Pages 61 to 120 (Chapters 5 and 6)

RARE AND PROBLEMATICAL TAXA FROM THE MUCH WENLOCK LIMESTONE FORMATION

by

LIAM GEORGE HERRINGSHAW

Thesis submitted to
The University of Birmingham
for the degree of
DOCTOR OF PHILOSOPHY

School of Geography, Earth and Environmental Sciences
University of Birmingham
September 2003

CHAPTER FIVE

ECOLOGY AND PHYLOGENETIC RELATIONSHIPS OF BRITISH SILURIAN ROSTROCONCHS

ABSTRACT. Taxa belonging to the extinct molluscan clade Rostroconchia are present throughout the Palaeozoic, but few have received detailed study. Four species of conocardiacean rostroconchs are described from the Much Wenlock Limestone Formation (Silurian: Wenlock) of England: *Mulceodens aedicula* sp. nov., *M. latus* sp. nov., *M*? *aequicostatus* (Phillips, 1848) and *Redstonia sima* sp. nov. In previous studies, *Mulceodens* and *Redstonia* have been placed in separate families, *Redstonia* in the Hippocardiidae, containing taxa with a prominent primary carina or hood, and *Mulceodens* in the more primitive, hoodless Bransoniidae. However, recent analyses have indicated that the two families are polyphyletic, with some 'bransoniids' being derived species in which the hood had been secondarily lost, and that *Redstonia* and *Mulceodens* belong to the same clade. This is supported here, with autecological investigation suggesting that morphological differences between *Mulceodens* and *Redstonia* represent adaptations of closely related taxa to different ecological niches - *Redstonia* living in much lower energy environments than *Mulceodens* - rather than indicating that they belong to separate families. Pending further study, all bransoniids and hippocardiids are placed here in a single group, the Hippocardiidae.

THE number of major groups within the Mollusca, and the relationships between them, are contentious topics and a widely accepted phylogenetic model is yet to be reached. This is partly because molecular and developmental analyses of the Mollusca are few and little attention has been paid to fossil data. Nonetheless, it is generally agreed that at least one extinct major clade can be recognized: the Rostroconchia, identified and diagnosed by Pojeta *et al*. (1972). They realized that taxa placed previously in extant molluscan classes, or even separate phyla (see Pojeta and Runnegar 1976; Runnegar 1978 for summary), in fact belonged to a single group. Present throughout the Palaeozoic, rostroconchs were most diverse during Ordovician times, declining subsequently until their extinction in the Permian. Despite their relative scarcity, post-Ordovician rostroconchs developed a number of highly unusual morphologies and were clearly a successful, if minor, element of Palaeozoic marine ecosystems.

Because of their rarity, rostroconchs have generally been overlooked or only briefly described. More research has been done following their recognition as a separate clade, but the focus has been either on Cambrian and Ordovician taxa, as part of studies into the early evolutionary history of the Mollusca (see e.g. MacKinnon 1985; Landing 1989, 1991; Cope

1996; T. M. Sanchez 1997, 1998, 2000; Kouchinsky 1999; Yi 2001), or on Carboniferous forms that are often notable for their large size and complex morphology (see e.g. Hoare *et al*. 1982, 1988, 2002; Hoare and Mapes 1990; Hoare 1990; Amler 1996; Quiroz-Barroso *et al*. 2000; Hoare and Aghababalu 2001). In comparison, Silurian and Devonian taxa have been relatively neglected. Using specimens from the Silurian of Britain, this study provides new information on rostroconch diversity during the mid-Palaeozoic, as well as on the palaeoecology of the group. It also shows that the current classification of post-Ordovician rostroconchs requires reassessment.

Recent work on Silurian rostroconchs has focused mainly on taxa from North America, with Johnston and Chatterton (1983) and Caldwell and Chatterton (1995) describing numerous species from the Wenlock and Ludlow of the Mackenzie Mountains, Canada, and Hoare (2000) documenting a new taxon from the Ludlow of California. Pojeta and Runnegar (1976) described Wenlock and Ludlow bransoniids and hippocardiids from Gotland, Sweden, but, since the class was erected, no rostroconchs have been recorded from the Silurian of the UK. Only a single species has been identified previously from the British Wenlock. Two specimens of *Pleurorhynchus aequicostatus* Phillips, 1848, were figured by Phillips (1848, pl. 16, figs 1–2), whilst a third example was recorded by Salter (1873, p. 151), but not figured. All were from the Much Wenlock Limestone Formation of the English Midlands and Welsh Borderlands. The species was referred to by subsequent authors (see section 5.3), but no further material was described and, until this study, these three specimens constituted the total known rostroconch fauna of the British Silurian. Based on specimens in the Lapworth Museum, University of Birmingham, three new species from the Much Wenlock Limestone Formation are described here, while additional examples of the existing species, *Mulceodens*? *aequicostatus*, have been discovered also.

5.1 ROSTROCONCH MORPHOLOGY

Rostroconchs are morphologically diverse (see e.g. Runnegar 1978, fig. 1, p. 320), but uniting them at class level is justified by the presence of a variety of synapomorphies. All forms had a univalved larval shell (*protoconch*) and a post-larval bivalved shell (*dissoconch*) with at least one shell layer running internally across the hinge line (Pojeta and Runnegar 1976). Along the opposite margin (*commissure*) the valves are never more than partly closed – early rostroconchs had a continuous opening, while in most later forms this was reduced to a gape or series of gapes. The dissoconch is often termed *pseudobivalved* (e.g. Runnegar 1978; Johnston and Chatterton 1983) as it was not functionally bivalved in the same way as the shells of bivalves and brachiopods.

Contrary to the etymology of the clade, many rostroconchs did not possess a rostrum, the structure being absent from most Cambrian and Ordovician species. It is distinct in later forms, however, particularly hippocardiids and conocardiids, and is one of the main criteria for separating the orders Conocardioida and Ribeirioida (see section 5.3).

