LAPWORTHELLIDS FROM THE LOWER CAMBRIAN STRENUELLA LIMESTONE AT COMLEY, SHROPSHIRE

by S. C. MATTHEWS

ABSTRACT. A sample of some 10 kg from the Strenuella Limestone (Lower Cambrian) of Comley, Shropshire, etched in 10% acetic acid, has produced over 1000 small fossils. These include 281 specimens of Lapworthella dentata Missarzhevsky. L. nigra Cobbold, already known from higher in the Comley succession, was not found in this sample. L. dentata typically occurs in the upper part of the Addabanian Stage in Siberia.

Callaway (1877) was first to recognize the presence of Cambrian rocks in the Comley area of Shropshire, and Lapworth (1888) first to identify the Lower Cambrian there. The major contribution on the Cambrian of Shropshire came in E. S. Cobbold's series of papers published 1909–1936. Descriptions of the succession of rocks at Comley and of the general geological setting of the area are available in Whittard et al. (1953) and in Greig et al. (1968). It would be appropriate to make special note here of two records of fossils obtained by etching limestone from Comley. Walliser (1958) collected a phosphatic problematicum, Rhombocorniculum comleyense, from a sample taken at Comley Quarry, and Reid (1959) found there Chancelloria, a heteractinellid sponge.

During 1962 the author visited Comley in the company of Dr. J. W. Cowie and Messrs. T. R. Fry and M. White, and assisted in reopening Cobbold's Excavation No. 2, situated 200 yards south of Comley Quarry (Cobbold 1909, p. 6; 1916, p. 4; 1925, pp. 371–372; 1927, p. 553; and especially 1933, pp. 473–476). At Excavation No. 2 it is possible to uncover a section which includes the Strenuella Limestone (Ac₄ in Cobbold's notation and the Protolenus Limestone (Ac₅). According to Cobbold these two units are almost entirely faulted out of the section exposed in Comley Quarry itself. A sample (approx. 10 kg) of the reddish-grey Strenuella Limestone from Excavation No. 2 was placed in 10% acetic acid, and the residue washed and then screened between 10- and 125-mesh sieves. The residue consisted mainly of fossil debris, much of it phosphatized. No attempt was made to concentrate a heavy fraction by flotation since there seemed to be little reason for discarding the incompletely phosphatized (and therefore relatively light) material present. Grains of phosphate and of glauconite were fairly common and some iron-manganese mineralization is also seen.

Picking from the considerable bulk of this residue has proceeded at various times during the last 10 years and the author's collection from the *Strenuella* Limestone now includes between 1100 and 1200 small fossils. Among them are trilobites (cephala, pleura, and pygidia—254 items), brachiopods (2), gastropods (14, most as phosphatic external moulds), sponges (10), hyolithids and hyolithellids (together 551, many fragmentary), and lapworthellids (281). Cobbold's faunal list for the *Strenuella* Limestone, Ac₄ (Cobbold 1921, p. 371), has more specific detail of

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trilobites, brachiopods, hyolithids, and hyolithellids than is offered here, but makes no mention of gastropods, sponges, nor lapworthellids. The lapworthellids now available are the subject of this paper. It is hoped to supply information on the other groups represented in the new collection at a later date.

THE PRESENT RECORD OF OCCURRENCE OF THE GENUS LAPWORTHELLA

The type of Lapworthella is L. nigra (Cobbold 1921, p. 359) from the Lapworthella Limestone (Ad), which Cobbold took to be the highest unit in the Lower Cambrian succession at Comley. The new finds in the Strenuella Limestone provide a lower record of the genus than was previously available from this particular area. However, Cobbold and Pocock (1934, p. 322) encountered L. nigra in Ac₄, Ac₅, and Ad at Rushton in the Wrekin area, and Rozanov and Missarzhevsky (1966, p. 93) mention that they obtained a Lapworthella cf. nigra from a Comley sample put at their dis-

posal by Prof. R. Koslowski.

