Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada

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Introduction

Retiolitids are, by virtue of their beautifully symmetrical and delicate meshwork structure, inherently fascinating organisms. However, because of these same features, as well as the small size of some, the structures, growth and development of these taxa are inadequately known.

The recovery of free, uncompressed specimens of retiolitids from limestone concretions in the Cape Phillips Formation of the Canadian Arctic Islands presented a unique opportunity. The specimens of most taxa are abundant, preservation is exquisite, and growth stages of most are present. Moreover, graptolite-bearing concretions occur in shales in more or less continuously exposed sequences ranging in age from mid Llandovery to early Ludlow.

In spite of the fact that Silurian retiolitids have long been known and illustrated, the numbers of isolated specimens are, with the exception of such classic studies as Tullberg (1883), Holm (1890), Wiman (1896), and especially Eisenack (1931, 1935, 1951, 1966), relatively few. The present study, in addition to recovering a number poorly known taxa, fills in some of the stratigraphic gaps left in earlier studies.

Material

The graptolite-bearing facies of the central and northern Arctic Islands have been named the Cape Phillips Formation by Thorsteinsson (1958). Graptolites are generally abundant both in compressed form in the shales, and uncompressed form in the enclosed limestone concretions (Thorsteinsson, 1958; Thorsteinsson and Kerr, 1968; Lenz, 1978). The Cape Phillips ranges in age from Late Ordovician (Ashgill) to Early Devonian, but graptolite-bearing nodules are most common in Llandovery to lower Ludlow strata.

Uncompressed graptolites, including the retiolitids of this study, were recovered from eight areas (fig. 1). The material studied was collected...
from strata of the mid Llandovery triangulatus or magnus zones to the latest Wenlock lundgrenil testis Zone or the apparently slightly younger nassa Zone. Only rare specimens of Holoretiolitidites were recovered from lower Ludlow strata. Age determinations of the retiolitids were by means of the associated monograptid faunas.

Systematic Paleontology

In this section, we focus discussion on the overall morphologic characteristics of the genera, and species are only briefly discussed. Furthermore, very little discussion is devoted to periderm fine structure since that aspect has already been admirably covered in the works of Andres (1977), Crowther and Rickards (1977), Bates and Kirk (1978) and Crowther (1981).

Family RETIOLITIDAE Lapworth 1873

Subfamily RETIOLITINAE Lapworth 1873, emended herein

Well developed reticula supported on a distinct clathria; sicula unsclerotized or partially sclerotized (prosicula and, rarely, metasicula); ancora stage stage well developed. Clathrial 'seams' face in, reticular 'seams' face out; surface fine structure of longitudinal striations composed of peridermal fibrils.

Remarks

The surface sculpture is consistent in all members in each of the two subfamilies. The variable occurrence of a prosicula and, rarely, metasicula, cannot be used as a diagnostic criterion of the subfamily (cf. Bulman, 1970, p. 108).

Genus PSEUDOPELGRAMATOGRAPTUS Pfibyl 1948

Diagnosis

Prosicula well developed. Virgella distally forming 4-pronged ancora which develops into basket-shaped corona formed of 2-3 crude rows of cells. Lateral bar from near apex of sicula splits into 2 parietal lists to form theca 1. Virgula moves quickly to ventral side of rhabdosome, alternately giving off short branches to 'left' and 'right'. Branch divides into short ventral and long dorsal, branch to form aboral list; these in turn divide and project laterally to form parietal lists. Zig-zag line on dorsal side alternately joins 'left' and 'right' thecal lists. Thecae orthograptid in profile, bases marked by a single median thread joining centre of thecal lip and aboral list of previous theca. Rhabdosome ovate in cross-section. Fine structure of lists comprises longitudinal striations only.

