REVISION OF THE SILURIAN GRAPTOLITE GENUS *RETIOLITES*

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ABSTRACT. The three *Retiolites* species, *R. geinitzianus*, *R. australis* and *R. angustidens*, may be distinguished only by differences in their dorso-ventral width (both the maximum attained and the rate of increase from the proximal end). Other characters used previously in specific discrimination are septal bar inclination and meshwork density. The former shows considerable intraspecific variation, with no consistent differences between the species. The latter is dependent upon the astogenetic stage of the specimen examined. Whilst *R. geinitzianus* and *R. angustidens* appear to have been of very widespread distribution, specimens of *R. australis* are known only from north of the Silurian equator. All three species have long stratigraphical ranges (for graptoloids) and are thus of little biostratigraphical utility other than in indicating a Telychian (Upper Llandovery) or Wenlock age.

MEMBERS of the graptolite genus *Retiolites* Barrande, 1850 are among the most beautiful and distinctive of all Silurian graptoloids. Surprisingly, despite the wealth of recent publications on Silurian retiolitids (e.g. Bates and Kirk 1978, 1984, 1986, 1987; Lenz and Melchin 1987*a*, 1987*b*; Bates *et al.* 1988; Kozłowska-Dawidziuk 1995), the most recent concerned with the taxonomy of *Retiolites* at the species level was published over half a century ago (Bouček and Münch 1944). Given the considerable and continuing interest in Silurian retiolitids, and the resurgence of studies into high-resolution graptolite biozonation and correlation (e.g. see Koren' 1995), it was clear that a taxonomic revision of the genus was long overdue; this is presented herein.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; BB, Bouček collection, Czech Geological Survey, Prague; BGS, British Geological Survey, Keyworth; BM(NH), The Natural History Museum, London; GSE, British Geological Survey, Edinburgh; L, National Museum, Prague; MV, Museum of Victoria, Melbourne, Australia; N, United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of the Russian Academy of Science, Novosibirsk; NMW, National Museums and Galleries of Wales, Cardiff; PŠ, Štorch collection, Czech Geological Survey, Prague.

SYSTEMATIC PALAEONTOLOGY

Terminology (Text-fig. 1). The terminology used herein is largely that of Bates (1990). The term 'septal bar' (Bates and Kirk 1978) is used for the thick and prominent lists (sb, Text-fig. 1), running at an angle to the rhabdosome axis towards the ventral sides of the rhabdosome. As noted by Kirk (1973, p. 10), the term 'parietal list' (used by Elles and Wood 1908, and more recently by e.g. Bulman 1970; Crowther 1981; Lenz and Melchin 1987*a*; Kozłowska-Dawidziuk 1995) is inappropriate for these structures as they do not enclose any body cavity (e.g. a theca). It is important to appreciate that the septal bars do not mark the junctions of interthecal septa with thecal walls (note that *Retiolites* do not possess interthecal septa). Thecae are rarely preserved, but it has been shown by Holm (1890, pl. 2, fig. 5; Pl. 1, fig. 4), Bates and Kirk (1978, pl. 12, fig. 2) and Lenz and Melchin (1987*b*, fig. 1) that the free ventral walls of the thecae are at a lower angle to the rhabdosome axis than the septal bars (see also Text-fig. 1); the arrangement of thecae depicted by Bulman (1970, fig. 59, 8) in the *Treatise* is incorrect.

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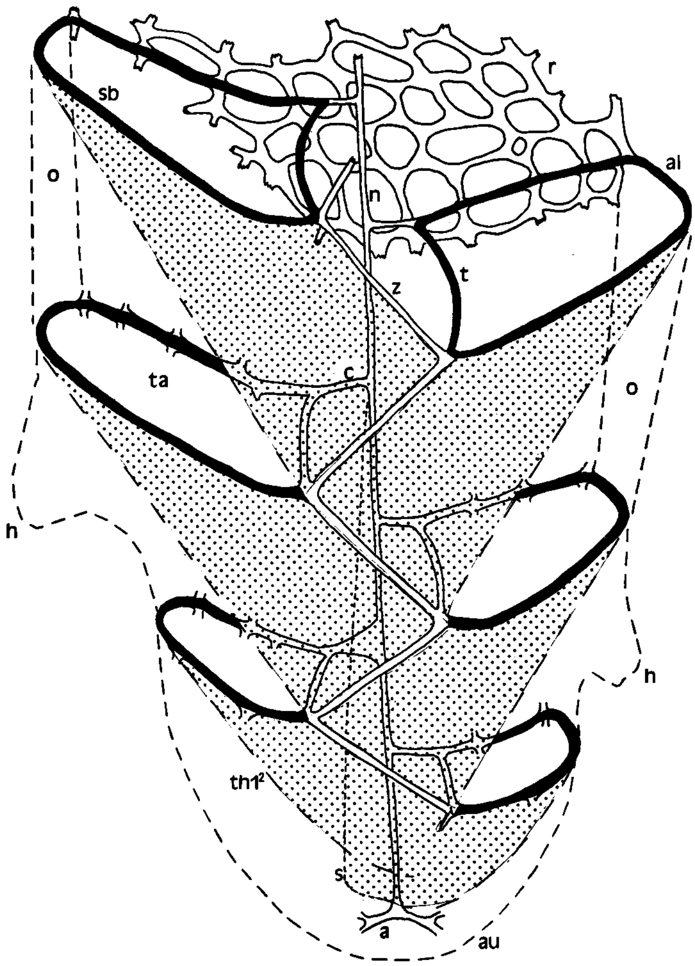


TEXT-FIG. 1. Diagrammatic representation of a *Retiolites* rhabdosome in reverse view, with the ancora sleeve largely stripped away so that the thecal framework is visible. The stippled area represents the (very rarely preserved) thin periderm of the sicula and proximal thecae. The dashed lines on the ventral sides of the rhabdosome show the ventral extent of the obverse and reverse ancora sleeve panels. The lists in solid black are those surrounding the thecal apertures. Abbreviations: a, ancora; al, thecal apertural lip; au, ancora umbrella; c, connecting rod; h, hoods over proximal orifices; n, nema; o, orifices; r, reticulum (ancora sleeve) – only a small part at the distal end of the obverse side of the rhabdosome is shown; s, sicula; sb, septal bar; t, transverse rod; ta, thecal aperture; th, theca; z, zigzag list.