The recent Russian literature refers to various forms of Lapworthella found in successions of early Cambrian age on the Siberian Platform. Missarzhevsky (1966) produced the first report of lapworthellids from Siberia and erected two new species, Lapworthella tortuosa and L. bella. These are from the Tommotian Stage, i.e. from lower horizons than those from which Missarzhevsky (in Rozanov et al. 1969, p. 164) later obtained L. dentata. Meshkova (in Zhuravleva et al. 1969) described three other species (L. lucida, L. marginata, and L. corniforma), also from Siberia. In 1967 Rozanov published a review (in English) of the work done on the Siberian faunas that contain lapworthellids. Bengtson (1968, 1970) has described Swedish representatives of some of the elements of these faunas, and Zakowa and Jagielska (1970) have discussed Polish material; but there is as yet no published record of actual lapworthellids from Sweden or Poland.

One should mention here what may be two further records of occurrence of Lapworthella. First, there is the material from Bornholm in which Poulsen (1942) identified four new species of Cobbold's (1935, p. 43) genus Stenothecopsis. According to Missarzhevsky (1966, fig. 1) these are lapworthellids. Second, Lochman's (1956) Stenothecopsis schodackensis may also be a lapworthellid. Missarzhevsky (1966, fig. 1), Rozanov and Missarzhevsky (1966, p. 92), Missarzhevsky and Rozanov (1968, Table 3), Missarzhevsky (in Rozanov et al. 1969, pp. 163–164) are consistently (despite occasionally irregular renderings of the American specific name) of this opinion. An answer to these questions of generic identity may emerge as information accumulates on the range of variation of lapworthellids. Further guidance may come from material (at present under preparation) which the author has collected at what can be presumed to be the type locality for Stenothecopsis, near Ste Geniès de Varensal, Hérault, France.

Though Rozanov and Missarzhevsky (1966, p. 93) recorded an L. cf. nigra from the Kameshkov horizon in the Altai, the work in Siberia has so far produced no firm identification of L. nigra, and therefore no clear indication of an equivalent of Cobbold's Lapworthella Limestone (Ad). However, the lapworthellids from the slightly older Strenuella Limestone of Comley compare well with the L. dentata

found in the upper part of the Atdabanian Stage in Siberia, and so establish a link between the Siberian stratigraphy and a classical western European Cambrian sequence.

SYSTEMATIC DESCRIPTION

Phylum and class uncertain

Order TOMMOTHDA Missarzhevsky 1970 (replacement name for CAMENIDA Missarzhevsky 1969)

Diagnosis (after Missarzhevsky, in Rozanov et al. 1969, p. 161, as Camenida Missarzhevsky ord. nov.). Small (a few mm long), phosphatic, conoidal, pyramidal shells with sloping walls, usually asymmetrical.

Remarks. The order contains the two families Lapworthellidae Missarzhevsky 1966 and Tommotiidae Missarzhevsky 1970 (replacement name for Camenida Missarzhevsky 1969). Bengtson (1970) offered an alternative view of the way in which these families might be allotted to orders: he found that the two families Tommotiidae and Tannuolinidae Fonin and Smirnova 1967 constitute a natural group with well-defined features, and proposed the Order Mitrosagophora to contain them. This order, he observed, would not satisfactorily accommodate the Lapworthellidae. He did not think it worth while to maintain Missarzhevsky's order Tommotiida (i.e. Camenida Missarzhevsky 1969, with the name changed as a consequence of Missarzhevsky's substitution of the generic name Tommotiia in 1970 for Camena pre-occupied). The reference to the Order Tommotiida made here should not be thought to imply rejection of Bengtson's interesting and well-argued proposals. Missarzhevsky's sense of the ordinal grouping is preferred because it is the more convenient one. It makes it possible to avoid for the present any commitment to, say, an Order Lapworthellida, and it is convenient again in that using Missarzhevsky's systematic terms, one may refer without hindrance to Missarzhevsky's stratigraphic proposals.

Family LAPWORTHELLIDAE Missarzhevsky 1966

Diagnosis (after Missarzhevsky 1969). Small, multilayered shells, pyramidal or cornute in form, composed of calcium phosphate. External surface with transverse sculpture which has almost no representation on the internal surface of the shell. Aperture at right angles (or only a small angle from that) to the axis of the shell, and with an outline ranging from ovate to rounded rectangular. Initial part of the shell tends to be pointed.

