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New Data on the Sclerite Morphology of the Tommotiid Species *Lapworthella fasciculata*

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Abstract—New morphological types of sclerites of the tommotiid species *Lapworthella fasciculata* Conway Morris et Bengtson are described from the Lower Cambrian of South Australia. These sclerites are composed of five fused elements. Two possible reconstructions of the scleritome of *Lapworthella fasciculata* are discussed.

Key words: tommotiid sclerites, Lower Cambrian, South Australia, reconstructions.

INTRODUCTION

Tommotiids are an enigmatic order-level group of Cambrian organisms the integument of which is composed of sclerites of different morphological types. The tommotiids are widely distributed in the Lower Cambrian of Russia (Siberian Platform), Mongolia, India, China, England, France, Scandinavia, the United States, Canada, Mexico, Australia, and Antarctica. In addition, they were found in the Middle Cambrian (Amgan Stage) of Scandinavia and Australia.

Their fossil remains are usually represented by isolated sclerites of different shapes (symmetrical or asymmetrical, cap- or saddle-shaped) ranging in size from one to several tens of millimeters. The basal cross section of the sclerite is also variable in shape, i.e., it can be rounded, oval, triangular, rectangular, or trapezoid (Pl. 1). The outer surface of the sclerites is usually ornamented by transverse ribs or, more rarely, by radial folds. The sclerites are composed of phosphate minerals (Rozanov *et al.*, 1969; Missarzhevsky, 1989; Bengtson *et al.*, 1990). Their wall is usually laminar, some forms have a framed microstructure of walls (Fonin and Smirnova, 1967). Occasionally, fused sclerites occur in addition to isolated sclerites. Possibly, the sclerite grew outward from its base in the uppermost portion of successive growth layers (Bengtson, 1983). However, another more feasible model that was developed by Landing (1984), on the basis of an analysis of longitudinal sections (Fig. 1), assumes that the sclerites grew by basal-internal accretion.

The complete scleritome of these problematic animals is still unknown. For a long time, judging from the superficial similarity of the external morphology, they were considered to have some affinity with another extinct problematic group, machaeridians, from the Ordovician–Carboniferous of Europe and Australia (Bengtson, 1970; Jell, 1979; Dzik, 1986). In machaeridians the integument is composed of several longitudinal rows of imbricate metameric sclerites. In addition, the tommotiids were compared with polyplacophorans (Landing, 1984). Nowadays, many researchers accept the reconstruction of the tommotiid scleritome suggested by Evans and Rowell (1990) for the species *Dailyatia braddocki* (Fig. 2).

There is no general agreement on the classification system of tommotiids. Landing (1984) recognizes four families within the order Tommotiida Missarzhevsky, 1970, i.e., Tommotiidae Bengtson, 1970; Tannuolinidae Fonin et Smirnova; 1967, Lapworthellidae Missarzhevsky, 1966; and Sunnaginiidae Landing, 1984. Dzik (1986) placed the orders Tommotiida Missarzhevsky,

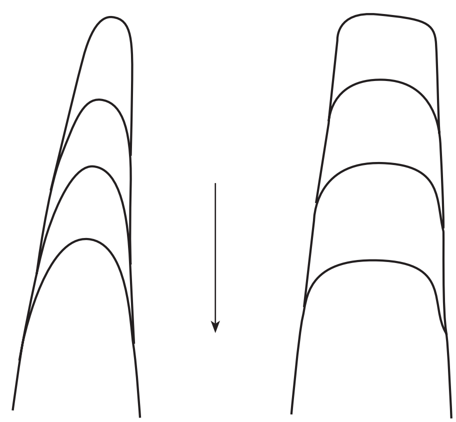


Fig. 1. Scheme of the sclerite growth in the tommotiid species *Lapworthella fasciculata* Conway Morris et Bengtson, 1990: (a) sclerite with a rounded basal cross section and (b) sclerite with a rectangular basal cross section; drawings after the photographs presented in the paper by Landing (1984, text-fig. 3); arrow indicates the growth direction; not to scale.

