REVISION OF THE SILURIAN GRAPTOLOIDE GENUS

RETIOLITES

by DAVID K. LOYDELL, PETR ŠTORCH and DENIS E. B. BATES

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 1987a, 1987b; Bates et al. 1988; Kozlowska-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.


SYSTEMATIC PALAEOONTOLOGY

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 rhombosome axis towards the ventral sides of the rhombosome. 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 1987a; Kozlowska-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 (1987b, fig. 1) that the free ventral walls of the thecae are at a lower angle to the rhombosome 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.

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 (1987b). The

**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; Bjerskov 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*, *Stomatograpthus tornquisti* Tullberg, 1883, is type species of *Stomatograpthus* 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 *Pseudorietiolites*, a taxon now accorded generic status (see e.g. Lenz and Melchin 1987a; Bates and Kirk 1992).
4. *Retiolites perlatus* var. *daironi* Lapworth, 1877. Like *perlatus*, this species is now assigned to *Pseudorietiolites* (e.g. Loydell 1993b).
6. *Retiolites macilentus* Törnquist, 1887. Moberg and Törnquist (1909) designated this as type species of their genus *Plectograpthus*.
7. *Retiolites nassa* Holm, 1890. Type species of *Gothagograpthus* Frech, 1897.
8. *Retiolites spinosus* Wood, 1900. Elles and Wood (1908) placed this species in a subgenus (*Gothagograpthus*); it was subsequently designated type species of *Spinograpthus* (see Bouček and Münch 1952).
10. *Retiolites praecursor* Kirsch, 1919. Originally described from the Aeronian *cometa* Biozone, this species was assigned tentatively to *Pseudorietiolites* by Bouček and Münch (1944). It is from significantly older strata than any described *Retiolites* sensu *stricto* and Kirsch’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. *maxima* 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 *Stomatograpthus grandis*. The horizon is quoted as *convolutus* Biozone (Aeronian), although it is possible (A. C. Lenz, pers. comm. 1996) that Ruedemann had confused ‘*Monograpthus* convolutus’ (Hisinger) with the Telychian species *Oktavites spiralis* (Geinitz).
12. *Retiolites obliquipenis* 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 *Stomatograpthus 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 1993a), 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 Zaslawskaya (1986) and to Spinograptus by Lenz and Melchin (1991) and Lenz (1993). Kozlowska-Dawidziuk (1995) noted differences between Berry and Murphy’s species and other Spinograptus species, suggesting that nevadensis (and S. apoxyi 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 minitus Ni, 1978. The type material has been examined recently by one of us (PS) 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 Kozlowska-Dawidziuk 1995 for details).

Chang and Sun (1947, pl. 1, fig. 9) illustrated what they considered to be a new variety, ’Retiolites geinitzianus [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 (1987a) reported Retiolites from the Homarian Stage (Upper Wenlock). Elsewhere, the extinction of Retiolites formed part of the mid Sheinwoodian ‘murchisonii [biotic crisis] Event’, recently identified by Storch (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 DIPLOGRATTOIDEA 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; Dimykteragratpatus 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 orthogaptid 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 *Reticolites* 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*). *Reticolites* has been used, almost without exception, by all writers since Suess (1851, p. 91).'

Haberfelder's (1936) genus *Dimykterograpthus* was distinguished from *Reticolites* by the presence of a membrane. However, Haberfelder 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 *Reticolites* 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 rhabdosome (Pl. 1, fig. 2) and at the distal end of the rhabdosome. Bouček and Münch (1944) were the first to recognize that *Dimykterograpthus* is simply a preservational variant of *Reticolites*.

*Stomatograpthus* Tullberg, 1883 has a structure almost identical to that of *Reticolites*, 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 *Stomatograpthus*. The ventrallymost lists of the ancora sleeve run at right angles to the septal bars (cf. Bulman 1970, fig. 95, 6 and 95, 5). In *Stomatograpthus* the ancora sleeve panels do not extend across the proximal ventral orifices.

*Reticolites geinitzianus* (Barrande, 1850)

Text-figures 2A, D, 3C

-- vp1850  *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 [= Stomatograpthus grandis Suess, 1851 sensu lato], ?33 [specimen is lost]).

1851  *Reticolites Geinitzianus* Barr.; Suess, p. 95, pl. 7, fig. 1a–g.

v.1852  *Graptolites venosus* (n. sp.) Hall, p. 40, pl. A.17, fig. 2a–c.


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

v.1908  *Reticolites (Gladiograpthus) Geinitzianus*, Barrande; Elles and Wood, p. 336, pl. 34, fig. 8a, c, (non b [= Stomatograpthus 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  *Reticolites 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  *Dimykterograpthus bončevi* n. sp. var. *latus* Haberfelder, p. 93, fig. 6.

v.1944  *Reticolites (Ret.) geinitzianus cf. angustidens* E. and W.; Bouček and Münch, p. 36, text-fig. 11f–i.

v.1944  *Reticolites (Retic.) geinitzianus geinitzianus* Barrande 1850; Bouček and Münch, p. 37, pl. 3, figs 2–5, text-figs 13c–h, 14c–d.

v.1944  *Reticolites (Retic.) robustus* n. sp., Bouček and Münch, p. 42, text-figs 12a, 13a–b, 15f.

non1966  *Reticolites geinitzianus* Barr.; Eisenack, p. 581, fig. 6 [= R. angustidens].