Remarks. Missarzhevsky (1966) referred Cobbold's two genera Lapworthella and Stenothecopsis to this family. In another paper published during that year (Missarzhevsky, in Rozanov and Missarzhevsky 1966). Camena Miss. (now Tommotia), Camenella Miss., and Kelanella Miss. were also allotted to the Lapworthellidae. Meshkova (in Zhuravleva et al. 1969, p. 166) again referred these five genera to the Lapworthellidae, although Missarzhevsky (in Rozanov et al. 1969, p. 162) was by this date including only Lapworthella, Stenothecopsis, and Fomitchella Miss. in the family, and was of the opinion that Camena (now Tommotia), Camenella, and Kelanella were better placed in the family Camenidae.

Genus LAPWORTHELLA Cobbold 1921

Type species (by original designation). Lapworthella nigra Cobbold 1921.

Diagnosis. See Cobbold 1921, p. 359.

Remarks. Seven species are known. If, as Russian authors have suggested, Poulsen's (1942) and Lochman's (1956) stenothecopsids are lapworthellids, the number of species would rise to 12. In that situation, however, it would become necessary to ask whether all of Poulsen's species should stand. Lochman (1956,

p. 1395) has already remarked that Poulsen was perhaps not justified in separating species on the basis of slight changes in the shape of the assumed aperture. Poulsen's stenothecopsid species, if transferred to *Lapworthella*, would need to be checked against Cobbold's *L. nigra* and also against the more recently

proposed Siberian forms.

Cobbold, in his diagnosis of the genus, observed that the shell of Lapworthella has two layers: an inner, of 'medium' thickness, and a very much thinner chitinous outer layer. Missarzhevsky (1966) refers to a more massive outer layer and a 'platy' inner layer in L. tortuosa-it seems obvious that these cannot be the same two layers that Cobbold mentioned. Lochman has described Stenothecopsis as having a 3-layered shell. The Stereoscan work done so far on the Strenuella Limestone lapworthellids brings no new information to bear on these questions. The shell-structure will be understood only when fine details have been studied with due regard to the possibility that certain features of the fabric may have arisen during diagenesis. Good information on primary fabric may eventually give some guidance on the affinities of the lapworthellids. The present state of this question is seen in the treatment given to Lapworthella in the Treatise of Invertebrate Paleontology (W), where Fisher (with a clear expression of his doubts) lists Lapworthella among the small conoidal shells whose affiliations are unknown at all levels up to and including phylum, and Howell (also making clear his doubts) includes Lapworthella among the worm order Sedentaria. The genus Stenothecopsis, which, it is generally agreed, may be a close relative of Lapworthella, has been referred tentatively to the Crustacea by Cobbold and Poulsen, and Fisher (1962) mentions phoronid, entoproctid, conulariid, and molluscan relationships as open, if not strong, possibilities. Müller (1966, 1971) has suggested that *Stenothecopsis* belongs among the paraconodonts (Müller 1962), although Müller and Nogami (1971), in an emended account of the suborder Paraconodontida, do not include Stenothecopsis in the list of constituent genera. An attribution to the paraconodonts would not, of course, immediately throw light on the zoological affinities of Stenothecopsis, nor, even indirectly, on those of its presumed relative Lapworthella.

Lapworthella dentata Missarzhevsky 1969

Plate 8, figs. 1-16; Plate 9, figs. 1-12

v*1969 Lapworthella dentata Missarzhevsky, 164, pl. 6, figs. 9, 14 (holotype), 19.

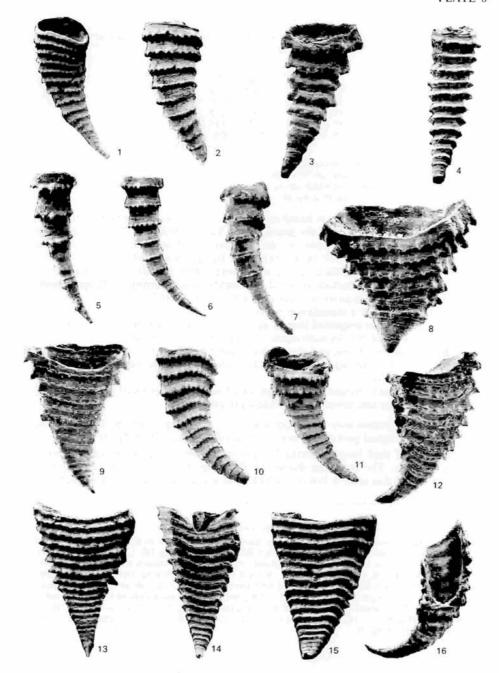
Material. 281 specimens. Figured specimens (numbers prefixed BU) are in the collections of the Geology Museum, University of Bristol.