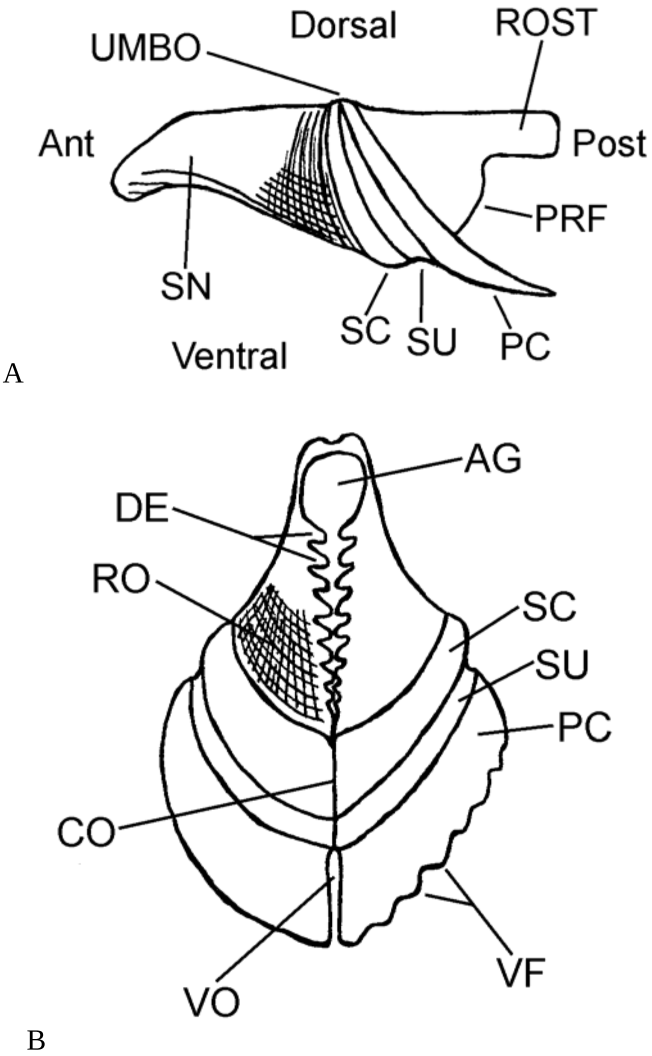
5.1.1 BODY ORIENTATION

As an extinct group of organisms without any known instances of preserved soft tissues, determining the anatomy and body orientation of rostroconchs is difficult. However, by comparison with other Conchifera (monoplacophorans, bivalves, scaphopods, gastropods and cephalopods), particularly bivalves, which are probably the closest relatives of rostroconchs (see section 5.2), the shell openings and commissure are regarded as ventral, with the hinge dorsal. The question of which end was anterior and which posterior is more problematical. Since the foot is an homologous character present in all extant conchiferan molluscs, Pojeta and Runnegar (1976) considered that rostroconchs must have had a foot, and that it would have protruded from the largest shell opening. Thus, the large gape at one end of the ventral margin was interpreted as functionally anterior and anatomically anteroventral, with the rostrum, positioned at the opposite end of the shell, being functionally and anatomically posterior. These interpretations are necessarily somewhat speculative, but the body orientation proposed has been accepted by all subsequent authors and is followed here.

The internal positions of muscle scars give further anatomical information, but the continuation of shell layers across the rostroconch hinge means that the two valves do not easily separate, and little is known of the internal anatomy of most species. Using natural and artificial moulds, however, Pojeta and Runnegar (1976) were able to identify two types of muscle – pedal and pallial – and reconstructions were produced showing the likely musculature of various genera (see Pojeta and Runnegar 1976, figs 4, 5). The implications for rostroconch palaeoecology are discussed below.

5.1.2 TERMINOLOGY

General rostroconch terminology used here follows Pojeta (1987*a*, pp. 359–374). Conocardiacean terms (see Text-fig. 5.1) are as defined by Caldwell and Chatterton (1995, p. 826), with amendments as follows: for clarity, *gape* is applied only to the large anterior shell opening; all other openings are referred to as *orifices* (e.g. rostral orifice; ventral orifice); the ridge of shell material running ventrally from the umbo, projecting beyond the ventral body margin and containing the ventral orifice is the *primary carina*, with the term *hood* applied



TEXT-FIG. 5.1. Rostroconch terminology; A, left lateral view, and B, antero-ventral view, showing typical conocardiacean morphology. AG, anterior gape; Ant, anterior; CO, commissure; DE, denticles; PC, primary carina; Post, posterior; PRF, pre-rostral field; RO, reticulate ornamentation; ROST, rostrum; SC, secondary carina; SN, snout; SU, sulcus; VF, ventral flanges; VO, ventral orifice.

only to the extremely large and sheet-like primary carina seen in some hippocardiids. The *secondary carina* is the ridge found to the anterior of the primary carina, normally less pronounced and always lacking an orifice, and which separates the body and snout. The term *secondary hood* is applied only to the ridge posterior of the primary carina in forms such as *Bigalea* Pojeta and Runnegar, in which a second ventral orifice is present. The body size classification of Hoare (1982) is used, with small rostroconchs defined as those less than 10 mm in length, medium-sized rostroconchs being between 10 and 20 mm long, and large rostroconchs having a length greater than 20 mm.