The prominent openings along the ventral sides of the rhabdosome (Pl. 1, fig. 2) should be termed orifices (o, Text-fig. 1) rather than apertures; they are not homologous with the thecal apertures. The latter are somewhat introverted (see Pl. 1, fig. 4; ta, Text-fig. 1). The inclination of a thecal aperture is the angle between the septal bar and the rhabdosome axis.

This paper is concerned only with the gross morphological features of *Retiolites* rhabdosomes; emphasis is placed on the distinguishing features of each species. For fuller descriptions (including micro- and ultrastructural detail) of chemically isolated *Retiolites* material from limestones and carbonate nodules, see Bates and Kirk (1978, 1986, in press) and Lenz and Melchin (1987*b*). The former authors also discussed the affinities, mode of rhabdosome secretion and palaeoautecology of *Retiolites* and other retiolitids (Bates and Kirk 1978, 1984, 1986, 1987, 1992, in press).

Measurements. Measurement of dorso-ventral width, both the maximum attained and the rate of expansion proximally, provides the easiest means of distinguishing between *Retiolites* species. For ease of comparison, measurements of rhabdosome dorso-ventral width are given below at specified distances (in mm) from the proximal end.

Some authors (e.g. Bouček and Münch 1944; Loydell and Cave 1993) considered the inclination of the septal bars to the rhabdosome axis to be of importance in differentiating species. This angle varies considerably intraspecifically (e.g. distally in *R. geinitzianus*, from 35–40° in the specimen illustrated by Loydell and Cave 1993, fig. 9a, to typically 55–60° in specimens from the *murchisoni* Biozone (Sheinwoodian) of Bohemia); it is not a diagnostic feature for any of the three species described below.

Measurements of meshwork density are quoted by several authors (e.g. Bouček and Münch 1944; Bjerreskov 1975), and the species *Retiolites densereticulatus* Bouček, 1931 was erected solely on the basis of its possession of a dense reticular meshwork. Scanning electron microscope studies have shown, however, that meshwork density in *Retiolites* is a function of astogeny, with more mature and 'gerontic' specimens having a denser meshwork (see e.g. Crowther 1981, pp. 92–94, pl. 15, fig. 5; Pl. 1, fig. 5).

Taxa described. Several species originally described under *Retiolites* do not belong in this genus and therefore are not described below. These are the following.

1. *Retiolites grandis* Suess, 1851. A junior synonym of *R. grandis*, *Stomatograptus törnquisti* Tullberg, 1883, is type species of *Stomatograptus* Tullberg, 1883.
2. *Retiolites rete* Richter, 1853. This rare species, recorded only from the lower Telychian of Germany, was placed by Bouček and Münch (1944) in their subgenus *Pseudoretiolites*, a taxon now accorded generic status (see e.g. Lenz and Melchin 1987*a*; Bates and Kirk 1992).
3. *Retiolites perlatus* Nicholson, 1868. Designated type species of *Pseudoretiolites* by Bouček and Münch (1944).
4. *Retiolites perlatus* var. *daironi* Lapworth, 1877. Like *perlatus*, this species is now assigned to *Pseudoretiolites* (e.g. Loydell 1993*b*).
5. *Retiolites perlatus* var. *obesus* Lapworth, 1877. Elles and Wood (1908) placed this in a subgenus of non-ancorate Ordovician 'retiolitid' (*Plegmatograptus*). Přibyl (1948) designated *obesus* type species of his genus *Pseudoplegmatograptus*.
6. *Retiolites macilentus* Törnquist, 1887. Moberg and Törnquist (1909) designated this as type species of their genus *Plectograptus*.
7. *Retiolites nassa* Holm, 1890. Type species of *Gothograptus* Frech, 1897.
8. *Retiolites spinosus* Wood, 1900. Elles and Wood (1908) placed this species in a subgenus (*Gothograptus*); it was subsequently designated type species of *Spinograptus* (see Bouček and Münch 1952).
9. *Retiolites eiseli* Manck, 1917. Designated type species of *Paraplectograptus* by Bouček and Münch (*in* Přibyl 1948; see also Bouček and Münch 1952).
10. *Retiolites praecursor* Kirste, 1919. Originally described from the Aeronian *cometa* Biozone, this species was assigned tentatively to *Pseudoretiolites* by Bouček and Münch (1944). It is from significantly older strata than any described *Retiolites sensu stricto* and Kirste's illustration (pl. 3, fig. 58) suggests that it is highly unlikely that the species should be placed in *Retiolites*.
11. *Retiolites geinitzianus* Barrande var. *maximus* Ruedemann, 1947. The authors have been unable to trace the single specimen assigned to this taxon by Ruedemann. The dimensions are comparable to those of *Stomatograptus grandis*. The horizon is quoted as *convolutus* Biozone (Aeronian), although it is possible (A. C. Lenz, pers. comm. 1996) that Ruedemann had confused '*Monograptus*' *convolutus* (Hisinger) with the Telychian species *Oktavites spiralis* (Geinitz).
12. *Retiolites obliquidens* Obut, 1949. The holotype, illustrated by Obut (1949, pl. 2, fig. 2a–b) and by Obut and Sobolevskaya (1966, pl. 4, fig. 1), is clearly a specimen of *Stomatograptus grandis* (Suess, 1851) *sensu lato*; stomata are prominent, particularly near the proximal end, and the rhabdosome's overall shape and

dimensions also match those of the latter species. Obut (1949, p. 16) stated that the holotype was collected from strata of early Wenlock age. Obut and Sobolevskaya (1966, p. 54) gave a rather different and somewhat more precise horizon for this specimen of '*spiralis* and *grandis*' Biozone (upper Telychian).

13. *Retiolites geinitzianus* var. *liangshanensis* Huo, 1957. This was distinguished by Huo from *R. geinitzianus* only 'by the greater length of the polypary'. Huo's specimens were destroyed during the 'Cultural Revolution' (Loydell 1993*a*), but from Huo's illustrations it seems that the species probably belongs in *Stomatograptus* (and almost certainly not in *Retiolites*).

14. *Retiolites nevadensis* Berry and Murphy, 1975. This species was assigned to *Agastograptus* by Obut and Zaslavskaya (1986) and to *Spinograptus* by Lenz and Melchin (1991) and Lenz (1993). Kozłowska-Dawidziuk (1995) noted differences between Berry and Murphy's species and other *Spinograptus* species, suggesting that *nevadensis* (and *S. apoxys* Lenz, 1993) form a group 'generically separate' from *Spinograptus*. Whatever the species' eventual generic assignment, it seems that it does not belong in *Retiolites*.