Description. Small cornute phosphatic shells. Transverse section rounded near pointed (apical) end, may approach rectangular form near open (apertural) end. External surface regularly ribbed, each rib more or less regularly toothed (cog-like) along its adapically directed free edge. Best developed teeth (seen on the most widely-developed shells) are recurved toward the apex. Internal surface relatively smooth, has low-relief bands which occur at same frequency as external ribs, and which like these are disposed at right angles to the curved axis of growth.

Measurements (mm). Abbreviations are: L = length, Aw = apertural width (i.e. the dimension measured left to right at the aperture of a specimen seen as in Pl. 8, fig. 13), Ad = apertural depth (i.e. the dimension

EXPLANATION OF PLATE 8

Figs. 1–16. Stereoscan micrographs of specimens of *Lapworthella dentata* Missarzhevsky. 1, BU 22182, × 25. 2, BU 22183, × 28. 3, BU 22181, × 40 (detail on Pl. 9, fig. 12). 4, BU 22180, × 40. 5, BU 22177, × 32. 6, BU 22178, × 22 (detail on Pl. 9, fig. 10). 7, BU 22179, × 27. 8, BU 22187, × 55. 9, BU 22188, × 37. 10, BU 22184, × 22 (detail on Pl. 9, figs. 1, 2, 4, 7). 11, BU 22185, × 24. 12, BU 22189, × 45. 13, BU 22190, × 30 (detail on Pl. 9, fig. 11). 14, BU 22191, × 26 (detail on Pl. 9, figs. 3, 5, 6, 8). 15, BU 22192, × 33 (detail on Pl. 9, fig. 9). 16, BU 22186, × 24 (note banded internal surface). All from the *Strenuella* Limestone (Ac₄ of Cobbold), Lower Cambrian, Comley, Shropshire.



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measured left to right at the aperture of a specimen seen as in Pl. 8, fig. 12), Nr = number of ribs, Nt = number of teeth on the immediately pre-apertural rib.

	Plate reference	L	Aw	Ad	Nr	Nt
BU 22178	Pl. 8, fig. 6	1-9	0-55	0.55	10	27
BU 22184	Pl. 8, fig. 10	1.9	0.95	0.95	12	38
BU 22190	Pl. 8, fig. 13	1.52	1.15	0.5	18	35
BU 22189	Pl. 8, fig. 12	1.15	1.15	0.5	11	39
BU 22187	Pl. 8, fig. 8	0.75	0.8	0.5	6	27
Holotype		1.10	0.45	0.35	8	*

Holotype measurements from Missarzhevsky 1969, p. 164.

* Missarzhevsky gives a reading (20-30) for the number of teeth per millimetre. He also gives a reading for wall-thickness (0·02-0·03 mm) which can be compared with 0·05 mm (at a rib) and 0·02 mm (interspace) for the specimen shown on Pl. 8, fig. 16.

Remarks. The identification is based on the fact that Lapworthella dentata is so far the only described species of the genus which has toothed ribs. The terms of the description above depart from the exact detail of Missarzhevsky's description (Missarzhevsky 1969, p. 164) in two relatively trivial respects only. Missarzhevsky described the internal surface merely as smooth. Here a shallow banding (Pl. 8, fig. 16) of the internal surface is noted. Missarzhevsky, referring to 30 specimens, described the curvature as weak. Here (281 specimens) it can be seen that the curved growth axis may have a cumulative redirection of more than 90°.

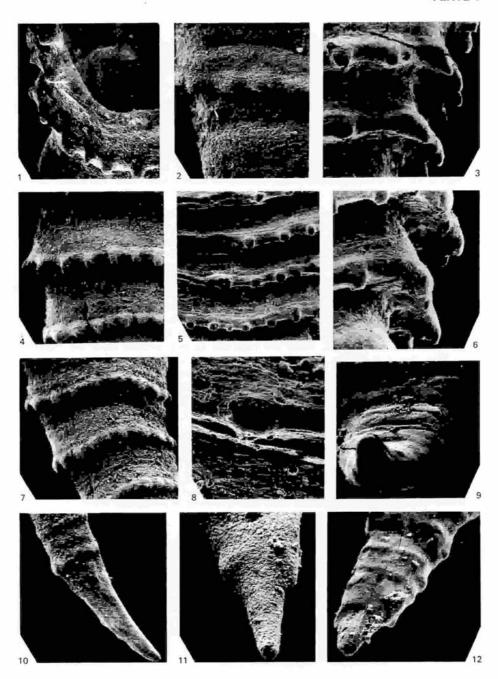
Missarzhevsky has suggested that *L. dentata* has more resemblance to *L. chodaca* (Loch.) (i.e. Lochman's *Stenothecopsis schodackensis*) than to any other described species. Size, general form, and the outward tapering of the ribs are said to match, but the cog-teeth on the edges of the ribs of *L. dentata* provide a clear means of distinguishing the two.