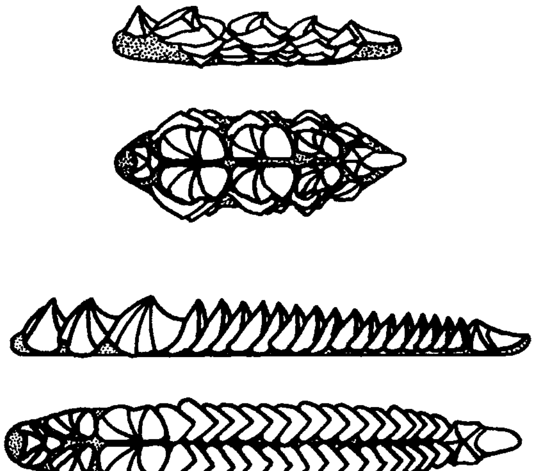
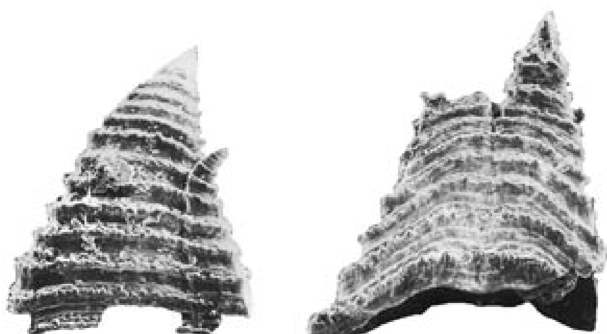


Fig. 2. Scleritome reconstruction of the tommotiid species *Dailyatia braddocki* (after Evans and Rowell, 1990).



(a) (b)

Fig. 3. Fused pairs of sclerites of the tommotiid species *Lapworthella schodackensis* (Lochman, 1956): (a) equal and (b) unequal sclerites (after Landing, 1984).

1970 and Sachitida He, 1980 into the class Machaeridia Withers, 1926. Laurie (1986) assigned the family Tommotiidae Bengtson, 1970, along with the families Tannuolinidae Fonin et Smirnova, 1967 and Lapworthellidae Missarzhevsky, 1966, to the order Mitrosagophora Bengtson, 1970. I support the system suggested by Esakova (Esakova and Zhegallo, 1996). On the basis of the sclerite general morphology, ornamentation, and microstructure, she split the tommotiids into six families, i.e., Tommotiidae Bengtson, 1970; Tannuolinidae Fonin et Smirnova, 1967; Lapworthellidae Missarzhevsky, 1966; Kelanellidae Missarzhevsky et Grigorieva, 1981; Kennardiidae Laurie, 1986; and Sunnaginiidae Landing, 1984. Eight tommotiid genera representing four families are present in the examined specimens from South Australia.

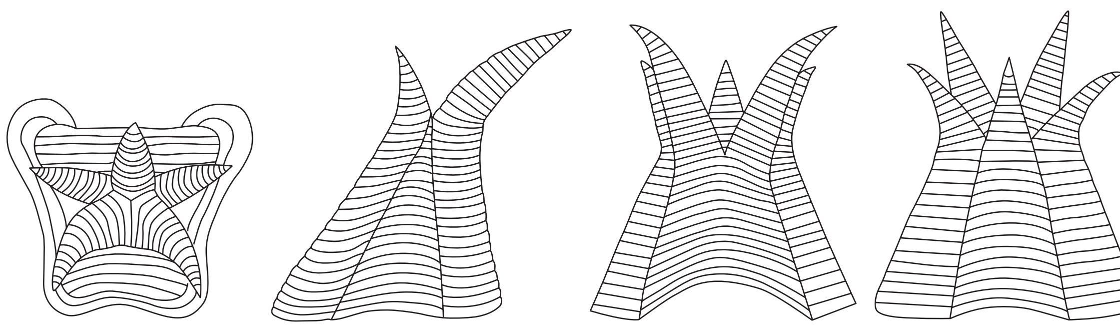
MATERIAL

I studied over five hundred rock samples from ten sections of the Lower Cambrian of South Australia. Only one sample (rock sample no. HG0, Horse Gully Locality, the base of the Parara Limestone) yielded ten specimens of similar fused sclerites of *Lapworthella fasciculata* Conway Morris et Bengtson (Pl. 2, figs. 1–7). Three scleritome fragments have satisfactory preservation, the other fragments are poorly preserved.