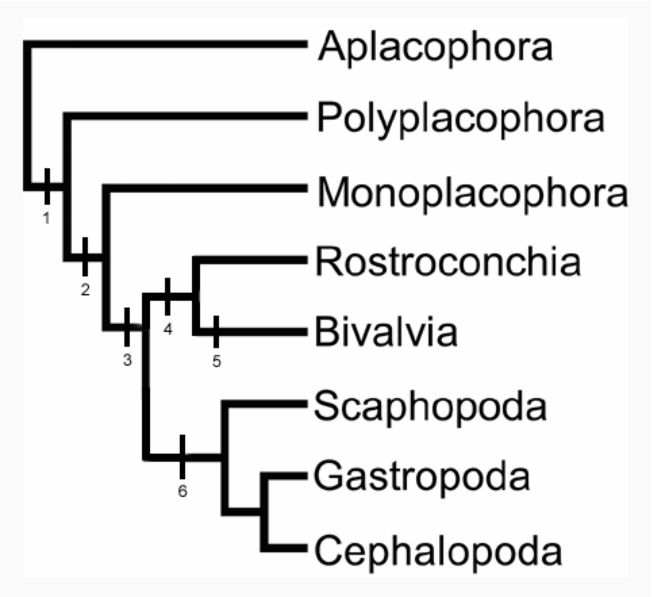
5.2 PHYLOGENETIC POSITION OF ROSTROCONCHS

In their review of molluscan phylogeny, Runnegar and Pojeta (1974) used fossil evidence to suggest that rostroconchs were the ancestors of both scaphopods and bivalves, and that together the three classes formed a subphylum (Diasoma) that diverged from monoplacophorans in the Early Cambrian. The relationships were described in greater detail by Pojeta and Runnegar (1976), who interpreted two simple Early Cambrian molluscs – *Heraultipegma varensalense* (Cobbold) and *Watsonella crosbyi* Grabau – as the first rostroconchs. It was argued that both evolved early in the Early Cambrian from a laterally compressed monoplacophoran such as *Anabarella plana* Vostokova, and then gave rise to the bivalves later in the Early Cambrian, and possibly also the scaphopods in the Ordovician (Pojeta and Runnegar 1976). Runnegar (1978) was less tentative, stating (p. 329) that bivalves 'undoubtedly' descended from rostroconchs by the middle Early Cambrian, and that scaphopods did likewise in either the Late Cambrian or Early Ordovician. This was disputed by MacKinnon (1985) who interpreted *Heraultipegma* as a laterally compressed monoplacophoran, and stated that the first rostroconchs were not present until the Upper Cambrian (MacKinnon 1985, p. 80). Thus, he argued that the earliest bivalves predated the earliest rostroconchs by at least 40 Ma and were more likely to have evolved from a separate lineage of laterally compressed monoplacophorans, although the possibility of a ghost lineage was not considered.

Wagner (1997) used a variety of phylogenetic approaches to examine the evolution of rostroconchs and, although concentrating primarily on morphological diversification within the class, concluded (Wagner 1997, p. 123) that the first rostroconchs were more closely related to a clade of early bivalves including *Tuarangia* than they were to the clade containing *Heraultipegma* and *Watsonella* (see Wagner 1997, fig. 3). Subsequently, Kouchinsky (1999) argued that *Heraultipegma* and *Watsonella* were synonyms, and that all species of the two genera should be transferred to *W. crosbyi*. He then carried out comparative examination of the shell microstructure of *Watsonella* with that of *Anabarella plana* and demonstrated similarities between the two, particularly in the fine-scale shell textures of the dorsal margins (Kouchinsky 1999). This led him to support the hypothesis of Pojeta and Runnegar (1976) and interpret *A. plana* as the ancestor of the earliest rostroconchs, as well as 'the first evolutionary step' (Kouchinsky 1999, p. 173) towards bivalves. Although retaining *Heraultipegma* as a separate genus, Yi (2001) agreed with Kouchinsky (1999) in stating that information from shell structure, mode of growth, shell morphology and stratigraphical occurrences indicated bivalves were descendants of a single, early branch of rostroconchs.

The relationship between rostroconchs and scaphopods is also controversial, due in part to the paucity of fossil scaphopods. The earliest species, *Rhytiodentalium kentuckyensis* Pojeta and Runnegar, 1979, from the Middle Ordovician of the United States, is preserved without fine morphological detail, and has not been universally accepted as an unequivocal member of the class. As no Silurian scaphopods are known, this has led some authors (e.g. Yochelson 1978, 1979; Engeser and Riedel 1996) to argue that the class did not appear until the Devonian, and a number of different models of scaphopod phylogeny have been proposed. Pojeta and Runnegar (1976, p. 43) thought scaphopods were 'probably well differentiated' by the mid-Ordovician, having originated from an elongate ribeiriid rostroconch similar to *Pinnocaris*, via fusion of the pseudobivalved rostroconch shell early in ontogeny. Yochelson (1978) disagreed, suggesting instead that scaphopods arose in the Devonian from an unknown, unshelled organism, but this has been generally discounted by subsequent workers. Steiner (1992) followed Runnegar and Pojeta (1974) in regarding scaphopods, rostroconchs and bivalves as a monophyletic group (Diasoma) but was unable to explain how scaphopods could have evolved from ribeiriids, as the changes in body plan were too great. The contrast in scaphopod and ribeiriid morphology led Engeser and Riedel (1996) to argue that scaphopods did not evolve from ribeiriids in the Ordovician. Instead, they regarded the morphological similarity of adult conocardiids and juvenile scaphopods (see Engeser and Riedel 1996, fig. 2) as indicating that the latter had evolved from the former by heterochrony, probably in the Devonian (Engeser and Riedel 1996, p. 123). A cladistically based revision of diasome systematics was produced (Engeser and Riedel 1996, fig. 3, p. 124), showing scaphopods to be an order of the class Rostroconchia rather than a class in their own right, thus resurrecting the rostroconchs from their extinct state. This was tentatively supported by Wagner (1997), who concluded (Wagner 1997, p. 116) that scaphopods 'probably do belong to the Rostroconchia as defined [by his analyses]…but the exact relationships…are problematic'.

