THE TAXONOMY AND SHELL CHARACTERISTICS OF A NEW ELKANIID BRACHIOPOD FROM THE ASHGILL OF SWEDEN

by LARS E. HOLMER

ABSTRACT. A new elkaniid brachiopod genus and species, *Tilasia rugosa*, is described from the Ashgill (Harju Series) Boda Limestone in the Siljan district (province of Dalarna), Sweden. It is the first record of the lingulacean family Elkaniidae from the Upper Ordovician. The material of *T. rugosa*, which is one of the largest described member of the family, is well preserved and allows an account of the micro-ornamentation and shell structure. The strongly rugose exterior has a divaricate ornamentation with minute rhomboid pits, previously not known among the elkaniids.

ELKANIID brachiopods are common and widely distributed mainly in the Upper Cambrian and Lower Ordovician (Tremadoc-lower Llanvirn); the family has not previously been recorded from beds younger than the Middle Ordovician.

Here a new genus and species, *Tilasia rugosa* from the Upper Ordovician (Ashgill) Boda Limestone in the Siljan district, province of Dalarna, Sweden (Text-fig. 1), is described. The rare but well preserved material of this large elkaniid also permits an account of the shell structure and micro-ornamentation, not previously known from this group.

MATERIALS AND METHODS

In the Siljan district, Lower Palaeozoic (Upper Cambrian? to Silurian) rocks crop out within a tectonically complex ring-structure, which probably represents a hypervelocity impact crater (Text-fig. 1; see Jaanusson 1982 for a review). The Boda Limestone (within the *Amorphognathus ordovicicus* Biozone: Bergström 1971) is a large (maximum diameter, 1000 m; thickness, 140 m), lens-shaped, stromatactis-bearing unit, with a high carbonate content. Although reef-like, it lacks an organic frame; it represents a carbonate mound, possibly comparable with modern lithoherms (Jaanusson 1979, 1982).

The phosphatic inarticulates (discinaceans) from these beds have previously been described by Lindström (*in* Angelin and Lindström 1880) and Holmer (1987). The stratigraphy and fauna of the Boda Limestone were summarized by Jaanusson (1958, 1982).

The material was prepared from the limestone by etching with 10% buffered acetic acid (see Jeppsson *et al.* 1985 for details); the outer or inner surfaces of the valves were covered with a layer of epoxy resin to avoid fragmentation during the etching process. To study shell structure, specimens embedded in epoxy resin were sectioned, polished and subsequently etched with 4% hydrochloric acid for 4 seconds; the counterparts of the sectioned valves were used to make thin sections for examination in transmitted light.

The type material is housed in the Department of Palaeozoology, Swedish Museum of Natural History (SMNH), and in the Department of Geology, University of Lund (LO). Detailed descriptions of the localities (Östbjörka, Boda, Jutjärn, and Skålberget; Text-fig. 1) in the Siljan district are given by Thorslund (1936; see also Jaanusson 1982).
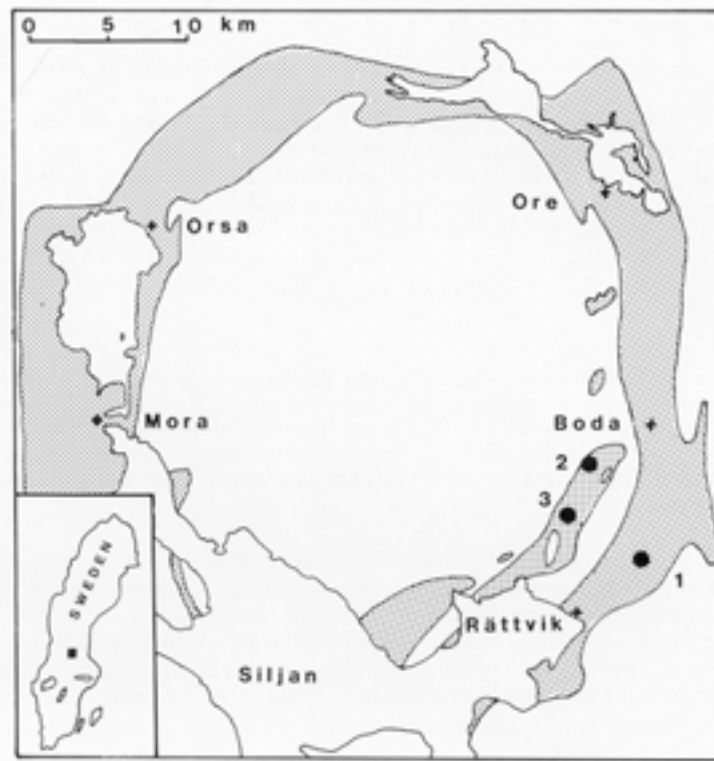
TEXT-FIG. 1. Location map of the Siljan district, province of Dalarna, Sweden, showing the ring-structure with Lower Palaeozoic rocks (shaded) and the localities investigated (filled circles). 1, Jutjärn; 2, Östbjörka; 3, Skålberget.