DISCUSSION

Fused sclerites with a single common internal cavity have been reported earlier, i.e., *Lapworthella* (Fig. 3) and *Tannuolina* and *Eccentrotheca* (Bengtson, 1970; Landing, 1984; Qian and Bengtson, 1989). However, all of them were formed by fusion of only two (equal or unequal) sclerite elements.

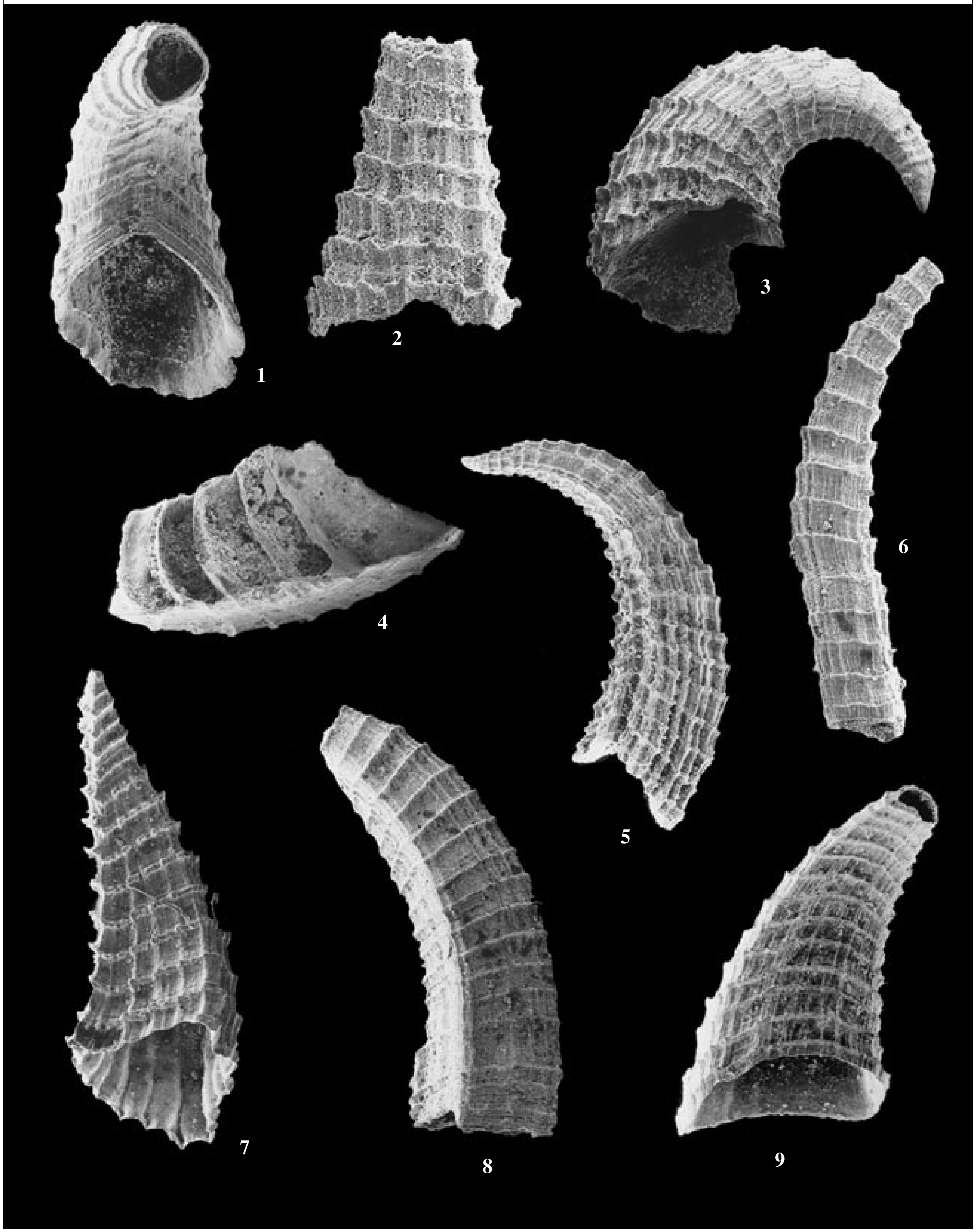
I have found fused sclerites that are less than 1 mm high and 0.5–0.6 mm wide and are composed of five elements (two larger elements and three smaller elements). These sclerites are bilaterally symmetrical. Each of the fused sclerites has a subtrapezoid basal cross section (Fig. 4) with two longer sides (one is concave, another is almost straight) and two shorter sides (both are concave). Two larger elements have irregular trapezoid basal cross sections, while three smaller elements have triangular cross sections. The elements are