Remarks

Characteristics of the genus are the irregularly-sized and shaped meshes of the reticula and the paired, proximo-laterally directed thecal spines (see for example Tornquist (1890), Elles and Wood (1908), Bouček and Münch (1944), Münch (1952), Schauer (1971), Hutt (1974), Lenz (1978). The genus is well known but the complex nature of the clathrium and reticulum has not been previously understood. This study, however, has shown that the clathrium, while more complex than that of for example Retiolites, is in most ways remarkably similar. The presence of stomata is previously unreported in the genus. The stomata are irregular in outline, show no indication of thick-
ened rims and, like those of Stomatograptus, are elevated above the area of the surrounding reticula.

The lack of any evidence of a lacinia requires comment. By analogy with the sclerotized ventral walls of the thecae of Stomatograptus, the lacinia must have been very delicate. Furthermore, most compressed specimens are without lacinia. In fact, some illustrations such as those of Figs. 223a,b,c of Elles and Wood (1908) and especially Text-fig. 12 of Hutt (1974) can, by comparison with the uncompressed material of this study, clearly be seen to be laterally flattened and distorted elements of the thecal lips and spines.

All specimens except one, recovered in this study are assignable to P. obtusus Lapworth. Parameters are as follows: maximum width of somewhat flattened fragments: 4.5 mm; thecae about 12 in 10 mm; mesh of reticula difficult to measure, 3-5 in 2 mm; spines at least 1.2 mm long. The one exception is presumably assignable to P. longispinus Bouéck and Münch because of its overall finer mesh (about 6 in 2 mm), 1-2 rows of finer ovate meshes along the lateral margins of the thecae, and spines at least 2.5 mm long.

Occurrence and Age

Found only at Laura Lakes area in the Late Llandovery turriculatus Zone.

Genus PSEUDORETIOLITES Bouéck and Münch 1944

Diagnosis

Prosicula characteristically present (pl. 1, fig. 7); metastoma rarely preserved (pl. 1, fig. 3). Corona developed from four-pronged ancora, hemispherical and basket-like, formed of 3-4 rows of gently spiralled lists joined to longitudinally arrayed lists (pl. 1, fig. 5). In specimens with metastoma, “struts” anchor sicula to reticula. First theca develops from clathrial list arising near top of sicula; remaining thecae developing in manner similar to that of Pseudoplegmatograptus. “Floor” of theca marked by long median list arising from aboral list of previous theca and connected to lip of theca. Lip of theca formed of fine, laterally elongate meshes, divided medially by a zig-zag list. Thecae distinctly orthograptid in profile, with moderately accentuated lips and curved, anterolaterally directed apertures. Reticulum moderately fine, meshwork polygonal, with meshes of more or less uniform size. Median region of both sides of rhombosome generally bear large, irregularly shaped, thin-walled stomata, the margins of which stand above the adjacent reticula. Stomata at least twice the size of reticulum mesh-size.

Remarks

Obut and Zaslavskaya (1976) tentatively suggested that Pseudoretiolitinae be assigned to a separate (new) subfamily Pseudoretiolitinae because of the presence of a metastoma. However, in view of the fact that the metastoma is rarely present (at least in our material), and that thecal development is essentially like that of Retiolites, the move seems unnecessary.

The corona, with its beautiful symmetry and nearly square meshes, the moderately regular reticular meshwork, the normally poorly-seen clathrium, and the dense mesh network forming the lip of theca, are all distinctive of the genus and are, we feel, sufficient justification for the retention of Pseudoretiolites as a separate taxon, unlike Bulman (1970) who placed it in synonymy with Retiolites. The basket-like corona is especially diagnostic, and make recognition of the genus easy.

Some studies, based on the study of flattened specimens, note the presence of ‘membranes’ (e.g. Perrett (1899), Elles and Wood (1908), Bouéck and Münch (1944), Münch (1952), Hutt (1974)). On the other hand, the excellent but flattened material of Chen (1983) gives no indication of ‘membranes’, while clearly showing the fine meshwork forming the lip of the thecae as is recognized in all our specimens. We have seen no sclerotization or membrane formation and offer no overall explanation, but we do suggest that the flattening of the fine meshwork of the thecae could readily lead to the appearance of a continuous membrane in these areas.