SYSTEMATIC PALAEONTOLOGY

Class LINGULATA Goryansky and Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULACEA Menke, 1828
Family ELKANIIDAE Walcott and Schuchert, 1908

Diagnosis. See Rowell (1965, p. H270).

Genera assigned. Monobolina Salter, 1866; *Elkania* Ford, 1886; *Broeggeria* Walcott, 1902; *Lamanskya* Moberg and Segerberg, 1906 [= ?*Dictyobolus* Williams and Curry, 1985]; *Elkanisca* Havlíček, 1982; *Tilasia* gen. nov.

Discussion. The detailed morphology of many of the elkaniid genera listed above remains poorly known, perhaps partly because they have usually been described from material from argillaceous sequences (e.g. *Broeggeria, Monobolina, Elkanisca*); well preserved complete specimens from carbonates have generally not been available.

The elkaniid affinity of *Monobolina* was recently questioned by Havlíček (1982, p. 50). However, the new data on the morphology of *M. plumbea* (Salter) presented by Lockley and Williams (1981, p. 15, figs 31–34) indicates that it belongs within the Elkaniidae. Lockley and Williams (1981) also

described the new species *M. crassa*, which extended the range of the family into the Middle Ordovician (Llandeilo).

The poorly known Lower Ordovician (Tremadoc) *Lamanskya* Moberg and Segerberg, 1906, from Öland, Sweden, was previously placed questionably among the Strophomenidina (Williams 1965, p. H863), but is now considered to be an elkaniid (Holmer 1989); the type (and only) species, *L. splendens* Moberg and Segerberg, is widely distributed in the Lower Ordovician of Sweden, and is currently being redescribed. The Irish Lower Ordovician genus *Dictyobolus* Williams and Curry, 1985 (type species *D. transversus* Williams and Curry), which is here referred to the elkaniids, appears to be a junior synonym of *Lamanskya* (Holmer unpublished). The likewise poorly known *Aulonotreta kuraganica* Andreeva, 1972 from the Lower Ordovician of the Ural Mountains probably also represents a new genus of the elkaniid brachiopods (L. E. Popov, personal communication 1989).

Genus TILASIA gen. nov.

Type species. Tilasia rugosa sp. nov.

Etymology. In honour of Daniel Tilas (1712–1772), who published the first detailed account of the Lower Palaeozoic strata of Dalarna (Tilas 1740).

Diagnosis. Large, transversely suboval, moderately and subequally biconvex, rugose shell; exterior pitted with rhomboid pits. Ventral pseudointerarea with wide propareas and deep, triangular pedicle groove; ventral umbonal muscle scar divided by anteriorly directed extension of the pedicle groove. Dorsal pseudointerarea with wide median groove and narrow propareas.

Species assigned. Tilasia rugosa sp. nov.;? *Obolus*? sp. 3 Cooper, 1956.

Tilasia rugosa sp. nov.

Text-figs 2–5

Holotype. SMNH Br133686, almost complete shell (width 26·6 mm, length 22·4 mm, thickness 10·0 mm) from the Boda Limestone, Jutjärn quarry, Siljan district, Dalarna (coll. M. Frye).

Paratypes. All material from the Boda Limestone, Siljan district, Dalarna; SMNH Br133691, incomplete dorsal valve, Skålberget quarry (coll. E. Jarvik; flank facies; locality 8 *in* Jaanusson 1982, fig. 3; SMNH Br102556*a*, incomplete dorsal valve (previously identified as fragmentary dorsal valve of *Orbiculoidea*? *gibba in* Holmer 1987, p. 320), Skålberget quarry (flank facies; coll. J. Martna); LO 5956, incomplete ventral valve, Östbjörka (coll. S. L. Törnquist); LO 5957 (not figured), incomplete ventral valve, Boda (coll. S. L. Törnquist). Total of two dorsal and two ventral valves.

Etymology. Latin *rugosus*, wrinkled; alluding to the rugose ornamentation.

Diagnosis. As for genus.

Description. Shell large (up to 26·6 mm wide and 22·4 mm long in one specimen), and moderately, subequally biconvex, 38 % as thick as wide (Text-figs 2A and 3E); transversely suboval in outline. Ornamentation strongly rugose (see also below) with regularly disposed, up to 0·5 mm high rugae, on average 0·5 mm apart (Text-figs 3A, D, F, I and 4A–F).

