the corner sulcus, the transverse ribs bend sharply toward the aperture, and within the corner sulcus the transverse ribs arch gently toward the aperture. Due to incomplete preservation or preparation, most reposited specimens do not display these features. Examples of specimens that do exhibit them include GSC 87242 (*R. penouili*; see Babcock and Feldmann, 1986b, fig. 35.3), USNM 409832 (*R. baini*), and NJSM 14960 (*R. sussexensis*). The corner anatomy is perhaps best displayed in NJSM 14960 (*R. sussexensis*), which includes an external mold of part of a single face and corner sulcus. The mold shows the abrupt bending of the transverse ribs on the shoulders (edges) of the corner sulcus, as well as the interlocking and adapertural curvature of the ribs within the sulcus. In addition, near the apertural end of the sulcus, the mold exhibits fine, closely spaced, adaperturally arching grooves that extend transversely across the sulcus. These grooves, of course, correspond to fine, transverse ridges.

Five additional characteristics of *Reticulaconularia* not noted by Babcock and Feldmann (1986b) and Babcock *et al.* (1987) are: (1) midline of each face marked by a low, straight, external ridge; (2) nodes located at the ends of the interspace furrows (Van Iten *et al.*, 1996), which are the short troughs between the interspace ridges; (3) long axes of the interspace ridges generally line up across the transverse ribs ("collinear from one interspace to another"; Sinclair, 1942, p. 160), forming superficially continuous ridges that parallel the corner sulcus of their respective half-face (and thus are inclined at a low angle to the facial midline); (4) interspace ridges extend across the full width of the interspace, with no tapering or constriction; (5) interspace ridges inclined at high angles (approximately 70°) to the transverse ribs. Many reposited specimens show the raised midline, and this feature is evident in previously published light photographs (see for example Babcock and Feldmann, 1986b, fig. 35.3). The midline ridge is similar in form to the interspace ridges flank-



Text-fig. 1　*Reticulaconularia sussexensis* (Herpers, 1949)

1. NJSM 10749, light photograph of part of an external mold of a face. Note (a) the collinear alignment of the interspace bars (preserved as troughs) and (b) the occurrence of the nodes (preserved as pits) at the ends of the interspace furrows (preserved as bars). ×12.
2. NJSM 14960, light photograph of part of an external mold of a corner sulcus. Note the alternation and interlocking of the ends of the transverse ribs in the sulcus. ×11.

ing it, and is lower than the transverse ribs. Where the transverse ribs meet the midline in alternation, the midline ridge may be slightly zigzagged. The nodes generally are difficult to discern, and on most specimens they cannot be distinguished (due to weathering and/or exfoliation or breakage of the outermost test lamellae). However, distinct, external molds of a large number of nodes are displayed on a single face of the holotype of *R. sussexensis* (NJSM 10749; this paper, Text-figure 1.1). In addition, preserved nodes, situated at the ends of the interspace furrows, occur on a single face of a specimen (USNM 3144) of *R. baini*. The nodes on this specimen are minute, widely spaced, and elongate longitudinally. As noted above, the relatively wide spacing and collinear alignment of the interspace ridges across the transverse ribs is what gives *Reticulaconularia* its characteristic, reticulate facial ornament. However, in some specimens (e.g., NJSM 10806), the interspace ridges of adjacent interspaces are locally offset. Inclination of the interspace ridges at high angles to the transverse ribs was noted by Herpers (1949) in his detailed description of a single specimen of *R. sussexensis* (Herpers, 1949). Herpers (1949, p. 4) also stated that "the bars [interspace ridges] in adjacent channels [interspaces] are not in line but are more or less offset." This statement is true if one uses a reference line perpendicular to the transverse ribs; however, the interspace ridges are inclined to the transverse ribs, and their long axes are collinear from one interspace to another. Thus, the only interspace ridges that are offset are those whose long axes are not collinear, a condition which does characterize parts of the faces of some specimens.

REDESCRIPTION OF *CHANGSHACONUS CARINATA* ZHU, 1985

Changshaconus carinata Zhu, 1985

(Text-fig. 2)

1985 *Changshaconus carinata* Zhu, p. 533, pl. II, figs. 9, 10.

Material A single specimen (the holotype), preserved in dolostone and consisting of part (NIGP 90249a) and counterpart (NIGP 90249b).

Age and horizon Middle Devonian, upper part of the Qiziqiao Formation.