Recent work on the ontogeny of scaphopods (Wanninger and Haszprunar 2001, 2002*b*) has produced a different hypothesis that rejects the monophyly of the Diasoma. Wanninger and Haszprunar (2001) showed that the scaphopod *Antalis* is univalved throughout its development, rather than having a bilobed stage that would ally it most closely with bivalves. A univalved shell was thus interpreted as plesiomorphic for all extant Conchifera (monoplacophorans, scaphopods, bivalves, gastropods and cephalopods), with a bivalved shell regarded as an autapomorphy of Bivalvia, and the Subphylum Diasoma was abandoned. This was further supported by their investigation of molluscan myogenesis (Wanninger and Haszprunar 2002*b*), which revealed that scaphopods have cephalic retractor



TEXT-FIG. 5.2. Possible phylogenetic position of rostroconchs with respect to extant molluscan clades (after Wanninger and Haszprunar 2001, 2002*b*). The primitive state, represented by the Aplacophora, is a spicule-bearing, worm-like body shape, with numerous, serially repeated dorso-ventral muscle sets. Derived character states as follows: 1, acquisition of sclerites, with reduction of serialization to eight sets of dorso-ventral muscles; 2, reduction of eight plates to single shell; 3, reduction of dorso-ventral muscles to fewer than eight sets; 4, lateral compression of single shell into two valves; 5, evolution of functionally bivalved shell; 6, reduction of dorso-ventral muscles to one or two sets and acquisition of cephalic retractor muscles.

muscles. These had only previously been observed in gastropods and cephalopods, and Wanninger and Haszprunar (2002*b*) interpreted their presence in scaphopods as homologous, leading to the recognition of a scaphopod, gastropod and cephalopod clade. Fossil molluscs were not discussed, so the position of rostroconchs in the revised phylogeny is unclear, and will remain so until a full phylogenetic analysis of fossil and extant taxa is carried out, but it presently appears likely that rostroconchs are most closely related to bivalves (Text-fig. 5.2). The evidence of Wanninger and Haszprunar (2001, 2002*b*) suggests that uniting the two groups with scaphopods to form the clade Diasoma cannot be supported, and it is not followed here.

5.3 SYSTEMATIC PALAEONTOLOGY

Institutional abbreviations. Specimens from the Lapworth Museum, University of Birmingham, are prefixed by BU. Other specimens described are in the Natural History

Museum, London (NHM), British Geological Survey, Keyworth (BGS) and the Swedish Museum of Natural History, Stockholm (SMNH).

Phylum MOLLUSCA Cuvier, 1797

Class ROSTROCONCHIA Pojeta, Runnegar, Morris and Newell, 1972

Order CONOCARDIOIDA Neumayr, 1891

Remarks. Pojeta and Runnegar (1976) identified three orders of rostroconch (the Ribeirioida, Ischyrinioida and Conocardioida), but subsequent classifications – most significantly the phylogenetic analysis of Wagner (1997) – have reduced this to just two: the simpler ribeirioids and the more complex conocardioids. As noted in section 5.1, one of the main criteria for separating the two orders is that conocardioids have a distinct rostrum, whereas ribeirioids do not. The other differences, as defined by Pojeta and Runnegar (1976), are as follows: conocardioids have only one shell layer that is continuous across the hinge (all layers continuous in ribeirioids); no pegmas (one or two in ribeirioids); a body that is elongated anteriorly (posteriorly in ribeirioids); dorsal clefts positioned either to the posterior or the posterior and anterior of the protoconch (absent from most ribeirioids, and positioned anterior of the protoconch if present); and, in most forms, a pallial line (absent from most ribeirioids).

In the light of the restriction of rostroconchs to two orders, the subdivision defined by Pojeta and Runnegar (1976) – two ribeirioid families (Ribeiriidae and Technophoridae), one ischyrinioid family (Ischyriniidae) and four conocardioid families (Eopteriidae, Bransoniidae, Hippocardiidae and Conocardiidae) – has had to be reassessed. The cladistic analyses of Wagner (1997) produced phylogenetic relationships that were 'very congruent with those proposed by Pojeta and Runnegar (1976)' (Wagner 1997, p. 126), and seven clades, approximating to each of the family-level taxa, were identified. The only difference between the classification of Pojeta and Runnegar (1976) and that of Wagner (1997) was that ischyriniids were recognized as a family within the Ribeirioida, rather than as a separate order.

Superfamily CONOCARDIACEA Miller, 1889

Remarks. Within the Conocardioida, Pojeta and Runnegar (1976) defined two superfamilies: the Eopteriacea, containing only eopteriids, and the trifamilial Conocardiacea (bransoniids + hippocardiids + conocardiids). The morphological characters that Pojeta and Runnegar (1976) used to erect the two superfamilies were that eopteriaceans always have dorsal clefts and anterior, ventral and posterior gapes, whereas conocardiaceans lack a ventral gape and have a rostral orifice (plus a ventral orifice in some forms) rather than a posterior gape.

Additionally, the rostrum is much more distinct in conocardiaceans, and their shells have a far more pronounced anterior elongation.