Ventral valve (of holotype) 1 mm longer than dorsal valve, 84% as long as wide, but less convex (about 1 mm difference), 15% as high as wide (Text-figs 2A and 3A, E). Interior of ventral valve not known in detail; ventral pseudointerarea 14–16 mm wide (in two specimens), occupying 50% of valve width, with well developed propareas, 1·3 mm wide; deep, triangular pedicle groove, 4·3 mm wide and 1·6 mm long; ventral umbonal muscle scar divided by anteriorly directed extension of pedicle groove (Text-figs 2B and 4G–I). An
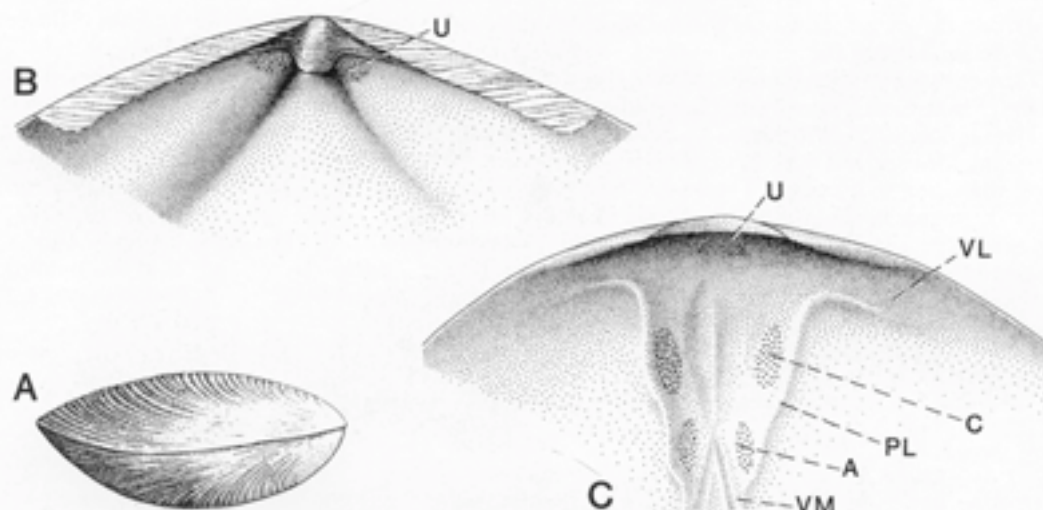
TEXT-FIG. 2. *Tilasia rugosa* sp. nov. A, lateral profile of complete shell, based on SMNH Br133686. B, ventral interior, based on LO 5956. C, dorsal interior, based on SMNH Br133686. All ×6. U, umbonal muscle scar; VL, *vascula lateralia*; C, central muscle scar; PL, platform; A, anterior lateral muscle scar; VM, *vascula media*.

unfigured, poorly preserved fragment of a ventral valve (No. LO 5957) shows a section through an elevated platform, directly anterior to the umbonal muscle scars, but the detailed morphology of the platform is not known.

Dorsal valve (of holotype) 80% as long as wide, and 23% as high as wide (Text-figs 2A and 3B, E). Dorsal pseudointerarea with median groove, 5·6 mm wide and 0·6 mm long; exact dimensions of propareas unknown, but they appear to be narrower than the ventral ones (Text-figs 2C and 3G–H). Dorsal umbonal muscle scar situated directly anterior to median groove; central and anterior lateral muscle scars situated on an elevated, subtriangular platform, 7 mm wide and 9 mm long, with low median septum; well-developed vascular markings with *vascula lateralia* diverging anterolaterally from umbonal muscle scar, and *vascula media* diverging anterior to anterior lateral muscle scars (Text-figs 2C and 3G–H).

Remarks on ontogeny. All the examined specimens represent adults. The early ontogeny of *T. rugosa* is not known; the apical region of the valves is fragmentary. The regularly shaped, biconvex shells do not show any major interruptions or changes in the growth pattern during the juvenile and adult stages; the major concentric rugae are formed at regular intervals. In an early part of the juvenile stage (when the shell is up to 3 mm wide and 2 mm long) the rugae are densely spaced, about 0·16 mm apart; during later growth stages they become gradually more widely spaced, up to 0·8 mm apart; a fully grown shell appears to have up to about fifty major rugae (Text-fig. 3A, D, F). In some specimens there are minor, more irregular rugae between the major ones (Text-fig. 4A–C).

Discussion. Tilasia rugosa differs from mot other elkaniids (such as species of *Broeggeria*, *Elkanisca*, and *Monobolina*) mainly in being more biconvex and strongly rugose. It is most similar to species of *Elkania*. However, *T. rugosa* differs in being less biconvex and more rugose; the thickness of the type species *E. desiderata* (Billings) (Rowell 1965, p. H270, fig. 164: 1a–c) is about two-thirds of its width and most species of *Elkania*, like *E. hamburgensis* (Walcott), are smooth, having only weakly developed growth lines (Rowell 1965, fig. 164: 1d–f).