One species, P. cf. decoratus Bouéck and Münch, has been recovered. It is characterized by a ovate rhambosome outline, thecae 14–12 in 10 mm, reticular meshwork 6–7 in 2 mm, maximum length of incomplete specimen 8.5 mm, and ovate stomata about 1.2 mm long.

Occurrence and Age

Found at Rookery Creek and southwest of Cape Manning in the triangulatus/magnus, convolutus and turriculatus zones; fairly common.

Genus RETIOLITES Barrande 1850 (not illustrated)

Remarks

Retiolites, particularly of the geinitzianus group, is widely known, and its morphology has been understood for nearly 100 years (see for example, Holm (1890), Bulman (especially illustration of 1938, fig. 40b), Bouéck and Münch (1944), and particularly the SEM studies of Bates and Kirk (1978) and Crowther (1981)).

Characteristics of the R. geinitzianus group include the relatively low, paraboloid-shaped corona made up of relatively few and coarse, polygonal meshes and the accompanying two large pores at the ‘top’ of the corona; the very robust clathria with strong parietal lists walled to the reticula and clearly marking the position of the thecae; the thecal apertures which distally are more or less parallel to the rhambosome; and the strong, fine, relatively uniform sized meshwork of the reticula. The development of ‘thecal hoods’ over the 3–4 proximal thecae is not widely known, although they and the succeeding ‘thecal con-
strictions' were illustrated by Crowther (1981). Specimens which otherwise are identical may or may not possess hoods and constrictions, although they are more common in, but not restricted to, stratigraphically lower specimens.

The presence of a prosicula in the geinitzianus group has been documented by Kühne (1953) and Obut and Zaslavskaya (1976). However, the present study shows that in the great majority of cases, no evidence of the prosicula remains, and that the nature of the prosicula is variable: some siculae are represented by a thickening, some by 2–3 threads, some by only the anterior portion and, most rarely, by a complete prosicula.

One species, R. geinitzianus denstreticulatus Bouček, is recognized in this study. It is characterized by a maximum uncompressed width of 3.5 mm, 14–11 thecae in 10 mm, thecae about 2 times longer than wide and inclined about 50° to the virgula and, above all, a fine reticulum. The meshes form 4–5 rows per theca and are spaced about 6 mm. It differs from R. g. angustidentis in possessing a much finer reticulum.

Occurrence and Age

Occurs commonly in every section; appears in the late Llandovery spiralis Zone and extends to the late Wenlock lundgreniites Zone. It is most abundant in the spiralis and grandis (= sakmaricus) zones.

Genus STOMATOGRAPTUS Tullberg 1883

Remarks

The overall similarity between the morphology of Retiolites and Stomatoograptus has long been recognized, and in fact Bouček and Münch (1944) in their diagnosis of the latter genus simply state (p. 46) "... sonst wie die Untergattung Retiolites". Furthermore, the walls of the stomata of various sizes are present in all Cape Phillips specimens, but it is interesting to note that in one fully developed, large specimen, stomata are irregular and even joined (pl. 2, fig. 1), a feature which surely must have weakened the rhabdosome and throws doubt on Rickards, et al. (1977, p. 31) statement that stomata "... are almost certainly a strengthening feature of the reticula". Furthermore, the walls of the stomata of some specimens are not in the least thickened.

The other diagnostic feature, that of the solid thecal walls, has not been observed in any of the Cape Phillips specimens. However, a close examination of the lists where the 'floor' of the theca would have been clearly shows thin and ragged remnants of the wall (pl. 2, fig. 4). It is probable therefore, that acid treatment destroyed the delicate walls. The supposed pore-bearing Retiolites described by Bjerrskov (1975) might then be explainable as a Stomatoograptus which has had its thecal walls destroyed.

The proximal end of the genus consistently shows the presence of a well developed prosicula, while the corona is crudely rounded, basket-shaped and composed of relatively small and regular polygonal meshes.