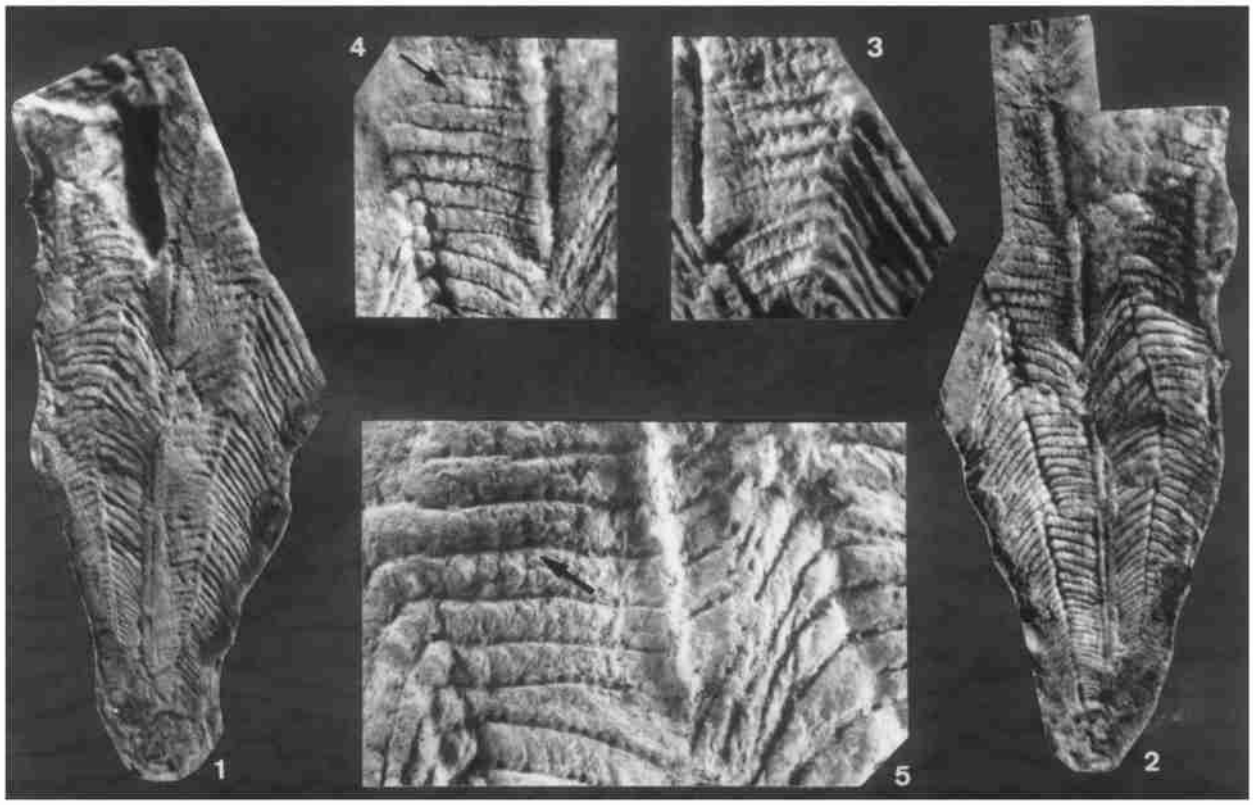
Locality Yuelu Mountain, Changsha, Hunan Province, South China.

Revised description Zhu's (1985) description of the single known specimen of *C. carinata* may be expanded as follows: Specimen compacted, incomplete, broken about 5 mm above the apex and with the faces locally distorted (sheared); specimen has four faces, two of which are embedded in rock matrix; apertural margin not preserved. Part (Text-fig. 2.1) approximately 11 mm long, with each of the two exposed faces having a maximum width of approximately 2.5 mm. Counterpart (Text-fig. 2.2) approximately 12 mm long and preserved primarily as an external mold. One face appears to have been slightly wider than the other, but due to compaction/distortion this is hard to determine. Angle of divergence of the two corners bordering a given face (apical angle) likewise difficult to determine, but it measures approximately 15° in the lower half of the "right" face of the part.

Corners sulcate and without internal thickening (carina). Midline of each face marked externally by a prominent, straight to slightly zigzagged, slender ridge that is slightly lower than the transverse ribs but higher than the interspace ridges flanking the midline; near the apical end of the part (Text-fig. 2.1), the midline ridge exhibits a narrow, central groove that may correspond to a low, internal carina.

Transverse ribs sharp-crested, nodose, straight or slightly arched, with the ends of approximately two-thirds of the transverse ribs meeting in opposition along the midline and the ends of the rest of the transverse ribs alternating there; angle formed by pairs of opposing or alternating transverse ribs ranges from approximately 115—126°; transverse ribs interrupted in the corner sulcus, with some ribs noticeably bent toward the aperture on the shoulders of the corner sulcus; ends of the transverse ribs of a given face alternate with the ends of the transverse ribs of the adjacent face (Text-fig. 2.5); transverse ribs number approximately 4 per mm near the apertural end and approximately 10—12 per mm at the apical end (NIGP 90249a), which is approximately 0.8 mm wide.