Lamanskya splendens Moberg and Segerberg, 1906 (p. 71, pl. 3: 17) and '*Aulonotreta*' *kuraganica* Andreeva, 1972 (p. 46, pl. 7: 1–3) differ in being more strongly biconvex; the thickness of the latter is up to three-quarters of its width; moreover, the dorsal platforms of these two species are much higher (Holmer unpublished; Andreeva 1972, pl. 7: 3).
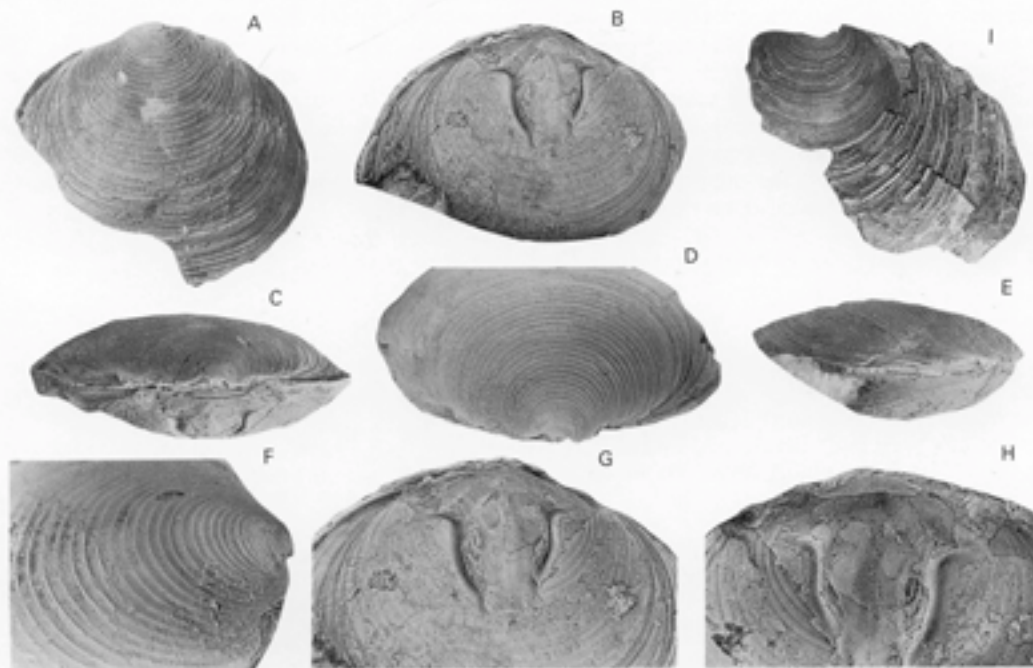
TEXT-FIG. 3. *Tilasia rugosa* sp. nov., Boda Limestone (Ashgill), Siljan district, Dalarna. A–H, holotype, complete shell, Jutjärn, SMNH Br133686; A, ventral exterior, ×2; B, internal mould of dorsal valve, ×2; C, posterior profile, ×2; D, oblique posterior view of ventral valve, ×2·5; E, lateral profile, ×2; F, oblique lateral view of ventral valve, ×2·5; G, detail of B, ×2·8; H, detail of latex cast of B, ×3·4. I, exterior of incomplete dorsal valve, Skålberget, SMNH Br102556a, ×2·5.

    T. rugosa is comparatively large for the family, the maximum width being almost 27 mm. Most other elkaniids (such as *Broeggeria*, *Elkania*, and *Elkanisca*) are generally up to 10 mm wide; only *Monobolina crassa* (maximum width 23 mm) and '*Aulonotreta*' *kuraganica* (maximum width 25 mm) are more than 20 mm wide. Cooper (1956, p. 193, pl. 9F; 16, 11A: 1) described a large, unnamed obolid, *Obolus*? sp. 3, from the Middle Ordovician Pratt Ferry beds of Alabama, USA. The interior of this species is unknown, but the strongly rugose exterior, and the general shape of the shell indicate that it might possibly be related to *Tilasia*.

    As noted above, *T. rugosa* is the youngest described elkaniid and the first record of the family from the Upper Ordovician (Harju Series).

Remarks on autecology. The type of environment in which *T. rugosa* lived is uncertain. The holotype is a complete, articulated shell, which has probably not been transported for any great distance after death, but its exact location within the carbonate mound is not known. The mound core of the Boda Limestone is generally poor in sedentary macro-organisms, and has dominantly a vagile fauna of trilobites, gastropods, cephalopods, and pelecypods (Jaanusson 1982, p. 28). Two dorsal valves, which were collected from the flank facies of the mound, are fragmentary and may have been transported.

    Although many fossil lingulaceans appear to have been infaunal burrowers comparable with their Recent representatives, this is an unlikely mode of life for *T. rugosa*. The following characters makes it comparatively poorly adapted for burrowing (see Bassett 1984 and Savazzi 1986 for a detailed

discussion of this life strategy): (1) The moderately biconvex shell is transversely suboval and wider than long (rather than elongate and 'streamlined' as in *Lingula*). (2) The visceral area and the sites of muscular attachments are more posteriorly placed as compared with other lingulaceans (the dorsal anterior lateral muscle scars are placed at about 40% the valve length from the posterior margin in *T. rugosa*, whereas in *Lingula*, for example, the ratio is about 60–70%). (3) The ornamentation is strongly rugose (rather than smooth, or with burrowing sculptures). Thus, *T. rugosa* was probably better adapted to some kind of epifaunal mode of life. The pedicle foramen appears to have remained open throughout ontogeny.

Occurrence. *T. rugosa* is restricted to the Ashgill Boda Limestone of Dalarna.

MICRO-ORNAMENTATION

Under the SEM, the etched rugose exterior of two dorsal valves revealed a regular pattern of pits covering the post-larval surface (Text-fig. 4A–F). The apical region of the valves is fragmentary, and the ornamentation is not known from this part of the shell.