Several taxa are recognized, or tentatively recognized, in this study; i.e. S. grandis grandis (Suess) (pl. 2, fig. 2), S. grandis imperfectus Bouček and Münch (pl. 2, figs. 1,4) and S. sp. (pl. 2, figs. 6,8,10). The first named taxon is characterized by having a maximum uncompressed width of 4 mm, thecal spacing of about 6.5 in 5 mm, thecae inclined at 50°–60° to the virgula, subrounded, heavy-rimmed stomata 0.6–0.7 mm in diameter and a dense reticula with uniform, fine mesh sizes. S. sp. imperfectus is incomplete, but 5 mm wide with thecae numbering 5 in 5 mm distally and inclined about 50°–60° to the virgula, thecal lips are acute and moderately projecting, and the reticular meshwork is coarser than that of S. grandis grandis. S. sp. possesses a slightly widening rhabdosome, thecae which are distinctly orthograptid in profile, numbering 5–6 in 5 mm, and inclined at 30°–50° to the virgula; the reticular meshwork is moderately fine proximally but becomes increasingly coarse and quadrate distally.

Most juvenile specimens from the highest range of the genus must, of necessity, also be assigned to 'S. sp.'.

Occurrence and Age

Large specimens are common in the spiralis and sakmaricus zones of most sections, and rarer juveniles occur in the late Wenlock lundgreniites Zone. S. grandis grandis is found only in the spiralis Zone.

Subfamily PLECTOGRAPTINAE Bouček and Münch, 1952; emended herein

Clathria well developed, sometimes without reticula, lacinia absent; development with ancora stage; proximal end of rhabdosome usually somewhat inflated (corona), narrowing distally and in some genera terminates in a slender tubular “appendix”. Virgula free or incorporated into ventral wall. Surface of lists pustulose on outside surface (pl. 3, fig. 6). Seams of the clathria and reticula generally face in and out, respectively.

Genus PLECTOGRAPTUS Moberg and Törnquist, 1909

Remarks

The genus is typically characterized by a clathria of open, subhexagonal meshes and a free, central virgula. P. macilentus, the type species, while not recovered uncompressed, occurs in
compressed form in Lower Ludlow strata of the Cape Phillips Formation (Jackson, et al., 1978).


Diagnosis
Virgula free, attached only to anca, extends only to level of theca 4 or 5. Corona of few lists, weakly rounded, rectangular in cross-section. Clathrium and reticulum complex and disorderly, meshes polygonal to triangular to quadrilateral, relatively fine proximally, becoming coarser distally. Thecae generally clineocoograptid proximally (pl. 3, fig. 13), more or less orthograptid distally. Thecae marked by one or two shorter, transverse, curved lists, the outer margins of which are sometimes joined by a vertical list, and by a longer and more projecting lower apertural lip. Rhabdosome rectangular in cross-section, widening abruptly proximally, and then maintaining constant width or widening very gradually. Occasional specimens narrow slightly distally. Seams of lists all face inward making distinction between clathrium and reticulum difficult; in this way it differs from other plectograptids.

Remarks
This subgenus is similar to the type Plectograptus macilentus in its possession of a free central virgula and rectangular cross-section; it differs markedly, however, in the possession of a complex and disorderly clathrium/reticulum. Bouček and Münch (1952) tentatively suggested that P. texor might be assignable to a new subgenus of Plectograptus.

Obut and Zaslavskaya (1976) noted the occurrence of a delicate prosicula in juvenile stages of S. parens; we have not recovered any prosicula-bearing specimens of P. (Sokolovograptus) texor.

We recognize one species, P. (Sokolovograptus) texor, from the Cape Phillips. It is characterized by an extremely variable meshwork, a width of 0.7–1.3 mm exclusive of apertural lips and 0.9–2.0 mm inclusive of apertural lips, a thecal spacing of 7–8 in 5 mm, and a length of at least 8 mm. P. (S.) texor differs from the species described as P.? bouceki by Rickards (1967), in being narrower, possessing more closely spaced thecae, and apparently possessing a coarser clathrial meshwork and somewhat different thecal apertural lists. It differs from S. parens Obut and Zaslavskaya primarily in being much wider, but is otherwise very similar and might possibly be conspecific.