15. *Retiolites minutus* Ni, 1978. The type material has been examined recently by one of us (PŠ) and is assignable to *Pseudoretiolites*.

In addition to the above are several other species, originally assigned to *Retiolites* by Eisenack (1951), now placed in the genera *Paraplectograptus*, *Neogothograptus*, *Holoretiolites*, *Spinograptus* and *Plectograptus* (see Kozłowska-Dawidziuk 1995 for details).

Chang and Sun (1947, pl. 1, fig. 9) illustrated what they considered to be a new variety, '*Retiolites geinizianus* [*sic*] var. *spinus* Chang (var. nov.)'. No description was provided, however, and thus this taxon is a *nomen nudum*. The illustration appears to be of a *Stomatograptus*.

Tectonic deformation. Tectonically deformed material which we have not examined personally (e.g. that of Romariz 1962; Schauer 1971; Obut. *et al.* 1988) is omitted from the synonymies below as it is not possible to determine from the illustrations the extent to which the original rhabdosome dimensions have been modified.

Stratigraphical ranges. Ranges quoted appear to apply to all areas except Arctic Canada, from which Lenz and Melchin (1987*a*) reported *Retiolites* from the Homerian Stage (Upper Wenlock). Elsewhere, the extinction of *Retiolites* formed part of the mid Sheinwoodian '*murchisoni* [biotic crisis] Event', recently identified by Štorch (1995) in the Barrandian area of the Czech Republic and undoubtedly of more widespread significance (see e.g. Loydell and Cave 1996).

Order GRAPTOLOIDEA Lapworth, 1873
Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTOIDEA Lapworth, 1873
Family RETIOLITIDAE Lapworth, 1873
Subfamily RETIOLITINAE Lapworth, 1873

Genus RETIOLITES Barrande, 1850
(= *Gladiolites* Barrande, 1850, *nom. suppr.* ICZN Opinion 199; *Gladiograptus* Lapworth *in* Hopkinson and Lapworth, 1875; *Dimykterograptus* Haberfelner, 1936)

Type species. *Gladiolites geinitzianus* Barrande, 1850, from the Motol Formation (Wenlock) of Bohemia.

Diagnosis. Sicula represented by virga and virgella, with traces of the prosicular rim; sicular walls normally preserved only as seams. Thecal framework consisting of an obverse nema and reverse zigzag list with connecting rods extending from the former to the thecae. Thecae orthograptid in outline, with introverted apertures; each thecal aperture defined by septal bars laterally, a transverse rod dorsally and a thecal lip ventrally; free ventral walls originate at dorsal transverse rods. Ancora sleeve commences with bifurcation of the virgella to give two primary lists, and further branchings to form the ancora umbrella; ancora sleeve forms two panels covering the obverse and reverse faces of the rhabdosome, panels convex, lists having seams on their external sides; lists making connection with the septal bars by 'plug-hole' junctions, where the inward-facing insertion seam on the septal bar is linked with the outward-facing seam on the ancora sleeve list. The spaces between the sleeve panels and the thecal framework form two external common canals. Ventral edges of the sleeve panels directed laterally, giving a straight appearance to the rhabdosome in lateral profile. Proximal end with distinctive triangular obverse and reverse orifices, and smaller orifices proximal to the lips of the first two thecae. Ventral faces of the rhabdosome formed of two series of orifices, each outlined by the ventral thecal lips and the lateral edges of the ancora sleeve panels; the ancora sleeve panels may extend across the first few orifices.

Remarks. Bulman (1929, p. 181) noted that *Retiolites* was an alternative name proposed by Barrande (1850, footnote, p. 68) for *Gladiolites* Barrande, 1850 'in case *Gladiolites* was not considered sufficiently distinct from *Gladiolus* (since at that time a fossil *Gladiolus* would have been named *Gladiolites*). *Retiolites* has been used, almost without exception, by all writers since Suess (1851, p. 91).'

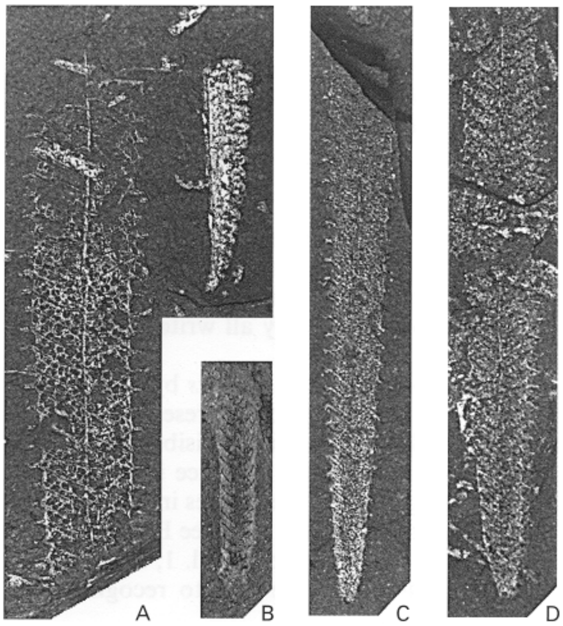
Haberfelner's (1936) genus *Dimykterograptus* was distinguished from *Retiolites* by the presence of a membrane. However, Haberfelner was observing simply the exceptional preservation of the very thin periderm between the lists of the ancora sleeve. This is sometimes visible in flattened bedding-plane material (see Bouček and Münch 1944, p. 19); its former presence is indicated in isolated specimens by seamed lists (see e.g. Bates 1987, pl. 4, figs 3–4). True orifices in the *Retiolites* rhabdosome occurred only on the obverse and reverse sides at the proximal end (see Bates and Kirk 1984, text-fig. 4g), ventrally, along almost the entire length of the rhabsosome (Pl. 1, fig. 2) and at the distal end of the rhabdosome. Bouček and Münch (1944) were the first to recognize that *Dimykterograptus* is simply a preservational variant of *Retiolites*.

Stomatograptus Tullberg, 1883 has a structure almost identical to that of *Retiolites*, but differs in two major respects: (1) in the presence of stomata, which form prominent pores in the ancora sleeve, often protruding as 'funnels': they form additional orifices, connecting the external common canals with the exterior of the rhabdosome; and (2) in the lateral profile, which is notched in *Stomatograptus*. The ventralmost lists of the ancora sleeve run at right angles to the septal bars (cf. Bulman 1970, fig. 95, 6 and 95, 5). In *Stomatograptus* the ancora sleeve panels do not extend across the proximal ventral orifices.