The pits are evenly distributed and closely packed, less than 10 μm deep, subequal in size and shape, elongate rhomboid, up to 100 μm long and 30 μm wide, with the largest dimension arranged
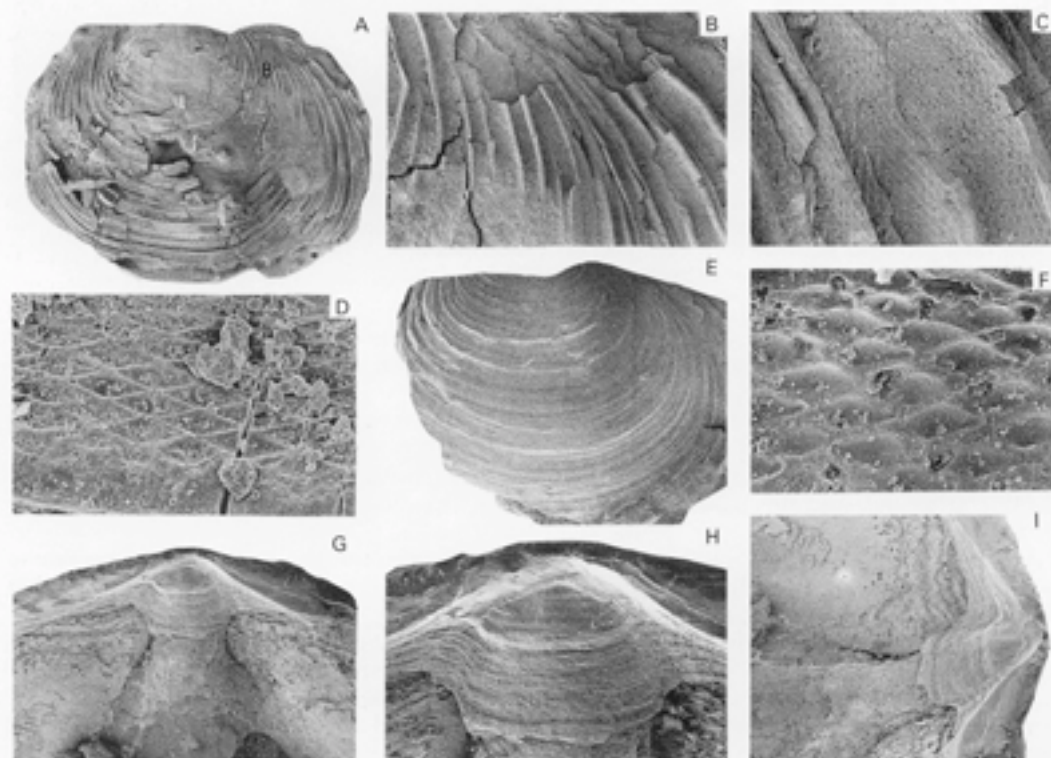
TEXT-FIG. 4. *Tilasia rugosa* sp. nov., Boda Limestone (Ashgill), Siljan district, Dalarna. A, exterior of incomplete dorsal valve, the location of B indicated, Skålberget, SMNH Br133691, ×5. B, C, D, details of A, ×19, ×60, ×150, respectively. E, exterior of partly exfoliated, incomplete dorsal valve (see also Text-fig. 3I), Skålberget, SMNH Br102556a, ×5. F, detail of E, ×196. G, interior of incomplete ventral valve, Östbjörka, LO 5956, ×10. H, detail of G, ×20. I, oblique lateral view of G, ×15.

perpendicular to the direction of growth (Text-fig. 4c). The geometry of the ornamentation could not be investigated in detail, owing to the considerable degree of fragmentation and exfoliation in the two available valves. However, the pits appear to be arranged in offset radiating rows (*sensu* Wright 1981, p. 446). Each rhomboid pit is defined by two pairs of parallel ridges (each up to 5 μm wide), which are disposed obliquely across the valve surface and intersect at about 30–40°. This type of sculpture is very suggestive of the so-called divaricate pattern of ornamentation, which is responsible for a wide range of sculptures (including burrowing terraces) in molluscs and arthropods, but it has also been reported from some lingulacean brachiopods (see Seilacher 1972 and Savazzi 1986 for reviews).

A divaricate ornamentation of pits has not previously been reported from the elkaniids, but the Lower Ordovician species *Dictyobolus* [= ?*Lamanskya*] *transversus* Williams and Curry (1985, p. 189, figs 2–7) and *Lamanskya splendens* Moberg and Segerberg have an essentially identical type of ornamentation; a similar type of sculpture also appears to be developed in '*Aulonotreta*' *kuraganica* Andreeva. As noted above, these taxa are here considered to belong within the family (Holmer, unpublished).