Nodes best seen on the counterpart (NIGP 90249b; Text-figs. 2.2, 2.4, 2.5), where they are



Text-fig. 2　*Changshaconus carinata* Zhu, 1985

1. NIGP 90249a, light photograph of the two exposed faces of the part. Specimen oriented with the apical end at the bottom of the photograph. Note the prominent ridge at the midline of each face and the central groove that may correspond to a low, internal carina (black arrow). ×9.
2. NIGP 90249b, light photograph of the counterpart of NIGP 90249a. ×9.
3. NIGP 90249a, detail (light photograph) of the apertural region of the "right" face of the part (Text-fig. 1.1). Note the poorly preserved nodes and the interspace ridges on the left side of the midline. ×17.
4. NIGP 90249b, detail (light photograph) of the upper half of the counterpart. Note the numerous molds of nodes to the left of the corner sulcus, and the occurrence of the nodes at the ends of the interspace ridges (preserved as external molds and therefore troughs) (black arrow). ×15.
5. NIGP 90249b, scanning electron photomicrograph (secondary electron mode) of part of a corner sulcus and the two faces on either side of it. Note the presence of (a) molds of nodes and (b) molds of interspace ridges. To the left of the corner sulcus, in the northwest quadrant of the photograph, note again that the nodes occur at the ends of the interspace ridges (black arrow). ×30.

preserved as external molds; nodes widely spaced, with approximately 9—10 nodes per mm near the apertural end and approximately 12 nodes per mm about 6 mm closer to the apical end; nodes located at the ends of the interspace ridges.

Interspace ridges widely spaced, lower and wider than the transverse ribs, collinear from one interspace to another and forming superficially continuous, longitudinal ridges that parallel the corner sulcus of their respective half-face and thus are inclined at a low angle to the facial midline (Text-fig. 2.3); interspace ridges extend across the full width of the interspace, with no apparent tapering or constriction.

Schott (apical wall) absent.

Discussion　The single currently known specimen of *C. carinata* is not as well preserved as the best specimens of *Reticulaconularia*, which show the reticulate facial ornament more clearly. Nevertheless, nearly all the anatomical characteristics exhibited by *Reticulaconularia* also occur in *C. carinata*. In *C. carinata*, the midline ridge and nodose transverse ribs are readily apparent, as are the interruption and alternation of the transverse ribs within the corner sulcus. The transverse ribs generally do not bend toward the aperture on the shoulders (edges) of the corner sulcus. However, this is also true of similarly preserved, external molds of the corner sulcus of *Reticulaconularia*. Moreover, the ends of a few of

the transverse ribs in *C. carinata* do show adapertural bending. This observation, coupled with the fact that adapertural bending is not readily apparent in poorly preserved external molds of the corner sulcus of *Reticulaconularia*, lead us to conclude that the transverse ribs of *C. carinata* were inflected toward the aperture on the shoulders (edges) of the corner sulcus. In other words, we predict that discoveries of better preserved *C. carinata* will demonstrate this characteristic conclusively.

Moving to the other aspects of the test's anatomy, the nodes and interspace ridges and furrows, all preserved chiefly as external molds, are best observed near the apertural end of the counterpart (Text-figs. 2.4, 2.5), on the "left" face (as seen with the apex pointing toward the observer). Here one can see clearly that the nodes are arranged in longitudinal files that parallel the corner of their respective half-face, and also that the nodes are located at the ends of the interspace ridges (which are preserved as troughs). The interspace ridges and furrows show perhaps the poorest preservation, and it is necessary to view them under low angle illumination in order to see that they are present and collinear from one interspace to another.

Comparisons *C. carinata* differs from the three species of *Reticulaconularia* in having the nodes located at the ends of the interspace ridges, and in having relatively low apical angles (approximately 15°). In addition, the midline ridge of *C. carinata* appears to be relatively higher than that of *Reticulaconularia*.