Retiolites geinitzianus (Barrande, 1850)

Text-figures 2A, D, 3C

vp?1850	*Gladiolites geinitzianus* Barrande, p. 69, pl. 4, figs 24–27 (*non* figs 16, 28–32 [= *R. angustidens*], ?17–19 [lectotype selected by Bouček and Münch 1944, probably = *R. angustidens*], 20–23 [= *Stomatograptus grandis* Suess, 1851 *sensu lato*], ?33 [specimen is lost]).
1851	*Retiolites Geinitzianus* Barr.; Suess, p. 95, pl. 7, fig. 1a–g.
v.1852	*Graptolithus venosus* (n. sp.) Hall, p. 40, pl. A.17, fig. 2a–c.
1883	*Retiolites Geinitzianus* Barr.; Tullberg, p. 41, pl. 1, figs 10–13, 16–17 (?14–15).
p1890	*Retiolites Geinitzianus* Barrande 1850; Holm, p. 18, pl. 2, figs 2–4 (*non* 5 [= *R. angustidens*]).
vp.1908	*Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande; Elles and Wood, p. 336, pl. 34, fig. 8a, c, (*non* b [= *Stomatograptus longus* Obut, 1949], d [= *R. angustidens*; specimen not traced, Strachan 1971, p. 87]), text-fig. 220a, d–e [cops Holm 1890], f (? c, *non* b [= enlargement of part of pl. 34, fig. 8b]).
1908	*Retiolites geinitzianus* Barrande var. *venosus* (Hall); Ruedemann, p. 469, pl. 29, figs 7–8; pl. 31, figs 6–8; text-fig. 449 [cop. Hall 1852].
1936	*Dimykterograptus bončevi* n. sp. var. *latus* Haberfelner, p. 93, fig. 6.
v.1944	*Retiolites* (*Ret.*) *geinitzianus* cf. *angustidens* E. and W.; Bouček and Münch, p. 36, text-fig. 11f–i.
v.1944	*Retiolites* (*Retiolites*) *geinitzianus geinitzianus* Barrande 1850; Bouček and Münch, p. 37, pl. 3, figs 2–5, text-figs 13c–h, 14c–d.
v.1944	*Retiolites* (*Retiolites*) *robustus* n. sp., Bouček and Münch, p. 42, text-figs 12a, 13a–b, 15f.
*non*1966	*Retiolites geinitzianus* Barr.; Eisenack, p. 581, fig. 6 [= *R. angustidens*].
1966	*Retiolites geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 15, pl. 3, figs 10–11 (?12–13 [short fragments]), text-fig. 7.



TEXT-FIG. 2. A, D, *Retiolites geinitzianus* (Barrande, 1850). A, holotype of *Retiolites robustus* Bouček and Münch, 1944; L 31629; middle Telychian, Bockendorf-Riechberg, Germany; note tectonic broadening, also affecting specimen of *Monograptus priodon* (Bronn), top right. D, BB 682; Litohlavy Formation, Praha-Pankrác; *tullbergi* (= *crenulata*) Biozone. B, *Retiolites australis* McCoy, 1875; lectotype, MV P12194; Springfield Sandstone, east bank of Maribyrnong River, north of Keilor, Victoria; *griestoniensis* Biozone. C, *Retiolites angustidens* Elles and Wood, 1908; holotype of *Retiolites densereticulatus* Bouček, 1931; L 31386; Motol Formation, Vyskočilka, Bohemia; *insectus* Biozone. All are ×2·5.

p1966	*Retiolites obliquidens* (Obut), 1949; Obut and Sobolevskaya, p. 18, text-fig. 9 (*non* pl. 4, fig. 1 [holotype = *Stomatograptus grandis* Suess, 1851 *s.l.*], fig. 2 [= *Stomatograptus* sp.]).
1967	*Retiolites geinitzianus* Barrande, 1850; Gailite *et al.*, p. 226, pl. 26, fig. 5, text-fig 40.
1967	*Retiolites angustidens* Elles et Wood, 1908; Gailite *et al.*, p. 228, pl. 26, fig. 7, text-fig. 42.
?1967	*Retiolites geinitzianus* Barrande, 1850; Obut *et al.*, p. 79, pl. 7, figs 7–8.
v.1970	*Retiolites geinitzianus angustidens* Elles and Wood; Toghill and Strachan, pl. 105, fig. 8.
1972	*Retiolites geinitzianus* Barrande, 1850; Koren', p. 72, pl. 1, figs 1–4.
1975	*Retiolites geinitzianus geinitzianus* Barrande; Berry and Murphy, p. 98, pl. 14, fig. 1.
1975	*Retiolites geinitzianus geinitzianus* (Barrande, 1850); Bjerreskov, p. 38, pl. 5, fig. F, table 3.
v*non*1984	*Retiolites geinitzianus* Barrande; Chen, p. 48, pl. 6, figs 3–4 [= *Pseudoretiolites dentatus* Bouček and Münch, 1944].
*non*1986	*Retiolites geinitzianus* Barrande; Fu and Song, p. 94, pl. 6, figs 12–13 [= *Stomatograptus grandis* (Suess, 1851)].
1987*b*	*Retiolites*; Lenz and Melchin, p. 354, fig. 1A–E.
.1992	*Retiolites geinitzianus geinitzianus* Barrande; White *et al.*, fig. 7h.
v1993	*Retiolites* sp. nov.; Loydell and Cave, p. 102, fig. 9a.
?1995	*Retiolites geinitzianus* Barrande 1850; Kozłowska-Dawidziuk, p. 281, figs 12A–B, 13.

Neotype. Loydell and Štorch (1996) have applied to the International Commission on Zoological Nomenclature to suppress Bouček and Münch's (1944, p. 37) lectotype selection and to designate as neotype specimen L 31612 (Bouček and Münch 1944, pl. 3, figs 2–4), from the Motol Formation (*Cyrtograptus murchisoni* Biozone) of Vyskočilka, Bohemia.

The choice of lectotype made by Bouček and Münch (1944, p. 37) was unfortunate. The specimen (L 27600) has dimensions comparable to those of *R. angustidens*, but, in being a small, mesial fragment, cannot be assigned confidently to this or any other species. Only those specimens that were figured by Barrande (1850, pl. 4, figs 16–32) are present in the collections of the National Museum, Prague. Of these, only two may, questionably, be assigned to *R. geinitzianus*. These are both short fragments, preserved obliquely, and neither is suitable as a type specimen.The proposed neotype is from the same locality as yielded the lectotype selected by Bouček and Münch.