Ornamentation comparable to that of the elkaniids is also known from three other brachiopod groups: (1) The problematic articulate brachiopod *Dictyonella* has rhomboid pits, very similar to those of *Tilasia* and arranged in a strict divaricate geometry (see Wright 1981 for a detailed discussion); however, this brachiopod is not otherwise comparable with the elkaniids. (2) Rhomboid, post-larval pits, only some 6 μm across, and arranged in divaricate rows have been described by Popov *et al.* (1982, fig. 1: 2) and Holmer (1986, fig. 40) from the thin-shelled Ordovician lingulacean *Paterula*. In the paterulids, the larval shell is also pitted, with minute, circular, cross-cutting pits, about 2–4 μm across, which are closely comparable with the larval pits of most acrotretaceans (see Biernat and Williams 1970). Popov *et al.* (1982, p. 103) suggested that both the larval and post-larval pits of *Paterula* represent moulds of a vesicular periostracum, as in the 'bubble raft' model originally proposed for the acrotretacean larval shell (Biernat and Williams 1970). It is entirely possible that the post-larval pits of *Tilasia* represent a cast of similar structures in the periostracum (see also Williams 1990). (3) Most paterinids (like *Dictyonina* and *Micromitra*) appear to have divaricate types of post-larval pitted ornamentation, whereas the larval shell is smooth (e.g. Rowell 1965); in *Dictyonites* and *Lacunites*, there are rounded, open perforations, 20–200 μm across, which penetrate the valves (Cooper 1956; Wright 1981; Holmer 1986, 1989), and the problematic phosphatic brachiopod *Volborthia* (sometimes doubtfully referred to the paterinids) possesses some kind of pitted, divaricate ornamentation, which has not been studied closely (Ushatinskaya *et al.* 1988, pl. 6: 6a).

Other types of pitted post-larval ornamentation have been reported and discussed by Wreight (1981), Savazzi (1986), and Holmer (1986, 1987, 1989).

SHELL STRUCTURE

Because of the limited material available, only a single fragment of the postero-lateral portion of a dorsal valve was sectioned (Text-fig. 5). The rugose exterior of this fragment is still covered by the calcareous matrix of the Boda Limestone (Text-fig. 5A).

The pitted ornamentation, described above, is developed in the outermost primary layer, which is only about 10 μm thick (Text-fig. 5E). In etched sections examined under the SEM, it has a densely granular appearance, but the size of individual apatite granulae could not be determined, and the layer appears to lack birefringence. The boundary to the secondary layer is not well defined (Text-fig. 5E), and the primary layer is not easily 'peeled off' as in some discinaceans (Holmer 1987).

The secondary layer is primarily built up of laminae, up to 0·3 mm thick, which are roughly wedge-shaped in section, and inclined at a low angle to the outer valve surface. The laminae have a porous appearance both under the SEM and the light microscope, and possess a well-developed baculate structure (*sensu* Holmer 1989), with criss-crossing slender apatite baculae, about 1–2 μm across (Text-fig. 5B, C). The detailed internal structure of the baculae could not be determined; they
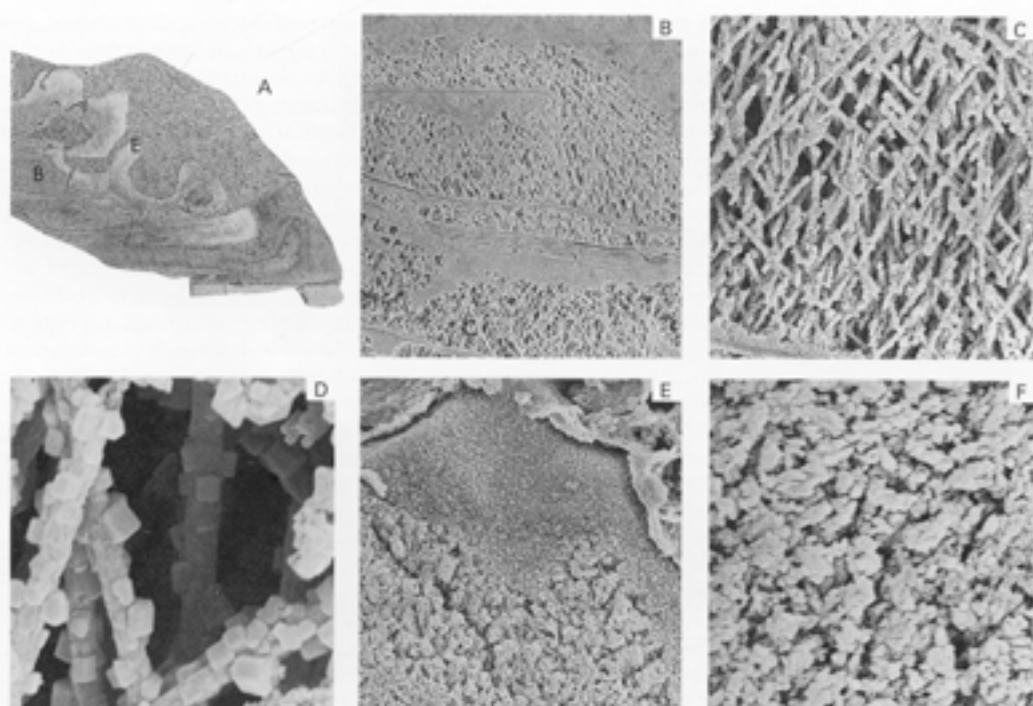
TEXT-FIG. 5. A, Polished and etched section through a fragment of a dorsal valve of *Tilasia rugosa* sp. nov., the location of B and E indicated, Boda Limestone (Ashgill), Skålberget, Siljan district, Dalarna, SMNH Br102556c, × 27. B, detail of A, the location of C is indicated, × 180. C, detail of B, × 750. D, detail of C, × 2250. E, detail of A, × 1660. F, detail of E, × 5900.