Changshaconus and *Reticulaconularia* are similar to all other conulariids except *Conulariella* Bouček, 1928 in having the transverse cross section square or slightly-moderately rectangular, and to all other conulariids except *Anaconularia* Sinclair, 1952 and *Conulariopsis* Sugiyama, 1942 in having the corners sulcate. *Changshaconus* and *Reticulaconularia* are further similar to *Climacoconus*, *Conularia*, *Conulariella*, *Ctenoconularia* Sinclair, 1952, *Flectoconularia* Waterhouse, 1979, *Malvinoconularia* Babcock *et al.*, 1987, *Notoconularia*, *Paraconularia*, and *Tasmanoconularia* Parfrey, 1982 in possessing transverse ribs whose longitudinal profile is trochoidal. As in *Ctenoconularia*, *Flectoconularia*, and *Tasmanoconularia*, as well as certain *Conularia* and *Paraconularia*, the transverse ribs of *Changshaconus* and *Reticulaconularia* are nodose, and their interspaces are crossed by interspace ridges and furrows. Like the interspace ridges of *Conularia* and *Paraconularia*, the interspace ridges of *Changshaconus* and *Reticulaconularia* extend across the full width of the interspaces. As in *Climacoconus*, *Notoconularia*, and *Paraconularia*, the transverse ribs of *C. carinata* and *Reticulaconularia* terminate, and their ends alternate and interlock, in the corner sulcus. As in *Climacoconus*, *Notoconularia*, and *Paraconularia*, the transverse ribs of *Changshaconus* and *Reticulaconularia* also are bent toward the aperture on the shoulders (edges) of the corner sulcus. Like the midlines of *Climacoconus*, *Glyptoconularia* Sinclair, and *Pseudoconularia* Bouček, 1928, the midlines of *Changshaconus* and *Reticulaconularia* are raised externally.

STATUS OF THE GENUS NAMES *CHANGSHACONUS* AND *RETICULACONULARIA*

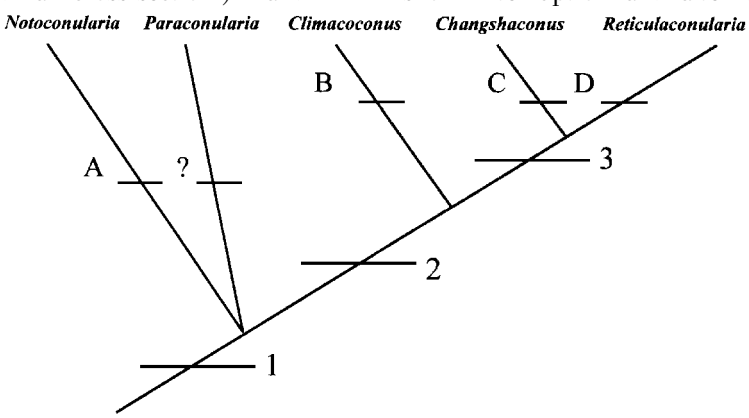
A logically necessary consequence of phylogenetic systematics (cladistics) is that a genus must contain at least two species in order to be a valid (monophyletic) taxon. Thus, unless it can be argued that *Changshaconus* as originally defined (Zhu, 1985) contains at least two species, this genus name should be dropped (and *C. carinata* assigned to a different genus) or, alternatively, *Changshaconus* should be redefined (rediagnosed) so that it includes at least two species. In our opinion, the detailed similarities uniquely shared by *C. carinata* and the three currently recognized species of *Reticulaconularia* probably are synapomorphies. In other words, we think that these four species probably were members of a single, monophyletic taxon that excluded all other conulariids (Text-fig. 3). The three species assigned by Babcock and Feldmann (1986b) and Babcock *et al.* (1987) to *Reticulaconularia* may have been more closely related to each other than any one of them was to *C. carinata*, but this hypothesis has yet to be tested. Until additional, better preserved material of *C. carinata* is collected, and a comprehensive analysis of phylogenetic relationships within Conulariida

successfully undertaken (see discussion in the following section), we prefer to retain the names *Changshaconus* and *Reticulaconularia*, with the understanding that one or both of them may have to be redefined (to eliminate paraphyly) or abandoned.

RELATIONSHIPS OF *CHANGSHACONUS* AND *RETICULACONULARIA* TO OTHER CONULARIIDS

Changshaconus and *Reticulaconularia* share detailed similarities in corner and facial anatomy with several other conulariids. In particular, bending and alternate arrangement (interlocking) of interrupted transverse ribs in the corner sulcus is a similarity uniquely shared with *Climacoconus*, *Notoconularia*, and *Paraconularia*. As in *Changshaconus* and *Reticulaconularia*, the transverse ribs of *Climacoconus*, *Notoconularia*, and *Paraconularia* are sharp-crested (trochoidal in longitudinal cross-section), and in some *Notoconularia* and *Paraconularia*, the transverse ribs are nodose and the interspaces crossed by interspace ridges. As in *Climacoconus*, the facial midline of *Changshaconus* and *Reticulaconularia* is the site of an external ridge.