Material. In addition to the type and figured specimens indicated in the synonymy, several hundred specimens from the Telychian and Sheinwoodian of Wales, Bohemia, Spain and Scotland.

Diagnosis. Broad *Retiolites*; dorso-ventral width increases rapidly from 2·2–3·1 mm (5 mm from the proximal end) to a distal maximum of *c*. 6 mm.

Measurements of dorso-ventral width. All specimens are flattened, with the exception of BGS RCV3332 (very low relief) and BGS RCV7145 (medium relief).* = proposed neotype.

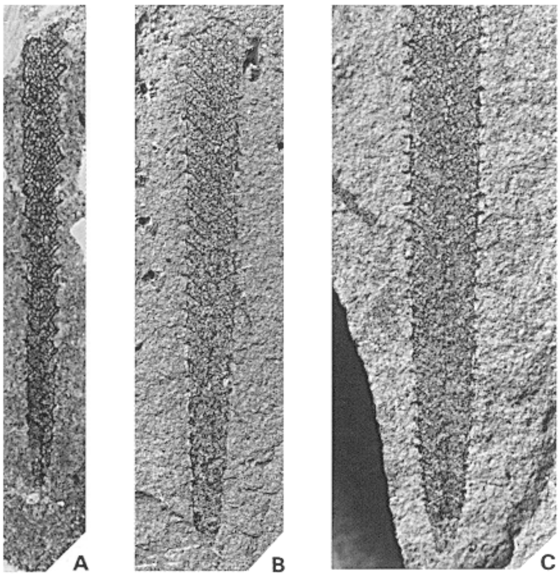
		Distance from proximal end (mm)					
Specimen no.	Biozone	5	10	15	20	30	50
BB 685	*murchisoni*	2·8	3·7	4·1	4·35	5·2	5·5
PŠ 701a	*murchisoni*	2·65	3·45	4·0	4·65	5·1	5·6
PŠ 703	*murchisoni*	2·75	3·9	4·25	5·1	5·1	
PŠ 704	*murchisoni*	2·9	3·55	4·0	4·3	4·5	
PŠ 707a	*murchisoni*	2·7	3·4	4·0	4·25	4·35	
PŠ 708	*murchisoni*	2·95	3·8	4·5	4·9	5·2	5·6
L 28334	*murchisoni*	2·7	3·7	4·25	4·9	5·5	5·95
L 28336	*murchisoni*	2·6	3·25	3·9	4·75	5·1	5·9
L 31612*	*murchisoni*	2·55	3·2	4·2	4·5	5·0	5·9
BGS RCV3332	*centrifugus*	2·5	3·0	3·45	3·35		
PŠ 702	*centrifugus*	2·6	3·4	4·1	4·25	4·6	
BGS RCV7145	*insectus*	2·4	3·1	3·5	3·85		
BB 688	*spiralis*	3·05	3·6	3·7	3·75	3·8	
BB 690	*spiralis*	2·4	3·1	3·65	3·8	4·2	
BGS RCV2402	*spiralis*	2·5	3·2	3·9	4·3	4·6	4·7
BGS RCV2496	*spiralis*	2·5	3·2	3·7	3·85	4·05	
BB 681	*tullbergi*	2·45	3·0	3·7	3·8	3·9	
BB 682a	*tullbergi*	2·2	3·1	3·5	3·8	4·2	
BB 684	*tullbergi*	2·3	3·0	3·5	3·6		
BB 686	*tullbergi*	2·3	3·05	3·8	3·8	4·1	
PŠ 688	*tullbergi*	2·9	3·2	3·95	4·55		
PŠ 689	*tullbergi*	2·25	3·0	3·85	4·1		

Remarks. Elles and Wood (1908) and Toghill and Strachan (1970) identified specimens of *R. geinitzianus* as *R. angustidens* Elles and Wood, 1908. The latter species differs, however, in its more gradual rate of increase in dorso-ventral width (see below). Short, mesial or distal fragments with a width of *c*. 4 mm might be difficult to assign confidently to one or other of these species, however.

In discussion of Hall's (1852) species *venosus*, Ruedemann (1908, p. 471) stated: 'I seriously doubt the specific difference of the American form [*R. venosus*] from *R. geinitzianus*, the genotype of *Retiolites*; for not only are the two exactly alike in dimensions and habit, but they tally also completely in the number of thecae within 10 mm and in their inclination'. He continued, 'We have for these reasons, for the present brought *R. venosus* as a variety under *geinitzianus*, allowing this distinction to stand less by virtue of differential characters than by that of different geographical distribution.' One of us (DKL) has examined Hall's material of *venosus* (AMNH 30957 and AMNH 502179); the specimens are indeed indistinguishable from *geinitzianus* and we follow Bouček and Münch (1944) in treating the two taxa as synonymous. Waterlot (1945, p. 65) considered *R. venosus* to be a senior synonym of *R. angustidens* Elles and Wood, 1908. This is clearly not the case.

Bouček and Münch's (1944) material of their species *Retiolites robustus* (Text-fig. 2A) is tectonically broadened *R. geinitzianus*. The width distally is 6·35–6·45 mm. Bouček and Münch suggested a horizon for this material of around the *crispus*/*griestoniensis* Biozone boundary (= *sartorius* Biozone *sensu* Loydell 1993*a*), but it may be from slightly higher than this (within the *griestoniensis* Biozone).

Obut and Sobolevskaya (1966, p. 18) recognized that SM A.21618 had been assigned incorrectly to *R. geinitzianus* by Elles and Wood (1908, explanations to pl. 34, fig. 8b, text-fig. 220b) and placed this specimen in *R. obliquidens* Obut, 1949 (a junior synonym of *Stomatograptus grandis* (Suess, 1851); see above). The specimen should, however, be assigned to another *Stomatograptus* species,



TEXT-FIG. 3. Proximal ends of the three *Retiolites* species; note the differences in dorso-ventral width. A, *Retiolites australis* McCoy, 1875; holotype of *Retiolites angustissimus* Obut and Sobolevskaya *in* Obut *et al.*, 1967; N 601B/6; Kolyma Formation, north-east Russia; '*spiralis* and *grandis* Biozone'. B, *Retiolites angustidens* Elles and Wood, 1908; PŠ 706; Motol Formation, Velká Ohrada, Bohemia; *grandis* Biozone. C, *Retiolites geinitzianus* (Barrande, 1850); PŠ 702; Motol Formation, Velká Ohrada, Bohemia; *murchisoni* Biozone (Sheinwoodian). All are ×2·5.