Occurrence and Age
Recovered in almost all sections, sometimes in considerable abundance. It is rare in the turriculatus Zone, and common in the spiralis to lundgreniitises zones.

Genus PARAPLECTOGRAPTUS Pitjyl, 1948
Diagnosis
Ancora four-pronged; corona simple, of few meshes, somewhat rhomboid in profile, and square in cross-section. Rhabdosome walls (clathrium) sharply angular. Virgula central proximally, quickly moving to ventral side and becoming incorporated in, and part of, ventral wall. Horizontal lists arise alternately on left and right sides of virgula and join outer walls. Dorsal wall either of zig-zag pleural lists connected directly to outer walls, or with very short horizontal lists connecting pleural lists to outer walls. Reticulum may or may not be present, lists generally few in number and finer than clathrium, sometimes more common in proximal region and absent in distal portions, and or may be more common along median line of rhabdosome. Clathrial seams in those of the reticulum face out.

Remarks
Paraplectoegraptus, as visualized in this study, incorporates the type Paraplectoegraptus eiseli (pl. 3, fig. 4) and "Plectoegraptus praemacilentus" of Bouček and Münch (1952) (pl. 3, figs. 2,5). In its simpler, more orderly morph this genus is superficially similar to Plectograptus (s.s.), but differs strikingly in possessing a virgula which is part of the ventral wall. The morphology of Paraplectoegraptus ranges from one with only a clathrium, to one with a more moderately complex but delicate reticulum over the clathrium. The clathrial structures of species recognized herein are essentially identical.

Bouček and Münch (1952), in their discussion of Plectograptus praemacilentus imply that the virgula of the Czech specimens is, like the typical Plectograptus, free throughout its length. However, an examination of their illustrations shows the virgula to be suspiciously straight throughout, an observation suggesting that the virgula in their material is probably attached. This is further suggested by an examination of flattened material from the Arctic identified as the same species by Lenz (1978). These flattened but well preserved specimens are clearly the same species as the uncompressed material studied herein, yet the attachment of the virgula to the ventral wall is recognizable only with difficulty, and then only after comparison with the uncompressed rhabdosomes. We suggest therefore that the virgula of the type P. macilentus of Czechoslovakia is attached.

Three species, P. eiseli, P. praemacilentus and P. sp. A are recognized in this study. P. eiseli has few reticular lists or none, is about 0.9 mm in width, and a thecal spacing of 6–7 in 3 mm, (slightly higher than that stated by Bouček and Münch (1952)). P. praemacilentus and P. sp. A (pl. 3, fig. 7) are characterized by the possession of a reticulum, that of the latter species being finer, denser and more disorderly over the entire surface, and/or more dense in the medial region. In some cases, the meshwork still retains a crude overall zig-zag pattern. The rhabdosome of both are generally parallel-sided, up to 1.4 mm in width, and thecae number 5–7.5 in 5 mm.

Eisenack (1951) illustrated "Retiolites tenuis", a species subsequently described as "Gothograptus tenuis" by Obut and Sobolevskaya (1965). By comparison with early growth stages of our material (pl. 3, fig. 9), we feel that Eisenack's species is nothing more than a juvenile stage of P. praemacilentus.

Occurrence and Age
Very common in most sections; P. praemacilentus ranges in age from the turriculatus Zone (rare) to the nassa Zone; P. sp. A ranges from the spiralis Zone to about the rigidas Zone (lower Wenlock). Both species are most abundant in upper Llandovery strata. P. eiseli is less common and ranges from the spiralis Zone to about "mid" Wenlock.