This sub-division of conocardioids was supported, on the whole, by Wagner (1997) whose phylogenetic analyses showed that a group of derived conocardioid taxa, equivalent to the Conocardiacea, did exist. However, the separation of that clade into the three families of Pojeta and Runnegar (1976) was much more difficult to justify (Wagner 1997). The monophyly of the most derived family, the Conocardiidae, was strongly supported, but the Bransoniidae and Hippocardiidae showed a high degree of polyphyly (Wagner 1997, figs 6–7; see Text-fig. 5.11). Pojeta and Runnegar (1976) had erected the two families principally on the basis that the primary carina of hippocardiids projected out beyond the shell margin, often forming a prominent hood, whereas the primary carina of bransoniids was absent or only weakly developed. However, Wagner's (1997) analyses indicated that hoodless (bransoniid) and hooded (hippocardiid) conocardiaceans do not form monophyletic groups, with some 'bransoniids' (including the type species, *Bransonia wilsoni* Pojeta and Runnegar, 1976, from the Permian of Australia) actually being derived conocardiaceans in which the hood had been secondarily lost. The probability that *Bransonia* and *Hippocardia* were polyphyletic had been noted by Pojeta and Runnegar (1976) and Caldwell and Chatterton (1995), but, despite verifying this, Wagner (1997, p. 129) retained a general relationship of primitive conocardiaceans ('bransoniids') being the sister group of 'hippocardiids' plus conocardiids. This relationship may be valid, and three conocardiacean clades may exist, but using the term 'bransoniid' to describe taxa belonging to the most primitive clade is inappropriate, since *Bransonia* probably does not belong to it (Text-fig. 5.11). Having studied only Wenlock taxa, it is not possible to attempt a detailed revision of the Conocardiacea, but neither can the retention of Bransoniidae as a family-level taxon containing the most primitive members of the superfamily be justified. It is more appropriate to place all 'bransoniids' and 'hippocardiids' in a single group, pending a more comprehensive analysis, and as both families were erected by Pojeta and Runnegar (1976), the International Code of Zoological Nomenclature (1999, article 24. 2, p. 30) states that the first reviser must select the name to take precedence. Given the greater ambiguity regarding the diagnosis of *Bransonia*, particularly over whether it is primitively or secondarily hoodless, the genus *Hippocardia* is more clearly defined, so Hippocardiidae is chosen.

Family HIPPOCARDIIDAE Pojeta and Runnegar, 1976

Diagnosis. Conocardiaceans with or without primary carina that is often prominent when present. Denticles normally absent or weakly developed, but prominent in some genera.

Ornamentation normally similar across anterior of shell; making junction between body and snout difficult to distinguish.

Remarks. Since the Conocardiidae was shown to be monophyletic by Wagner (1997) and contains just two genera – *Arceodeomus* and *Conocardium* – the Hippocardiidae by definition includes all other conocardiacean genera, making it paraphyletic. This is not an ideal situation, but deemed preferable to the existing, polyphyletic classification of Bransoniidae and Hippocardiidae. Conocardiids have no primary carina or hood, have much more anteriorly elongate bodies than other conocardiaceans, always have denticles or shelves in the anterior gape, and pronounced, tubular rostra. Additionally, the separate shell regions of snout, body and rostrum are usually very distinct from one another, having different ornamentation patterns, as opposed to hippocardiids, where the distinctions, particularly between body and snout, are often less clear.

Genus MULCEODENS Pojeta and Runnegar, 1976

Type species. *Mulceodens jaanussoni* Pojeta and Runnegar, 1976 from the Wenlock and Ludlow of Gotland, Sweden. By original designation.

Diagnosis. Conocardiaceans with short rostra, rounded snouts having a constriction separating dorsal and ventral parts, and prominent denticles in anterior gape that touch, or almost touch, across the gape. Primary carina absent or only weakly developed.

Remarks. Four species of *Mulceodens* were recognized by Pojeta and Runnegar (1976, p. 73), but only the type was discussed in detail, being described as a small form with alternating marginal denticles, distinct rostral clefts, and a strong constriction of the snout. The three other taxa – *Mulceodens bifarius, M. denticulatus* and *M. eboraceus,* all from the Middle Devonian of the USA – were mentioned only briefly. Working on rostroconchs from the Silurian of Canada, Johnston and Chatterton (1983) added two small, new, Wenlock species – *M. schneideri* and *M. wilsoni* – both of which had a primary carina. This led them to suggest (Johnston and Chatterton 1983, p. 847) that *Mulceodens* might belong to the Hippocardiidae *sensu* Pojeta and Runnegar, 1976, but Caldwell and Chatterton (1995) retained the genus in the Bransoniidae when erecting another species, *M. johnstoni*, also from the Wenlock of Canada. Their phylogenetic analysis of bransoniid and hippocardiid relationships (Caldwell and Chatterton 1995, p. 821-825), however, indicated that *Mulceodens* was a derived member of the Hippocardiidae. This was based on *Mulceodens* being monophyletic, a conclusion not reached by Wagner (1997). His analysis placed the three Canadian species together, but *M.*

jaanussoni and *M. eboraceus* fell into separate clades entirely, with the type species being apparently most closely related to a group of Ordovician and Silurian hippocardiids (see Wagner 1997, fig. 6).

Clearly, further work needs to be carried out to ascertain both the true number of species of *Mulceodens* and the relationship of the genus to other conocardiaceans. Based on Wagner's (1997) analysis of previously described species, only *M. jaanussoni* is included without question here. Even then, there is a good deal of morphological variability shown by the thirteen paratypes of *M. jaanussoni* (see Pojeta and Runnegar 1976, pl. 34, figs 1-16) when compared with the holotype (Pojeta and Runnegar 1976, pl. 35, figs 1-3, 11-12). For example, specimen SMNH Mo.18547 (Pojeta and Runnegar 1976, pl. 34, fig. 13) has opposing rather than alternating denticles in its anterior gape, whilst SMNH Mo.18546 (Pojeta and Runnegar 1976, pl. 34, fig. 13) is much wider in anterior view than the holotype. Having not examined the type material, though, the approach of Johnston and Chatterton (1983) is followed, with *M. jaanussoni* interpreted as having been morphologically variable, rather than comprising a suite of separate species.

The species described below as *Mulceodens*? *aequicostatus* (Phillips, 1848) is doubtfully assigned to the genus: until a more stable classification has been determined, and taxa can be less ambiguously defined, it would be inappropriate to place the species in a new genus.