are covered by numerous minute apatite granulae, which sometimes are cube-shaped, up to 0·5 μm across (Text-fig. 5D); these structures are possibly related to secondary cyrstal growth during diagenesis.

In the inner part of each lamina the interbacular spaces are empty, which causes the baculae to stand out in relief in etched sections; on the outer zone, directly beneath the primary layer, these spaces appear to be filled by a granular apatite matrix (Text-fig. 5B–D, F). The thick baculate laminae are separated by thin, homogenous lamellae, consisting of minutely granular apatite (Text-fig. 5B). The apatite of the secondary layer is strongly birefringent, and the main preferred orientation of the *c*-axes appears to be roughly normal, or at a high angle to the laminae; only in some of the thin granular lamellae are there indications of a different preferred *c*-axis orientation, parallel relative to the lamellae.

The shell structure of *Tilasia* is nearly indentical to that of other Lower Palaeozoic lingulaceans discussed by Holmer (1989). The shell structure of most Lower Palaeozoic lingulaceans can be interpreted in the light of what is now known about Recent *Glottidia*, which has a well-defined primary layer and a baculate structure penetrating the organic laminae of the secondary layer (see Iwata 1982; Watabe and Pan 1984; Pan and Watabe 1988 for details).

Holmer (1987) and Ushatinskaya *et al.* (1988) noted that the shell structure of fossil discinaceans is comparable with that of the lingulaceans, and that they can also be compared with their Recent representatives (see Iwata 1982).

Ushatinskaya *et al.* (1988, p. 49; see also Hewitt 1980; Popov and Ushatinskaya 1986;

Ushatinskaya and Zezina 1988) suggested that the shell structures present in both the fossil and Recent phosphatic brachiopods could have been formed by a complete *post-mortem* redistribution of phosphate, and phosphatization of the organic matter in the shell. One of the main reasons for this proposal seems to be that phosphatic, rod-like strutures, somewhat similar to the brachiopod baculae, have been described by Hewitt and Stait (1985) from the phosphatized connecting rings of some Ordovician cephalopods.

There are two kinds of rod-like structures present in the cephalopod connecting rings; the first type apparently represent secondarily phosphatized spicules, originally consisting of aragonite (Hewitt and Stait 1985, figs 5 and 7), whereas the second type is formed by 'dendritic granular crystals on the interior of the connecting ring' (Hewitt and Stait 1985, fig. 2). For obvious reasons, the phosphatized aragonite spicules are most unlikely to be comparable with the baculae described from lingulacean and discinacean brachiopods. The second irregular, dendritic pattern of granular apatite 'rods' appears to have grown in contact with the surface represented by the connecting ring, rather than representing isolated criss-crossing rods as in the lingulacean baculae. Moreover, the sections of Recent *Glottidia*, examined by Iwata (1982), Watabe and Pan (1984), and Pan and Watabe (1988) were prepared using freshly killed specimens; it is highly unlikely that a complete redistribution of phosphate could have occurred in these specimens as was suggested by Ushatinskaya *et al.* (1988).

REFERENCES

ANDREEVA, O. N. 1972. Brachiopods from the Ordovician Kuragan Suite in the southern Urals. *Paleontologicheskij Zhurnal*, **1972**, 45–56. [In Russian].

ANGELIN, N. P. and LINDSTRÖM, G. 1880. *Fragmenta Silurica e dono Caroli Henrici Wegelin*. Samson and Wallin, Holmiae [Stockholm], 60 pp.

BASSETT, M. G. 1984. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology*, **32**, 237–263.

BERGSTRÖM, S. M. 1971. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America. *Geological Society of America Memoir*, **127**, 83–157.

BIERNAT, G. and WILLIAMS, A. 1970. Ultrastructure of the protegulum of some acrotretide brachiopods. *Palaeontology*, **13**, 491–502.

COOPER, G. A. 1956. Chazyan and related brachiopods. *Smithsonian Miscellaneous Collection*, **127**, 1–1245.

HAVLÍČEK, V. 1982. Lingulacea, Paterinacea and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sborník geologických věd, Paleontologie*, **25**, 9–82.

HEWITT, R. A. 1980. Microstructural contrasts between some sedimentary francolites. *Journal of the Geological Society of London*, **137**, 661–667.

—— and STAIT, B. 1985. Phosphatic connecting rings and ecology of an Ordovician ellesmerocerid nautiloid. *Alcheringa*, **9**, 229–243.