S. longus Obut, 1949, which is characterized by a less rapid increase in dorso-ventral width than *S. grandis*.

Loydell and Cave (1993) identified two specimens from Buttington Brick Pit, Wales as belonging to a new species, because of the low angle of the septal bars to the rhabdosome axis. Septal bar inclination is highly variable within *Retiolites* species and these specimens are assigned herein to *R. geinitzianus*.

Stratigraphical range. Telychian Stage (Upper Llandovery), to Sheinwoodian Stage (Lower Wenlock); ?*crispus* Biozone, *sartorius–murchisoni* biozones. *R. geinitzianus* appears to be least common in the upper Telychian, in which *R. angustidens* tends to be the numerically dominant *Retiolites* in graptolite assemblages (see abundance data in e.g. Bjerreskov 1975; Loydell and Cave 1996).

Retiolites australis McCoy, 1875

Plate 1, figure 3, Text-figures 2B, 3A

v.*1875 *Retiolites australis* McCoy, p. 36, pl. 20, fig. 10.
p1934 *Stomatograptus australis* (McCoy); Keble and Harris, p. 181, pl. 22, fig. 5d (*non* fig. 5a–c).
.1965 *Retiolites angustidens* (Elles et Wood), 1908; Obut *et al.*, p. 38, pl. 2, fig. 11.
.1966 *Retiolites angustidens* (Elles et Wood), 1908; Obut and Sobolevskaya, p. 16, pl. 3, figs 14–16, text-fig. 8.
.1967 *Retiolites angustissimus* Obut et Sobolevskaya, sp. nov., Obut *et al.*, p. 81, pl. 7, figs 9–11.
1973 *Retiolites angustidens* Elles et Wood, 1908; Kul'kov and Obut, p. 228, fig. 2, 12.
p1978 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Lenz, p. 33, fig. 15C, H.
1981 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 20, pl. 6, fig. 1.
.1981 *Retiolites geinitzianus densireticulatus* Bouček, 1931; Crowther, p. 89, pl. 15, text-fig. 29A.
p.1988 *Retiolites geinitzianus densereticulatus* Bouček; Lenz, p. 1965, pl. 2, fig. I (?F2, *non* G–H [= *R. angustidens*]).
1989 *Retiolites geinitzianus densereticulatus* Bouček; Melchin, fig. 13A.

Lectotype. Specimen MV P12194, figured McCoy 1875, pl. 20, fig. 10 (figured herein as Text-fig. 2B); from the Springfield Sandstone, Geological Survey of Victoria locality Ba57, on the east bank of the Maribyrnong River, 1·2 km north of Keilor, Victoria. The associated graptolites are indicative of the mid Telychian *griestoniensis* Biozone (Andrew Sandford, pers. comm.). Keble and Harris (1934, p. 182) referred to this specimen as holotype; McCoy had not designated it as such, however, and, as there are several other syntype specimens (MV P12195), it is more correct to consider the specimen selected by Keble and Harris as the lectotype and those specimens labelled MV P12195 as paralectotypes.

Material. In addition to the lectotype and paralectotypes, all of which are flattened, several three-dimensional isolated specimens from the *sakmaricus* Biozone (upper Telychian, Llandovery), Cape Phillips Formation, Cape Phillips, Cornwallis Island, Arctic Canada.

Diagnosis. Narrow *Retiolites* with a proximal dorso–ventral width of 1·35–1·5 mm (5 mm from the proximal end) increasing gradually to a distal maximum of 2·1–2·4 mm.

Remarks. The lectotype has not previously been illustrated accurately. McCoy (1875, p. 37) noted that 'the lithographer has altered the drawing [pl. 20, fig. 10] so as to render it too gradually and regularly tapering' and that the 'cell boundary lines should diverge at a rather more acute angle and be straighter [than illustrated]'. Keble and Harris's figure (1934, pl. 22, fig. 5d) is inaccurate both in terms of its stated magnification (which suggests a dorso-ventral width of 2·8 mm, cf. the true maximum distal dorso-ventral width in the lectotype of 1·95 mm) and in its failure to portray the basically straight and nearly parallel-sided nature of the rhabdosome margins and the amount of visible detail of the reticulum. Loydell (1993*a*) suggested that '*Retiolites australis* appears, from M'Coy's description and illustrations, to be a senior synonym of *Retiolites angustidens*'. The two taxa are not synonymous, however; *R. australis* differs in its lesser dorso-ventral width throughout its length.

Stratigraphical range. The Australian type material is from the *griestoniensis* Biozone. The range of the conspecific *R. angustissimus* Obut and Sobolevskaya (*in* Obut *et al.*, 1967; Text-fig. 3A) was stated as '*griestoniensis* and *spiralis*' Biozone to '*spiralis* and *grandis*' Biozone. Lenz (1988) illustrated a specimen from the *sakmaricus* Biozone of northern Canada, the same biozone as yielded the chemically isolated specimen illustrated in Plate 1, figure 3. The species has not been reported from the Wenlock, however, and thus its total known range is from the *griestoniensis* Biozone to approximately the base of the Wenlock.

Retiolites angustidens Elles and Wood, 1908

Plate 1, figures 1–2, 5, Text-figures 2C, 3B

vp.1850 *Gladiolites Geinitzianus* Barrande, p. 69, pl. 4, figs 16, 28–32, ?17–19, 33 (*non* figs 20–27) [see synonymy of *R. geinitzianus*].

p1890 *Retiolites Geinitzianus* Barrande 1850; Holm, p. 18, pl. 2, fig. 5 (*non* figs 2–4 [= *R. geinitzianus*]).

p1908 *Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande; Elles and Wood, p. 336, pl. 34, fig. 8d only [see synonymy of *R. geinitzianus*].

*.1908 *Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande Var. *angustidens*, nov.; Elles and Wood, p. 338, pl. 34, fig. 9a–c.

v.1931 *Retiolites geinitzianus densereticulatus* n. var., Bouček, p. 306, fig. 16a.

1936 *Dimykterograptus bončevi* n. sp., Haberfelner, p. 92, fig. 5.

v.1944 *Retiolites* (*Retiolites*) *geinitzianus angustidens* Elles and Wood, 1908; Bouček and Münch, p. 34, pl. 2, figs 1–4, text-figs 11a–e, 12b–e.