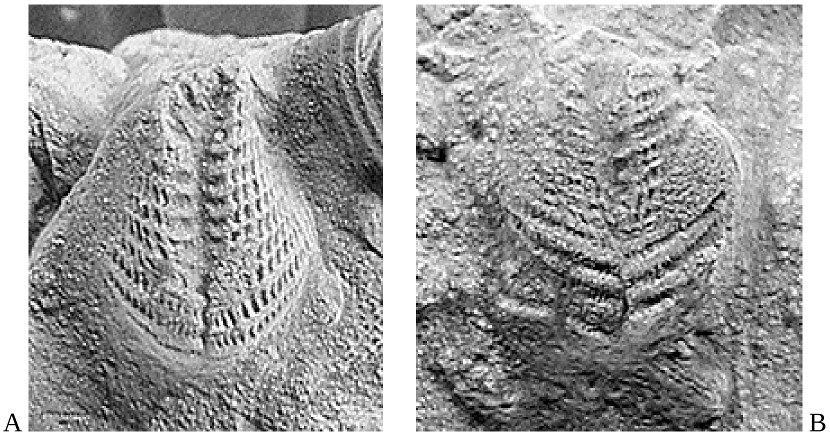
Mulceodens aedicula sp. nov.

Text-figs 5.3, 5.4

Derivation of name. From the Latin, *aedicula*, a small building or temple, in reference to the body and snout ornamentation resembling, in miniature, the exterior of a Roman building, particularly the Colosseum. Noun in apposition.

Type material. BU 4354 from the Much Wenlock Limestone Formation of Wren's Nest Hill, Dudley, England, is designated the holotype, with BU 4353 and 4356, and specimens on slabs BU 4366 and 4367, all from same locality as holotype, designated paratypes. BU 4365, an incomplete specimen from Wood Cross, Hurst Hill, near Dudley, England, is questionably assigned to the same species.

Diagnosis. *Mulceodens* with pronounced reticulate shell ornamentation, radial ribs more prominent towards posterior of body. Denticles oppose in anterior gape, becoming alternate posteriorly along commissure.

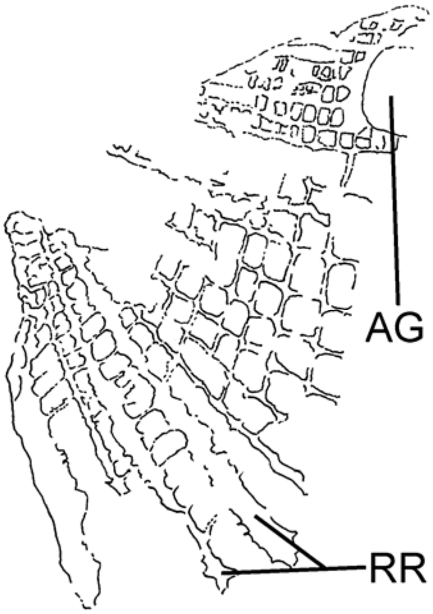


TEXT-FIG. 5.3. *Mulceodens aedicula* sp. nov., Much Wenlock Limestone Formation, Dudley, England. A, Antero-ventral view of holotype BU 4354, showing opposing denticles in anterior gape, and coarse, reticulate body ornament; x 7. B, Antero-ventral view of paratype BU 4356, showing prominent radial ribs and possible orifice at ventral end of specimen; x 8.

Description. All specimens small, with only ventral and lateral surfaces of shell anterior seen; dorsal and posterior parts unknown. Snout constriction clear, but lacking prominent scarf-like ridge around anterior gape. In antero-ventral view, widest point of shell approximately coincident with closure of anterior gape. Shell slightly rounded, with ventral margin convex in lateral view. Anterior gape open for most of antero-ventral margin; commissure relatively short.

No specimen of *Mulceodens aedicula* is complete, but the holotype BU 4354 (Text-fig. 5.3A) is the best preserved, with only the tip of the snout broken off. It is approximately 6.5 mm long and shows most of the antero-ventral surface, including the anterior gape with five sets of opposing denticles preserved, the next six sets of denticles alternating. BU 4356 (Text-fig. 5.3B) also displays the antero-ventral surface, with three opposing sets and five alternating sets of denticles, but more of the snout is missing and the anterior gape is incompletely preserved. At the posterior end of the commissure, however, there is a possible ventral orifice not seen in the holotype. The specimen on slab BU 4366 (Text-fig. 5.4) shows the right lateral surface of the body and snout, with the reticulate ornament being finer towards the anterior, and more prominent radial ribs being present at the posterior. Specimen BU 4353 and the specimen on slab BU 4367 are fragmentary and add little to the knowledge of the species.

BU 4365 is incomplete, but larger than the holotype, approximately 9 mm long and 4 mm high. Only the ventral surface is clearly seen, the anteriormost portion of the snout being



TEXT-FIG. 5.4. *Mulceodens aedicula* sp. nov., Much Wenlock Limestone Formation, Dudley, England. *Camera lucida* drawing of right lateral surface of paratype on slab BU 4366, showing part of anterior gape (AG) and prominent radial ribs (RR); x 15.

broken off, and the commissure is open towards the posterior, with denticles apparently closing the ventral margin towards the anterior. It cannot be allied with certainty to any of the species described here, but is morphologically closest to *M. aedicula* and is thus placed tentatively in that taxon.

Remarks. The constriction of the snout of *Mulecodens aedicula* is less pronounced than that of *M. jaanussoni*, without the prominent scarf-like ridge around the anterior gape, and the shell ornamentation is more distinct, with the radial ribs in particular having strong relief. In antero-ventral view, the widest point of *M. aedicula* is level with the closure of the anterior gape, whereas in the holotype of *M. jaanussoni* the widest point is nearer the anterior. The anterior gape of *M. aedicula* is slightly longer than that of *M. jaanussoni* and at least five of the sets of denticles within it are in opposition, rather than alternating as in *M. jaanussoni*.