(a) (b) (c) (d)

Fig. 4. Reconstruction of the fused sclerites of *Lapworthella fasciculata* Conway Morris et Bengtson, 1990: (a) top view, (b–d) three different views.

Plate 1



arranged in a checkerboard pattern and are deflected outwards, the smaller elements and larger elements are bent in opposite directions. All the fused sclerites under study are inclined to the long concave side.

The external ornamentation of the majority of sclerites is represented by transverse ribs and suggests that all five sclerites fused simultaneously. However, it is possible that the two larger elements appeared on the animal body prior to the three smaller elements. The same number of ribs on the lower part of each fused sclerite proves the simultaneous fusion of all elements (Pl. 2, fig. 1b).

All fused sclerites are comparable in size with numerous singular sclerites of *L. fasciculata.* Since all known fused sclerites are smaller than singular sclerites, the singular sclerites do not represent younger ontogenetic stages of the animal. The singular sclerites fused after they were fully grown and covered the entire animal body. Large singular sclerites occur in association with numerous singular sclerites of smaller size. This fact suggests that not all of the sclerites had the possibility or necessisarily had to fuse.

The following conclusions can be drawn from the find of new sclerite morphotypes of *Lapworthella*.

(1) The existence of fused sclerites shows that one isolate sclerite could not be a separate organism. This is also supported by the narrow and irregular shapes of cross sections of the aperture of fused sclerites in other species, i.e., *Lapworthella schodackensis* (Lochman); *Eccentrotheca kanesia* Landing; Nowlan, et Fletcher (Landing, 1984); and *Eccentrotheca guano* Bengtson (Bengtson *et al.*, 1990). Apparently, the sclerites were closely spaced on the body of an unknown animal and could merge to form an external skeleton.

(2) The existence of fused sclerites composed of unequal elements suggests that in the same animal sclerites varied in size; therefore, the number of sclerites could increase during the entire lifetime of the organism. A similar conclusion was already made after the find of fused sclerites of *Lapworthella schodackensis* composed of two unequal elements (Landing, 1984).

(3) Pointed and usually curved sclerites primarily served a protective function; however, their supportive function is also quite possible. The fusion of closely spaced sclerites apparently increased the durability (inflexibility) of the animal's integument.

(4) The presence of dextral and sinistral singular sclerites suggests that the animal has bilateral symmetry. As mentioned above, the fused sclerites are also bilaterally symmetrical. Therefore, such fused sclerites can be arranged on the animal body either (a) along the longitudinal axis of the animal (the symmetry plane of the fused sclerite coincides with the symmetry plane of the animal) or (b) in pairs so that the symmetry plane of