The Comley representatives of *L. dentata* all satisfy the terms of the description given above. They are, nevertheless, widely variable:

- 1. The axial curvature may vary from about 35° (Pl. 8, fig. 5) to about 110° (Pl. 8, fig. 15; and the apical part of this same individual shown on Pl. 9, fig. 9).
- 2. The ratio of shell length: apertural width (see table of measurements above) is widely variable. The specimen shown on Pl. 8, fig. 8 is the minimal case found. Shells in which this ratio is low (i.e. which have a relatively large angle of increase)

EXPLANATION OF PLATE 9

Figs. 1-12. Lapworthella dentata Missarzhevsky. Stereoscan micrographs to illustrate local details of certain of the specimens figured on Pl. 8. 1, 2, 4, 7, BU 22184 (see Pl. 8, fig. 10): 1, apertural detail, ×75; 2, detail of fourth rib from (broken) adapical end.; ×200; 4, detail of seventh and eighth ribs, ×100; 7, detail of fourth, fifth, and sixth ribs, ×100. 3, 5, 6, 8, BU 22191 (see Pl. 8, fig. 14): 3 (×220), 6 (×290), detail of curved teeth found on ribs situated near apertural end; 5 (×120), detail of teeth at approximately two-thirds length from apical end; 8 (×500), detail of single tooth situated immediately below centre in fig. 5. 9, apical detail (×200) of BU 22192 (see Pl. 8, fig. 15). 10, apical detail (×100) of BU 22178 (Pl. 8, fig. 6). 11, apical detail (×170) of BU 22190 (Pl. 8, fig. 13). 12, apical detail (×160) of BU 22181 (Pl. 8, fig. 3).



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tend to achieve eventually a rectangular apertural outline. Their toothed ribs are more powerfully developed and the teeth found in the relatively wide, adaperturally situated part of the shell can (as Missarzhevsky observed) show an adapically directed recurvature. Shells with a large angle of increase may also show a minor rib developed under the curving teeth of the major rib (Pl. 9, figs. 5, 8).

3. The apertural margin may vary in outline from rounded to near-rectangular, and may not lie entirely within one plane (see Pl. 8, fig. 10, and note the corresponding layout of the ribs). The form of the outline of the apertural margin (near rectangular, say, or rounded) may be recognized in the (early?) adaptical part of a shell, almost in the region where ribbing is first distinguishable (Pl. 9, figs. 9–12). The toothed effect is not yet evident at this point, but can be clearly seen (later?) at about half-length.

It may be noted that wide variations of form can be found among specimens whose lengths are comparable. The variation, it seems, should not be regarded as ontogenic. Variants have, at one extreme (e.g. Pl. 8, fig. 5), slim form, with a rounded aperture, relatively infrequent ribs, flat interspaces showing unelaborated interruptions of growth, ribs provided with relatively few teeth, and these teeth relatively straight, their axes disposed almost parallel to the axis of growth of the whole shell. At the other extreme (e.g. Pl. 8, figs. 13-15), the wider shells may have near-rectangular apertural outlines, have more frequent ribs, and the numerous teeth on each rib in the wider (later?) part of the shell are curved, with the axis of each tooth, in its proximal part, disposed at a relatively large angle (but less than 90°) to the axis of growth of the whole shell. What are regarded as intermediate cases are figured on Pl. 8, figs. 1, 2, 10, 11. There is no evident break in the range of variation, and since all specimens show the toothed effect characteristic of L. dentata they are all referred to that species. L. nigra, it should be noted, has annular banding, and the bands may have free adapical edges; but there is no record of a denticulate free edge.

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> s. c. MATTHEWS Geology Department Queen's Building University Walk Bristol Bs8 1TR

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