We hypothesize that the detailed, uniquely shared similarities in corner anatomy noted above constitute a synapomorphy uniting *Changshaconus* + *Reticulaconularia*, *Climacoconus*, *Notoconularia*, and *Paraconularia* in a single, monophyletic taxon that excluded all other conulariids (Text-fig. 3). This hypothesis is at odds with the classification of conulariids proposed by Sinclair (1952), which implies that *Climacoconus* was more closely related to *Ctenoconularia* (subfamily Ctenoconularinae Sinclair, 1952) than it was to *Notoconularia* or *Paraconularia* (subfamily Paraconularinae Sinclair, 1952). As indicated by our inspection of actual specimens (e. g., GSC 94784), *Ctenoconularia* does show interruption and alternation of the transverse



Text-fig. 3　Cladogram summarizing our interpretation of the phylogenetic relationships between *Changshaconus* + *Reticulaconularia* and *Climacoconus*, *Notoconularia*, and *Paraconularia*. Conulariids that we think were not members of this group include *Anaconularia*, *Archaeoconularia*, *Conularia*, *Conulariella*, *Conularina*, *Conulariopsis*, *Eoconularia*, *Flectoconularia*, *Glyptoconularia*, *Malvinoconularia*, *Metaconularia*, *Pseudoconularia*, and *Tasmanoconularia*. Putative synapomorphies: (1) transverse ribs interrupted in the corner sulcus, with the transverse ribs of one face alternating and interlocking with the transverse ribs of the adjacent face; transverse ribs of both faces bent sharply toward the aperture on the shoulders (edges) of the corner sulcus; (2) midline of the four faces marked by an external ridge; (3) interspaces with interspace ridges that line up across the transverse ribs (producing a reticulate facial ornament). Putative autapomorphies: (A) central portion of the corner sulcus raised; (B) faces strongly corrugated; transverse ribs lack nodes and interspaces lack ridges; (C) transverse ribs with nodes that are located at the ends of the interspace ridges; (D) transverse ribs with nodes that are located at the ends of the interspace furrows. The authors are unaware of any anatomical features that can be interpreted as autapomorphies for the genus *Paraconularia*, and therefore we suggest that this taxon as currently defined (Babcock and Feldmann, 1986b) may be paraphyletic.

ribs in the corner sulcus. However, the transverse ribs do not bend on the shoulders (edges) of the corner sulcus, and they terminate well short of the center (midline) of the sulcus. Also unlike *Changshaconus* and *Reticulaconularia*, the interspace ridges of *Ctenoconularia* extend only about half-way across an interspace, and they parallel the facial midline (as opposed to the corner sulcus).

Sinclair's (1952) families and subfamilies were adopted by Xu and Li (1979), who erected a new subfamily, called Hunanoconulariinae, and presented a cladogram (Xu and Li, 1979, figure 3) summarizing their interpretations of the phylogenetic relationships among all families and subfamilies interpreted by these authors as conulariids. Unfortunately, Xu and Li (1979) did not offer any putative synapomorphies for the proposed branch points of their cladogram.

Because of uncertainty surrounding the phylogenetic relationships of the Conulariida to other taxa, it is difficult to test alternative hypotheses of phylogenetic relationships within Conulariida using outgroup-based, cladistic parsimony analysis. Nevertheless, several authors (e.g., Kiderlen, 1937; Bischoff, 1978; Werner, 1966, 1967; Van Iten, 1991, 1992a,b; Jerre, 1994; Van Iten *et al*., 1996) have argued that conulariids were most closely related to scyphozoan or cubozoan cnidarians, and that conulariid tests were homologous to finely lamellar, tubular thecae of coronatid scyphozoans. Coronatid thecae exhibit a conulariid-like ornament consisting of coarse, non-nodose, transverse ridges and finer, longitudinal ridges that line up across the transverse ridges (e.g., Werner, 1966, 1967). In some coronatids, the inner thecal lamellae exhibit a single series of longitudinally arrayed, thorn-like invaginations in the perradial and interradial planes of four-fold symmetry. The four series of thecal invaginations in the perradial symmetry planes have been interpreted as homologous to conulariid corners (Van Iten, 1991, 1992a,b; Van Iten *et al*., 1996), which in many genera are invaginated (sulcate). Assuming, as originally proposed by Werner (1966, 1967), that coronatids are the nearest living relatives of conulariids, and that coronatid thecae and conulariid tests are homologous structures, it may be possible to use coronatids as an outgroup for analysis of phylogenetic relationships within Conulariida. Of course, such a test will require a far more extensive analysis of conulariid species and anatomical characters than is appropriate for this article, and thus at present we simply offer this approach as a possible avenue for future research.

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