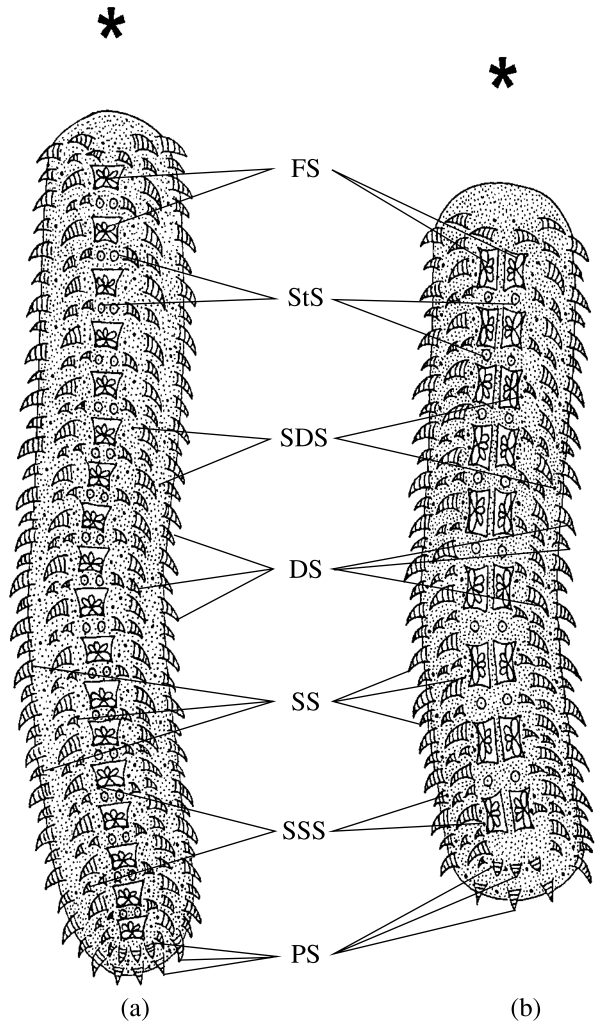


Fig. 5. Scleritome reconstruction of the tommotiid species *Lapworthella fasciculata* Conway Morris et Bengtson, 1990. Designations: (FS) fused sclerites; (StS) straight sclerites; (DS) dextral sclerites; (SDS) small dextral sclerites; (SS) sinistral sclerites; (SSS) small sinistral sclerites; (PS) posteriorly bent sclerites; (*) indicates the anterior end of the animal.

the sclerite is perpendicular to the symmetry plane of the animal.

(5) In case (a), the fused sclerites, which were arranged along the longitudinal axis of the animal, have their long, almost flat sides as their anterior parts, their long concave sides as their posterior parts, and the short

Explanation of Plate 1

Figs. 1–9. *Lapworthella fasciculata* Conway Morris et Bengtson in Bengtson *et al.*, 1990, singular sclerites; Lower Cambrian, Botoman Stage, *Bemella communis* Beds; South Australia, Yorke Peninsula, Horse Gully, basal part of the Parara Limestone, rock sample HG0: (1) specimen no. 4664/3396, dextral sclerite with a suboval basal section, ×50; (2) specimen no. 4664/3718, straight sclerite with a subrectangular basal section, ×90; (3) specimen no. 4664/3421, dextral sclerite with an oval basal section, ×60; (4) specimen no. 4664/3373, internal structure of sclerite, ×45; (5) specimen no. 4664/3388, sinistral sclerite with a subtriangular basal section, ×40; (6) specimen no. 4664/3716, dextral sclerite with a triangular basal section, ×65; (7) specimen no. 4664/3363, sinistral sclerite with a triangular basal section, ×45; (8) specimen no. 4664/3407, sinistral sclerite with a subquadrangular basal section, ×40; and (9) specimen no. 4664/3378, dextral sclerite with a rectangular basal section, ×55.