?1949 *Retiolites geinitzianus* Barrande var. *angustidens* Elles; Obut, p. 16, pl. 2, fig. 1a–b.

1963 *Retiolites* (*Gladiograptus*) *geinitzianus* var. *angustidens* Elles and Wood; Willefert, p. 26, text-fig. 31.

*non*1965 *Retiolites angustidens* (Elles et Wood), 1908; Obut *et al.*, p. 38, pl. 2, fig. 11 [= *R. australis*].

1966 *Retiolites geinitzianus* Barr.; Eisenack, p. 581, fig. 6.

*non*1966 *Retiolites angustidens* (Elles et Wood), 1908; Obut and Sobolevskaya, p. 16, pl. 3, figs 14–16, text-fig. 8 [= *R. australis*].

1967 *Retiolites densereticulatus* Bouček, 1931; Gailite *et al.*, p. 227, pl. 26, fig. 6, text-fig. 41.

*non*1967 *Retiolites angustidens* Elles et Wood, 1908; Gailite *et al.*, p. 228, pl. 26, fig. 7, text-fig. 42 [= *R. geinitzianus*].

?1966 *Retiolites* ex. gr. *geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 19, pl. 4, fig. 3.

v*non*1970 *Retiolites geinitzianus angustidens* Elles and Wood; Toghill and Strachan, pl. 105, fig. 8.
.1975 *Retiolites geinitzianus angustidens* Elles and Wood; Berry and Murphy, p. 99, pl. 14, fig. 2.
1975 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 38, pl. 5, figs D–E, table 3.
p1978 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Lenz, p. 33, (*non* fig. 15C, H [= *R. australis*]).
*non*1981 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 20, pl. 6, fig. 1 [= *R. australis*].
.1982 *Retiolites geinitzianus angustidens* Elles and Wood; Howe, pl. 2, fig. e.
v*non*1984 *Retiolites geinitzianus angustidens* Elles and Wood; Chen, p. 49, pl. 5, fig. 14, pl. 6, figs 6–8 [= *Pseudoretiolites dentatus* Bouček and Münch, 1944], fig. 5 [= indet. retiolitid], figs 10–11 [= *Pseudoretiolites perlatus* (Nicholson, 1868)].
1986 *Retiolites geinitzianus angustidens* Elles et Wood; Fu and Song, p. 94, pl. 7, fig. 2 (? fig. 1).
p.1988 *Retiolites geinitzianus densereticulatus* Bouček; Lenz, p. 1965, pl. 2, figs G–H (?F2, *non* I [= *R. australis*]).
1989 *Retiolites geinitzianus angustidens* Elles and Wood; Melchin, fig. 12C.

Lectotype. Selected by Bouček and Münch (1944); GSE 5629, figured Elles and Wood 1908, plate 34, figure 9a; from the north end of Falbogue Bay, on the west side of Meikle Ross, Kirkudbright Bay, Scotland.

Material. In addition to the type and figured specimens indicated in the synonymy, several hundred specimens from the Telychian and Sheinwoodian of Bohemia, Wales, northern England and Scotland.

Diagnosis. *Retiolites* with dorso-ventral width increasing gradually from 1·8–2·4 mm (5 mm from the proximal end) to a distal maximum of *c*. 4 mm.

Measurements of dorso-ventral width. All specimens are flattened, with the exception of BGS RCV4721 (very low relief).

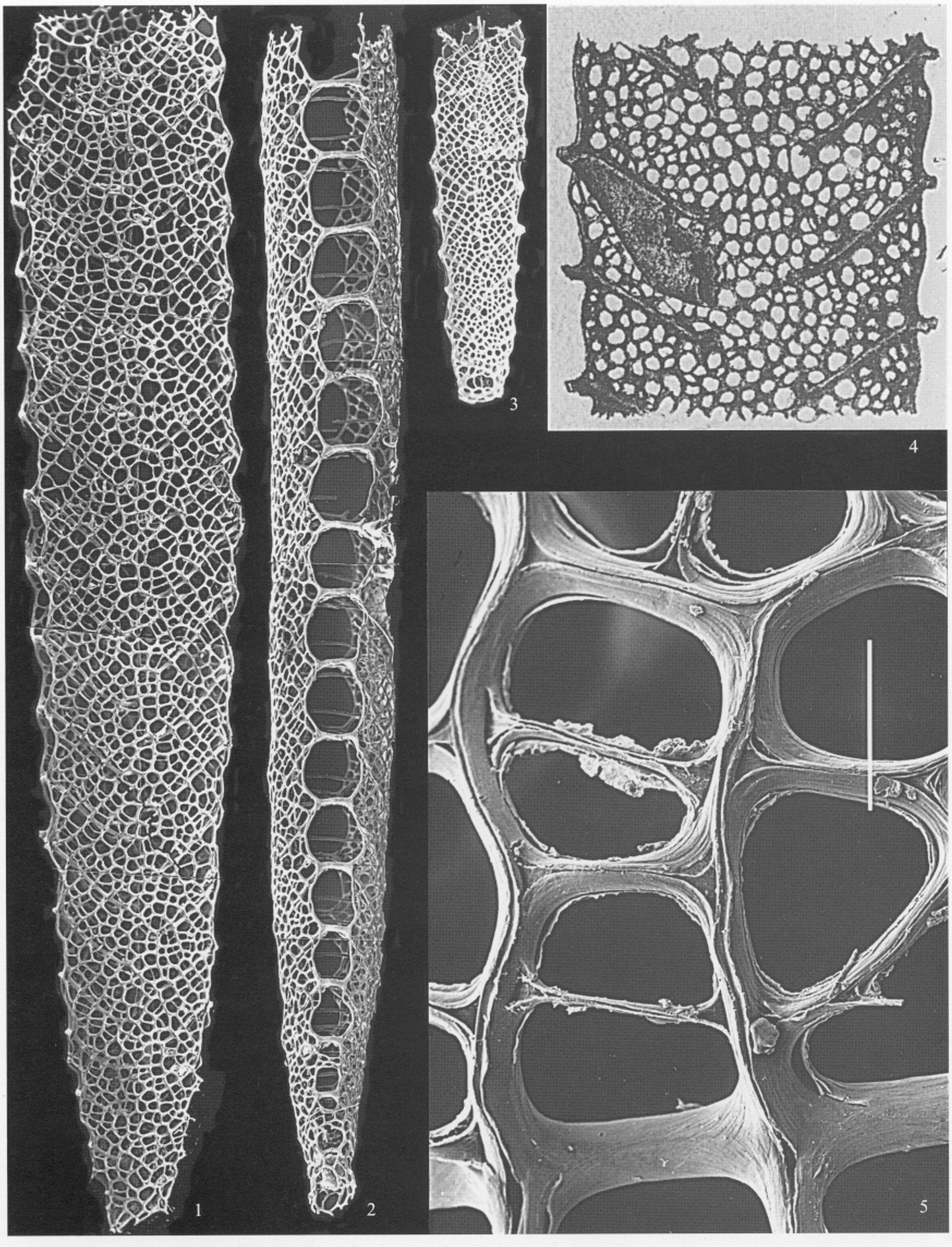
		Distance from proximal end (mm)					
Specimen no.	Biozone	5	10	15	20	30	50
L 28337	*murchisoni*	1·9	2·5	3·2	3·45	3·9	
BGS RCV4721	*centrifugus*	2·2	2·7	3·0	3·1	3·2	
BB 689a	*insectus*	2·1	2·9	3·4	3·55	3·55	
PŠ 709	*insectus*	2·2	2·95	3·55	3·55		
L 28340b	*insectus*	2·2	2·9	3·2	3·45		
PŠ 706	*grandis*	1·95	2·6	3·0	3·25		
L 28322	*spiralis*	2·4	3·05	3·1	3·5	3·9	
BB 687	*tullbergi*	1·95	2·3	2·65	2·75	2·9	