Genus GOTHOGRAPTUS Frech, 1897
Diagnosis (based primarily on G. eisenacki Obut and Sobolevskaya, 1965)
Corona rounded, width nearly equal to maximum width of rhabdosome which is attained at the level of the first theca, composed of a few irregular clathrial lists. Coronal meshwork made finer through addition of reticular lists, but maintains two large, adjacent basal-lateral pores. Rhabdosome of most specimens narrow rapidly distally and thecae generally number 3–4 per side. Clathrial pattern complex and irregular; reticulum well developed, relatively fine, list widths becoming coarser with maturity. Thecae long, outer margins undulose (pl. 2, figs. 13,14), overall rather similar in profile to those of Pseudoglycograptus, apertures generally horizontal. Meshwork of tubular appendix finer than that of more proximal regions. Virgula moves to ventral side early in development, but becomes at-
tailed to, and incorporated in, ventral wall about two-thirds along length of typical rhabdosome, then joined by alternating left and right bars for remainder of length; extends beyond rhabdosome. Seams of clathrium face in, and those of reticulum face out.

Remarks
The species recognized in this study, *G. eisenacki*, characteristically possesses only 3–4 thecae per side, but may range from 2 to 5 or rarely more; typically narrows rapidly distally and, most uniquely, possesses thecae more like those of *Pseudoglyptograptus* than *Climacograptus*. It differs from the type additionally in being consistently smaller, in possessing a relatively coarser reticulum (particularly that of the thecal margins), and in that the virgula is free for a relatively much greater part of its length. No hint of such thecal hoods as illustrated for *G. nassa* by Wiman (1896) is present.

Occurrence and Age
Found only at Laura Lakes area and Rookery Creek in the latest Wenlock *nassa* beds.

Genus *HOLORETIOLITES* Eisenack, 1951
Remarks
The genus is represented by only two partial specimens, probably assignable to *H. simplex* (Eisenack) (1935) from Lower Ludlow strata. The thecae are climacograptid and appear to number 2 per side, the clathrium is simple and more or less zig-zag, and the distal appendix is not developed. The fine structure is pustulose.

Occurrence and Age
Found only at Laura Lakes area in Lower Ludlow strata.

Stratigraphic Distribution of Retiolitids

The present study extends or modifies the stratigraphic ranges of the taxa *Retiolites*, *Stomato­graptus*, *Paraplectograptus* and *Plectograptus* (Sokolovograptus). In most cases, the ranges of the genera are considerably extended beyond that shown in the literature, particularly that of Rickards, et al. (1977).

A composite of the zonal schemes of Thorsteinsson (1958) and Lenz (1978) from the Arctic Islands, and Lenz (1982) from the northern Cordillera, is used as a standard against which to display the stratigraphic ranges of the taxa recognized in this study (Table 1). It must be emphasized that the study is a preliminary one, and that subsequent recovery of additional material and taxonomic revision could alter the ranges somewhat.

In their section on the evolution of the retiolitids, Rickards, et al. (1977) relied heavily on their assessment of the stratigraphic ranges of the taxa. In view of the much extended ranges of most of the genera and species recovered in this study, it is clear that the evolutionary history must be completely reevaluated. Furthermore, much more attention must be directed to the development of the clathrium and reticulum in order to understand the phylogenetic relationships.

Acknowledgements. Hermann Jaeger very kindly sent photographs of isolated specimens of *Plectograptus macilentus*, and Peter Crowther offered a number of written comments on retiolitids in general. R. Thorsteinsson directed Melchin to the Cape Manning section, and A. D. McCracken collected some material from Marshall Peninsula and Rookery Creek. Financial support for field and laboratory studies was through a Natural Sciences and Engineering Research Council operating grant to Lenz; transportation costs to the field were supplied to Melchin by the Northern Research Group of the University of Western Ontario; and air support in the field was through the Polar Continental Shelf Project of the Department of Energy, Mines and Resources.
Dansk sammendrag

De retilolide grasplolitlægter Pseudoretilolites, Pseudoplegmatograptus, Paraplectograpthus, Plectograpthus, Retiolites, Somatograptus, Gothographitus og Holoretilolites beskrives fra den arktisk canadiske Cape Phillips Formation. Den biostratigrafiske spændvidde er fra mellem llandovery (magnus/triangulatus zonen) til nedre ludlow (nilsoni zonen).

På basis af overflade ornamentikken bliver Retiolitidae og Plectograptinae emenderede. Paraplectograpthus emenderes til også at inkludere former med et retikulum.

References