Plate 2

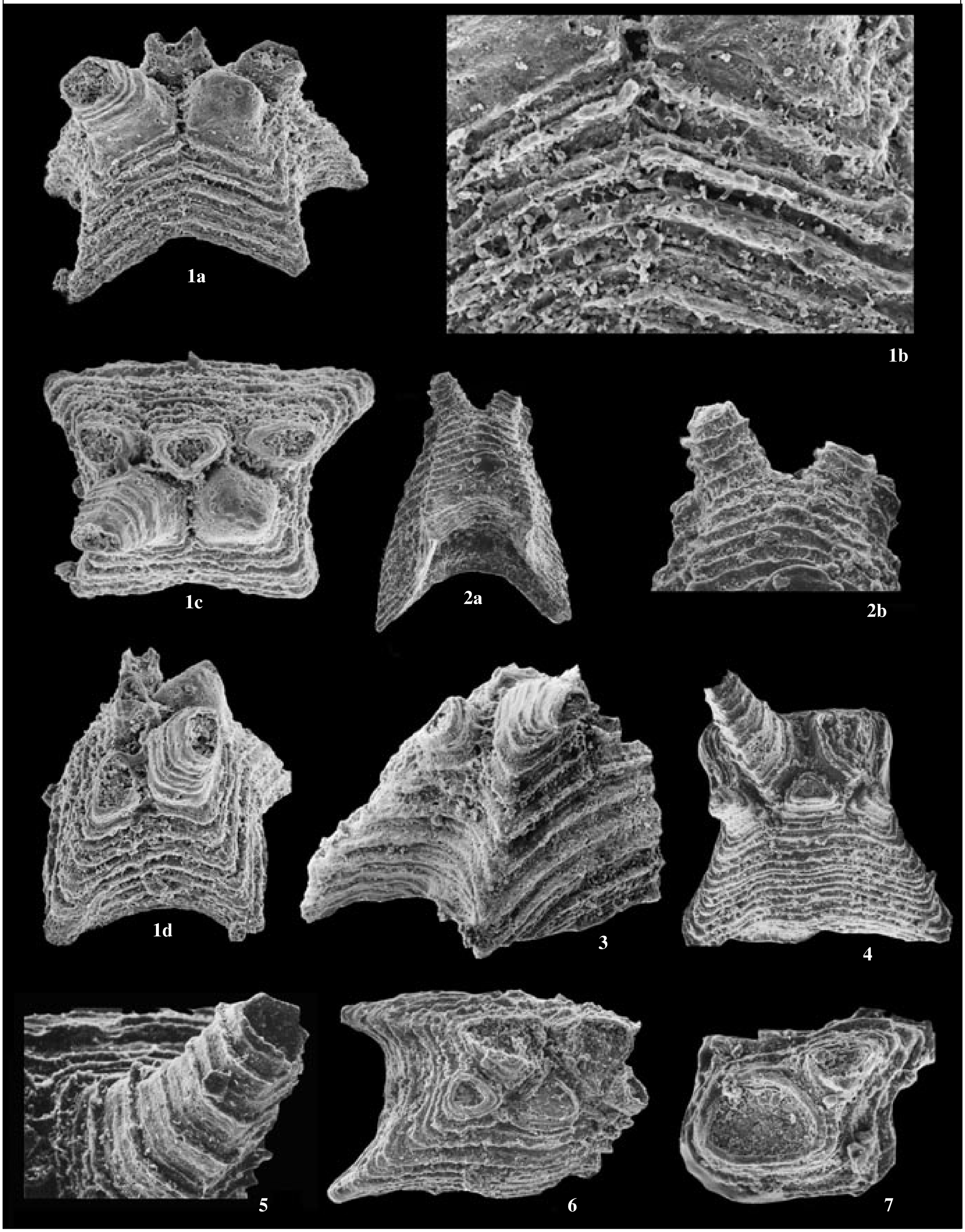


Table 1. Joint occurrence of isolated sclerites of *Lapworthella fasciculata* with other representatives of the order Tommotiida

Tommotiid species \ Specimen no.	HG0	HG1	HG5	HG9	HG12	Cur10	SH11	SH23	CURD 1B 382.4 m	Minlaton-1 376.6 m	Minlaton-1 496.9 m	Minlaton-1 531.6 m	Minlaton-1 585.5 m
Camenella reticulosa Conway Morris							+						
Dailyatia ajax Bischoff	+	+	+	+	+	+	+		+	+	+		
Eccentrotheca guano Bengtson	+											+	
Lapworthella fasciculata Conway Morris et Bengtson	+	+	+					+					+
Kennardia reticulata Laurie	+	+											
Kulparina rostrata Conway, Morris, et Bengtson	+												
Paterimitra pyramidalis Laurie	+												
Sunnaginia sp.							+						

Table 2. Occurrence of isolated sclerites of *Lapworthella fasciculata*

Sclerite morphotype \ Specimen no.	HG0	HG1	HG5	SH23	Minlaton-1 585.5 m	SYC-101 221.45 m	SYC-101 222.25 m	SYC-101 245.0 m
Dextral	96	2	1			1	2	1
Sinistral	62	2		1	1	1	1	
Straight	18							
Posteriorly bent	11	1						

concave sides as their lateral parts. This is due to the fact that all known fragments of the scleritome are inclined to the long concave side, i.e., to the posterior end of the animal body (Fig. 5a). In case (b), sclerites arranged in pairs could apparently form two rows on either side of the longitudinal axis of the animal, with their long flat sides being in contact with each other (Fig. 5b). It should be noted that in both cases fused sclerites can be restricted to the anterior and/or posterior ends rather than occuring along the entire animal.