1966  *Reticolites geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 15, pl. 3, figs 10–11 (?12–13 [short fragments]), text-fig. 7.
p1966  Retiolites obliquidens (Obut), 1949; Obut and Sobolevskaya, p. 18, text-fig. 9 (non pl. 4, fig. 1 [holotype = Stomatograpthus grandis Suess, 1851 s.l.]), fig. 2 (= Stomatograpthus sp.).

1967  Retiolites geinitzianus Barrande, 1850; Gailit et al., p. 226, pl. 26, fig. 5, text-fig 40.

1967  Retiolites angustidens Elles and Wood, 1908; Gailit 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.

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; Berry and Murphy, p. 98, pl. 14, fig. 1.

1984  Retiolites geinitzianus Barrande; Chen, p. 48, pl. 6, figs 3–4 [= Pseudoretiolites dentatus Bouček and Münch, 1944].

1986  Retiolites geinitzianus Barrande; Fu and Song, p. 94, pl. 6, figs 12–13 [= Stomatograpthus grandis (Suess, 1851)].

1987b  Retiolites; Lenz and Melchin, p. 354, fig. 1A–E.

1992  Retiolites geinitzianus geinitzianus Barrande; White et al., fig. 7h.

1993  Retiolites sp. nov.; Loydell and Cave, p. 102, fig. 9a.


Neotype. Loydell and Storch (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 (Cystrograptus 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, unquestionably, 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.
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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.

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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. Waterloo (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 1993a), 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,
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. angustidenis 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 2a, 3A

v.*1875 Retiolites australis McCoy, p. 36, pl. 20, fig. 10.
1934 Stomatographus australis (McCoy); Keble and Harris, p. 181, pl. 22, fig. 5d (non fig. 5a–c).
1965 Retiolites angustidenis (Elles et Wood), 1908; Obut et al., p. 38, pl. 2, fig. 11.
1966 Retiolites angustidenis (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 angustidenis Elles et Wood, 1908; Kul’kov and Obut, p. 228, fig. 2, 12.
1978 Retiolites geinitzianus angustidenis Elles and Wood, 1908; Lenz, p. 33, fig. 15c, h.
1981 Retiolites geinitzianus angustidenis Elles and Wood, 1908; Bjerreskov, p. 20, pl. 6, fig. 1.
1981 Retiolites geinitzianus densereticulatus Bouček, 1931; Crowther, p. 89, pl. 15, text-fig. 29A.
1988 Retiolites geinitzianus densereticulatus Bouček; Lenz, p. 1965, pl. 2, fig. 1 (θr2, non g–h [= R. angustidenis]).
1989 Retiolites geinitzianus densereticulatus Bouček; Melchin, fig. 13A.

Lectotype. Specimen MV P12194, figured McCoy 1875, pl. 20, fig. 10 (figured herein as Text-fig. 2n); 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 griesontiensiis 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 (1993a) suggested that *Retiolites australis* appears, from McCoy'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, 3a

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

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

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

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

*Retiolites (Gladioquarts) Geinitzianus* var. *angustidens* Elles and Wood; Willefert, p. 26, text-fig. 31.

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

*Retiolites (Gladioquarts) Geinitzianus* var. *angustidens* Elles and Wood; Willefert, p. 26, text-fig. 31.

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

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

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

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

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

*Retiolites ex. gr. geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 19, pl. 4, fig. 3.
vnon1970 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 b–e, table 3.
p1978 Retiolites geinitzianus angustidens Elles and Wood, 1908; Lenz, p. 33, (non fig. 15c, H [= R. australis]).
non1981 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.
vnor1984 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 (?r2, 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).

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Biozone</th>
<th>Distance from proximal end (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>L 28337</td>
<td>murchisoni</td>
<td>1.9</td>
</tr>
<tr>
<td>BGS RCV4721</td>
<td>centrifugus</td>
<td>2.2</td>
</tr>
<tr>
<td>BB 689a</td>
<td>insectus</td>
<td>2.1</td>
</tr>
<tr>
<td>PŠ 709</td>
<td>insectus</td>
<td>2.2</td>
</tr>
<tr>
<td>L 28340b</td>
<td>insectus</td>
<td>2.2</td>
</tr>
<tr>
<td>PŠ 706</td>
<td>grandis</td>
<td>1.95</td>
</tr>
<tr>
<td>L 28322</td>
<td>spiralis</td>
<td>2.4</td>
</tr>
<tr>
<td>BB 687</td>
<td>tallbergi</td>
<td>1.95</td>
</tr>
</tbody>
</table>

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
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).

**PALAEOBIOGEOGRAPHY**

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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LOYD ELL ET AL.: SILURIAN GRAPTOLITES


DAVID K. LOYDELL
Geology Department
University of Portsmouth
Burnaby Building
Burnaby Road
Portsmouth PO1 3QL, UK

PETR ŠTORCH
Geological Institute
Academy of Sciences of the Czech Republic
Rozvojová 135
Praha 6 Lysolaje
165 02, Czech Republic

DENIS E. B. BATES
Institute of Geography and Earth Sciences
University of Wales, Aberystwyth
Ceredigion SY23 3DB, UK

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