Mulceodens latus sp. nov.

Text-figs 5.5, 5.6

Derivation of name. From the Latin, *latus*, broad, wide, referring to the species being much wider in antero-ventral view and flatter in lateral view than the type species, *M. jaanussoni*.

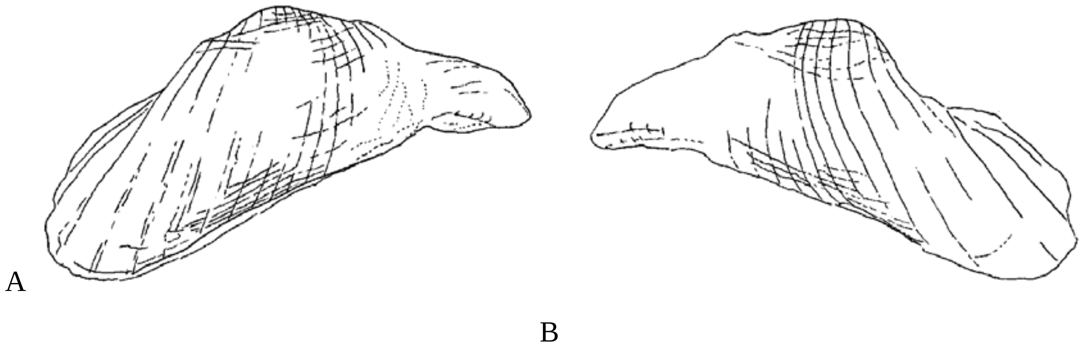
TEXT-FIG. 5.5. *Mulceodens latus* sp. nov., Much Wenlock Limestone Formation, Dudley, England. A, Antero-ventral view of holotype BU 4364, showing long, straight commissure and reticulate ornamentation; x 8. B, Postero-dorsal view of same specimen, showing dorsal depression running between umbones towards snout, and concentric ridges of pre-rostral field; x 8.

Holotype. BU 4364, the only specimen, from the Much Wenlock Limestone Formation of Wood Cross, near Hurst Hill, Dudley, England.

Diagnosis. *Mulceodens* with body and snout very rounded in antero-ventral view, slender and flattened in lateral view, with commissure forming straight ventral margin. Snout slightly downturned, distinctly constricted, with shell relatively thick around anterior gape. Pre-rostral field with three concentric ridges positioned ventrally beneath rostrum.

Description. Holotype of medium size, approximately 11.5 mm long, 5 mm high, 9.5 mm wide. Reticulate ornamentation very similar across body and snout, making distinction difficult. Denticles present in anterior gape but imperfectly preserved; anterior gape relatively short, commissure makes up most of length of ventral margin (Text-fig. 5.5A). Antero-dorsal margin slightly convex in lateral view. Rostrum missing; posterior of shell with dorsal depression along line of hinge (Text-fig. 5.5B).

Remarks. *Mulceodens latus* is quite different from the holotype of *M. jaanussoni* (Pojeta and Runnegar 1976, pl. 35, figs 1-3, 11, 12), being very much wider in antero-ventral view (Text-fig. 5.5A) and much thinner in lateral view (Text-fig. 5.6), with a thicker ridge around the constricted anterior gape. However, it is rather similar in antero-ventral view to paratypes



TEXT-FIG. 5.6. *Camera lucida* drawings of *Mulceodens latus* sp. nov., Much Wenlock Limestone Formation, Dudley, England. A, right lateral, and B, left lateral views of holotype BU 4364, showing slender body morphology and downturned snout; x 5.

SMNH Mo.18546 and 18547 (Pojeta and Runnegar 1976, pl. 34, figs 12–14). As noted above, there is a good deal of morphological variability between the specimens originally assigned to *M. jaanussoni* and it may be that these paratypes are better referred to another taxon. However, they are smaller than the holotype of *M. latus*, not as slender in lateral view, have a concave antero-dorsal margin in lateral view, and a thinner ridge around the anterior gape, and are retained in *M. jaanussoni* here. *M. latus* differs from *M. aedicula* in being wider and more rounded in antero-ventral view, very much flatter in lateral view, and in having a downturned snout with a more pronounced constriction around the anterior gape.

Mulceodens? *aequicostatus* (Phillips, 1848)

Text-fig. 5.7

* 1848 *Pleurorhynchus aequicostatus* Phillips, p. 359, pl. 16, figs 1-2.

1859 *Pleurorhynchus aequicostatus* Phill.; Murchison, p. 253.

1873 *Pleurorhynchus aequicostatus* Phill.; Salter, p. 151.

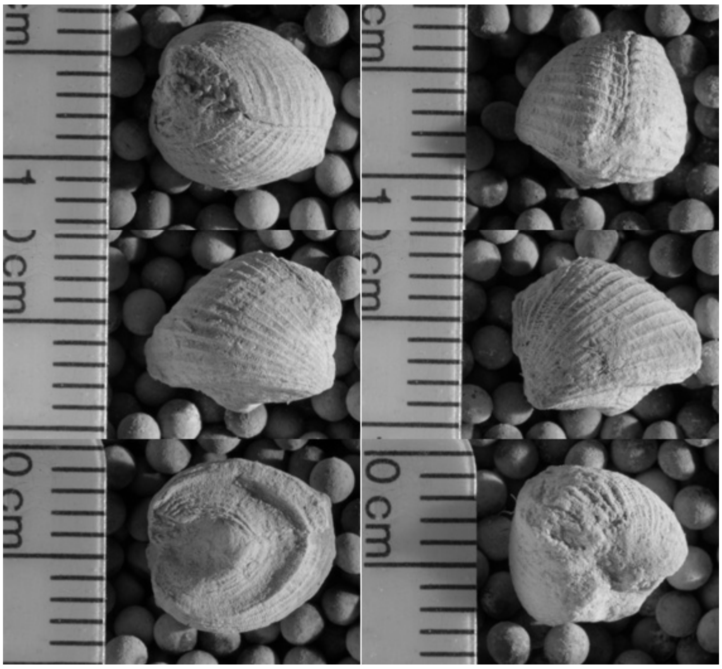
1875 *Pleurorhynchus aequicostatus*; Baily, p. xliii, pl. 21, figs 6a-c.