HOLMER, L. E. 1986. Inarticulate brachiopods around the Middle–Upper Ordovician boundary in Västergötland. *Geologiska Föreningens i Stockholm Förhandlingar*, **108**, 97–126.

—— 1987. Discinacean brachiopods from the Ordovician Kullsberg and Boda limestones of Dalarna, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar*, **109**, 317–326.

—— 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata*, **26**, 1–172.

IWATA, K. 1982. Ultrastructure and calcification of the shells in inarticulate brachiopods. Part 2. Ultrastructure of the shells of *Glottidia* and *Discinisca*. *Journal of the Geological Society of Japan*, **88**, 957–966. [In Japanese].

JAANUSSON, V. 1958. Leptaena limestone. 189–191. *In* MAGNUSSON, N. H. (ed.). *Lexique stratigraphique international*, 1(2c), 1–498.

—— 1979. Carbonate mounds in the Ordovician of Sweden. *Izvestya Akademii Nauk Kazakhckoj SSR, Seriya Geologicheskaya*, 4, 92–99. [In Russian].

—— 1982. Ordovician in Dalarna. 15–42. *In* BRUTON, D. L. (ed.). Field excursion guide. IV International Symposium on the Ordovician System. *Paleontological Contributions from the University of Oslo*, 279, 1–217.

JEPPSSON, L., FREDHOLM, D. and MATTIASSON, B. 1985. Acetic acid and phosphatic fossils – a warning. *Journal of Paleontology*, 59, 952–956.

LOCKLEY, M. G. and WILLIAMS, A. 1981. Lower Ordovician Brachiopoda from mid and southwest Wales. *Bulletin of the British Museum of Natural History*, (Geology), 35, 1–78.

MOBERG, J. C. and SEGERBERG, C. O. 1906. Bidrag till kännedomen of ceratopygeregionen med särskild hänsyn till dess utveckling i Fogelsångstrakten. *Lunds Universitets Årsskrift*, 2, 1–116.

PAN, C.-M. and WATABE, N. 1988. Shell growth of *Glottidia pyramidata* Stimpson (Brachiopoda: Inarticulata. *Journal of Experimental Marine and Biological Ecology*, 119, 45–53.

POPOV, L. E. and USHATINSKAYA, G. T. 1986. On secondary changes in the microstructure of calcium-phosphatic shells of inarticulate brachiopods. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya*, 10, 135–137. [In Russian].

—— ZEZINA, O. N. and NOLVAK, J. 1982. Microstructure of the apical parts of inarticulates and its ecological importance. *Byuleten' Moskovskogo obshchestva ispytatelej priody, otdel biologicheskij*, 87, 94–104. [In Russian].

ROWELL, A. J. 1965. Inarticulata. H260–H269. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part H. Brachiopoda 1(2)*. Geological Society of America and University of Kansas Press, Lawrence, Kansas, 927 pp.

SAVAZZI, E. 1986. Burrowing sculptures and life habits in Paleozoic lingulacean brachiopods. *Paleobiology*, 12, 46–63.

SEILACHER, A. 1972. Divaricate patterns in pelecypod shells. *Lethaia*, 5, 325–343.

THORSLUND, P. H. 1936. Siljansområdets brännkalkstenar och kalkindustri. *Sveriges Geologiska Undersökning, Series C*, 398, 1–64.

TILAS, D. 1740. Mineral-Historia öfwer Osmunds-berget uti Rättwiks Sochn och öster-Dalarne af Daniel Tilas. *Swenska Wetenskaps Academiens Handlingar för Månaderna Januar. Februar. Martius*, 1, 202–209.

USHATINSKAYA, G. T. and ZEZINA, O. N. 1988. On the probable post-mortem redistribution of phosphatic matter in older inarticulate brachiopods. *Doklady AN SSSR*, 300, 700–703. [In Russian].

—— ZEZINA, O. N., POPOV, L. E. and PUTIVTSEVA, N. V. 1988. Microstructure and mineral composition of brachiopods with calcium phosphate shells. *Paleontologicheskij Zhurnal*, 1988, 45–55. [In Russian].

WATABE, N. and PAN, C.-M. 1984. Phosphatic shell formation in atremate brachiopods. *American Zoologist*, 24, 977–985.

WILLIAMS, A. 1965. *Lamanskya* Moberg and Segerberg, 1906. H863. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part H. Brachiopoda 2(2)*. Geological Society of America and University of Kansas Press, Lawrence, Kansas, 927 pp.

—— 1990. Biomineralization in the lophophorates. 67–82. *In* CARTER, J. G. (ed.). *Skeletal biomineralization: patterns, processes and evolutionary trends*. Van Nostrand Reinhold, New York, 399 pp.

—— and CURRY, G. B. 1985. Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. *Bulletin of the British Museum of Natural History*, (Geology), 38, 183–269.

WRIGHT, A. D. 1981. The external surface of *Dictyonella* and of other pitted brachiopods. *Palaeontology*, 24, 443–481.

L. E. HOLMER

Institute of Palaeontology
Box 558
S-751 22 Uppsala, Sweden