Remarks. *Retiolites densereticulatus* Bouček, 1931 was considered to be distinct from *R. angustidens* because of its denser reticular meshwork. Meshwork density has been shown to be a function of

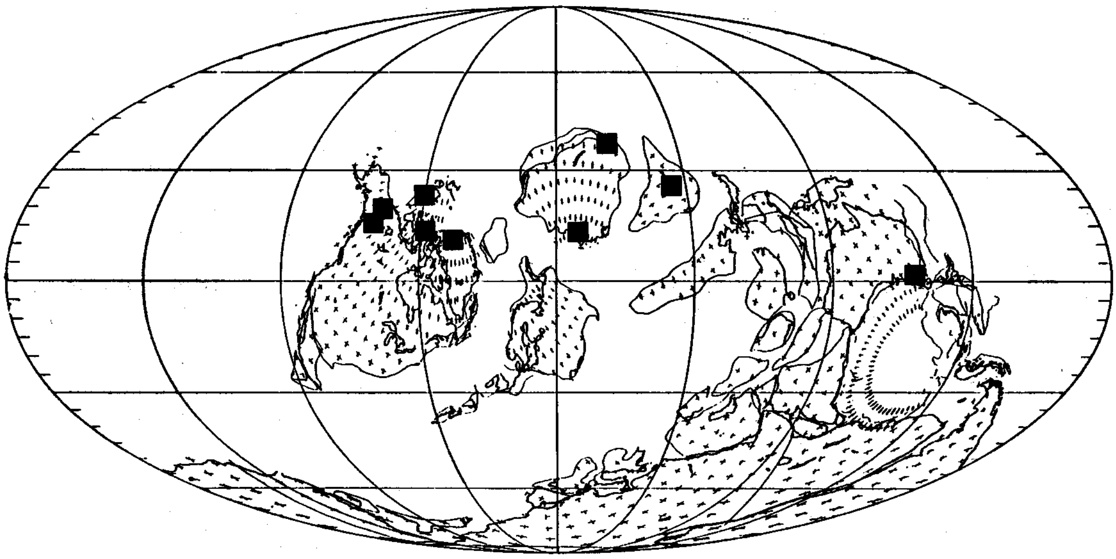
EXPLANATION OF PLATE 1

Figs 1–2, 4–5. *Retiolites angustidens* Elles and Wood, 1908. 1–2, 5, NMW 91.52G.812; Lower Visby Formation, 0·5–1 m below lowest of three main bentonites, 500 m south of Stenkyrkehuks fyr, Gotland. 1–2, obverse and ventral views respectively of rhabdosome; note the orifices opening ventrally (2); these orifices should not to be confused with the thecal apertures (see fig. 4 and Text-fig. 1); both × 15. 5, small part of meshwork, showing lists secreted late in astogeny, causing an increase in meshwork density; × 265. 4, copy (at twice original publication size) of Holm's 1890, plate 2, figure 5; note the presence of a theca, the apertural margin of which runs along the septal bar; the thecal aperture is introverted.

Fig. 3. *Retiolites australis* McCoy, 1875; NMW 91.52G 1330; upper *sakmaricus* Biozone (Telychian), Cape Phillips Formation, Cornwallis Island; × 10.



LOYDELL *et al.*, *Retiolites*



TEXT-FIG. 4. Localities yielding *Retiolites australis* McCoy (black squares) plotted on Llandovery world palaeogeographical map of Scotese and McKerrow (1990). Note that the position and orientation of Siberia are uncertain (discussions at James Hall Meeting, Rochester, August 1996). The record from Pearya (Bjerreskov 1981) is plotted in north Greenland; collision between Pearya and Laurentia took place late in the Telychian (T. De Freitas, pers. comm. 1996).

astogeny, however (see above), and as the taxa are identical in all respects they are synonymized herein. Incidentally, the lectotype of *R. angustidens* has a reticular meshwork just as dense as that of the holotype of *R. densereticulatus* (Text-fig. 2c). In terms of dorso-ventral width, *R. angustidens* is intermediate between *R. australis* and *R. geinitzianus.*

Bjerreskov (1975) noted a median row of pores on an internal mould of this species and suggested (as had Bouček and Münch 1944) that the genera *Retiolites* and *Stomatograptus* were closely related.

Stratigraphical range. Telychian (*crispus* Biozone; Melchin 1989)–Sheinwoodian (*murchisoni* Biozone).

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Specimens of *Retiolites* are encountered in the majority of graptolite collections made from late Telychian and early Sheinwoodian strata throughout the world, although the literature reviewed in the preparation of this paper suggests that the genus was not as common in the seas bordering the various microcontinents that now make up China as elsewhere; here, other retiolitids (particularly species of *Stomatograptus*) appear to have been more common than *Retiolites.*

Whilst both *R. geinitzianus* and *R. angustidens* appear to have had a very widespread distribution, *R. australis* is known only from strata deposited north of the Silurian equator (Text-fig. 4). This restricted geographical distribution matches that of several other late Telychian graptoloids (Melchin 1989, p. 1744).

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