It is possible, however, that tommotiids, like halkieriids, have sclerites that have been thought to belong to different genera and species. For this reason, the co-occurrence of singular sclerites of the tommotiid species *L. fasciculata* with other sclerites of this group was studied (Table 1). Sample no. HG0 has yielded fused sclerites that belong to the species *L. fasciculata* and to five other tommotiid genera. In other samples, singular sclerites of *L. fasciculata* co-occur with sclerites of *Dailyatia ajax* Bischoff (rock sample nos. HG1 and HG5) and *Kennardia reticulata* Laurie (rock sample no. HG1). These data are inadequate to reveal the pattern of the co-occurrence of *L. fasciculata* with other tommotiid taxa. Representatives of all other genera differ from the sclerites of *L. fasciculata* in shape, size,

Explanation of Plate 2

Figs. 1–7. *Lapworthella fasciculata* Conway Morris et Bengtson in Bengtson *et al.*, 1990; Lower Cambrian, Botoman Stage, *Bemella communis* Beds; South Australia, Yorke Peninsula, Horse Gully, basal part of the Parara Limestone, rock sample HG0: (1) specimen no. 4664/5400, fused sclerite: (1a) oblique top view, ×160; (1b) fragment of ornamentation in the fusion zone of sclerites, ×450; (1c) top view, ×160; (1d) oblique top view, ×160; (2) specimen no. 4664/3776: (2a) fused sclerite, ×65; (2b) fragment of the upper part of the sclerite, ×135; (3) specimen no. 4664/3614, oblique top view, ×150; (4) specimen no. 4664/3701, top view, ×110; (5) specimen no. 4664/3466, ornamentation fragment, ×235; (6) specimen no. 4664/3759, top view, ×130; and (7) specimen no. 4664/3934, fragment of a fused sclerite, top view, ×150.

and external ornamentation. However, such wide variations do not preclude the possibility that sclerites assigned to different genera and species belong to different parts of the body of a single animal. This assumption is supported by the find of *Halkieria* from the Lower Cambrian Buen Formation of Greenland (Conway Morris and Peel, 1990). The external skeleton of this *Halkieria* is composed of numerous small sclerites, which are different in morphology but similar in ornamentation, while the anterior and posterior ends bear a pair of larger sclerites, which are strikingly different in shape and ornamentation from the other elements.

It is possible that the Australian sclerites, which have been assigned to different genera (*Lapworthella, Dailyatia*, and *Kennardia*) and occur in the same samples, belong to one animal despite the difference in shape and external ornamentation.

In addition, a statistical analysis of singular sclerites of *L. fasciculata* has been made (Table 2). It should be noted that only rock sample no. HG0 is representative and, hence, statistically valid. The other rock samples contain too few (one to five) specimens and, thus, are nonrepresentative and cannot be analyzed statistically. In rock sample no. HG0 dextral sclerites outnumber sinistral sclerites by approximately 30%, although dextral and sinistral sclerites are thought to be equal in number. For every 100 dextral sclerites there are about two fused sclerites.

The new data make possible two different reconstructions of the animal scleritome (Fig. 5). It is clear that dextral and sinistral singular sclerites were located on the right and left sides of the body, respectively. The straight singular sclerites and posteriorly bent singular sclerites were apparently arranged along the central axis of the animal, especially as they are greatly outnumbered by the dextral and sinistral sclerites (Table 2).

In conclusion, it may be said that new finds similar to the fused sclerites of *L. fasciculata* described in this paper will provide a more exact reconstruction of the lapworthellid appearance.

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