1884 *Pleurorhynchus aequicostatus*; La Touche, p. 72, pl. 14, figs 477-8. [suggested *Pleurorhynchus* was probably synonymous with *Conocardium*.]

1910 *Conocardium aequicostatus* Phillips; Hind p. 544.

1927 *Pleurorhynchus aequicostatus* Phillips; Reed, p. 546. [but Reed noted that it bore a closer resemblance to *Lunulicardium insulare* Reed, 1927 than other species of *Conocardium*.]

1938 *Lunulicardium*? *aequicostatum*; Stubblefield, p. 40 [with brief synonymy list].



TEXT-FIG. 5.7. *Mulceodens*? *aequicostatus* (Phillips, 1848). Lectotype NHM PL168, from the Much Wenlock Limestone Formation of Dudley, England. Anterior view (top left); ventral view (top right); left lateral view (centre left); right lateral view (centre right); posterior view (bottom left) and dorsal view (bottom right). Scale bar increments = 1 mm. [Photograph courtesy of NHM]

Type material. Lectotype, designated by Stubblefield (1938), NHM PL168, from the Much Wenlock Limestone Formation of Dudley, England and paralectotype BGS 24146, from Dormington Wood, Woolhope, Herefordshire, England.

Other material. BGS 24142–5, all from Much Wenlock Limestone Formation of Wenlock Edge, Shropshire, England.

Description. Small form, height (9.2 mm) only slightly greater than width (8.6 mm), giving shell distinctive rounded, almost globular appearance. Ornament reticulate, but radial ribs much more distinct than co-marginal ribs; same across body and snout, making them indistinguishable. Pre-rostral field with prominent concentric ridge positioned ventrally beneath short rostrum. Primary carina absent.

Remarks. A re-description of *Mulceodens*? *aequicostatus* is included here for purposes of completeness, but at the time of this study paralectotype BGS 24146 and specimens BGS 24142–5 were on loan to another worker and not available for examination, so the diagnosis and generic placement of the taxon is based upon the lectotype alone (Text-fig. 5.7). The species is questionably assigned to *Mulceodens* on the grounds that denticles are present in the anterior gape, the ornamentation is reticulate, no primary carina is present, and the rostrum is short. However, as the shell is incomplete in both anterior and dorsal views (see Text-fig. 5.7), it cannot be determined whether the snout is constricted, or downturned, or whether the layout of denticles in the anterior gape is similar to that of other species. Additionally, in lateral view, the anterior and posterior parts of the hinge line do not form a continuous plane either side of the umbo as in *M. jaanussoni* (Pojeta and Runnegar 1976, pl. 35, fig. 3) but tilt at different angles, so that the hinge line is close to rectangular in lateral view. *M*? *aequicostatus* does not unequivocally belong to any previously described conocardiacean genus, but it is inappropriate to erect a new taxon without having examined the other specimens, and the species is questionably referred to *Mulceodens* until its true systematic position can be clarified.

Genus REDSTONIA Caldwell and Chatterton, 1995

Type species. *Bigalea tercierae* Johnston and Chatterton, 1983 from the Wenlock of the Mackenzie Mountains, north-western Canada. By original designation.

Emended diagnosis. Conocardiaceans with constricted snouts, anterior end drooped in lateral view, dorsal and ventral margins straight thereafter. Posterior end of snout demarcated by distinct secondary carina with up to three pronounced ridges, separated from primary carina by narrow sulcus. Primary carina forms obvious hood, often curved posteriorly and projecting well beyond rest of body; with leaf-shaped ventral flanges. Anterior gape of elongate teardrop shape; denticles normally absent or very weakly developed. Rostrum long, with inflated pre-rostral area. Reticulate ornament across body and snout, coarsest on snout, fine on secondary carina and sulcus, very fine on primary carina.

Remarks. *Redstonia* was erected by Caldwell and Chatterton (1995) after their phylogenetic analysis of bransoniids and hippocardiids revealed *Bigalea* Pojeta and Runnegar, 1976 to be polyphyletic. Three species were included in *Redstonia*: *Bigalea visbyensis* Pojeta and Runnegar, 1976, from Visby, Gotland, Sweden, *B. tercierae* Johnston and Chatterton, 1983, and *B. buskasi* Johnston and Chatterton, 1983, both from the Mackenzie Mountains, Northwest Territories, Canada. *R. sima* sp. nov. is the first new species to be identified, although Wagner's (1997) phylogenetic analyses suggested that two Ordovician species of *Hippocardia* – *H. cooperi* and *H. richmondensis* – might be early examples of *Redstonia*. *H. cooperi* (see e.g. Pojeta and Runnegar 1976, pl. 45, figs 10-14) is the better preserved of the two and, in terms of body and snout ornamentation, primary carina/hood morphology, and shape of anterior gape, strongly resembles the existing members of *Redstonia*.

Stratigraphical range. *Redstonia tercierae*, *R. buskasi* and *R. visbyensis* are known solely from strata of Wenlock age. *R. sima* sp. nov., described below, is present in the Much Wenlock Limestone Formation, which is unequivocally Wenlock in age, but the holotype and six of the paratypes are preserved in a lithology more typical of the overlying Lower Elton Formation, which is at least partly of Ludlow age (see appendix for further discussion). Thus, the genus may have persisted beyond the end of the Wenlock.

Redstonia sima sp. nov.

Text-figs 5.8, 5.9

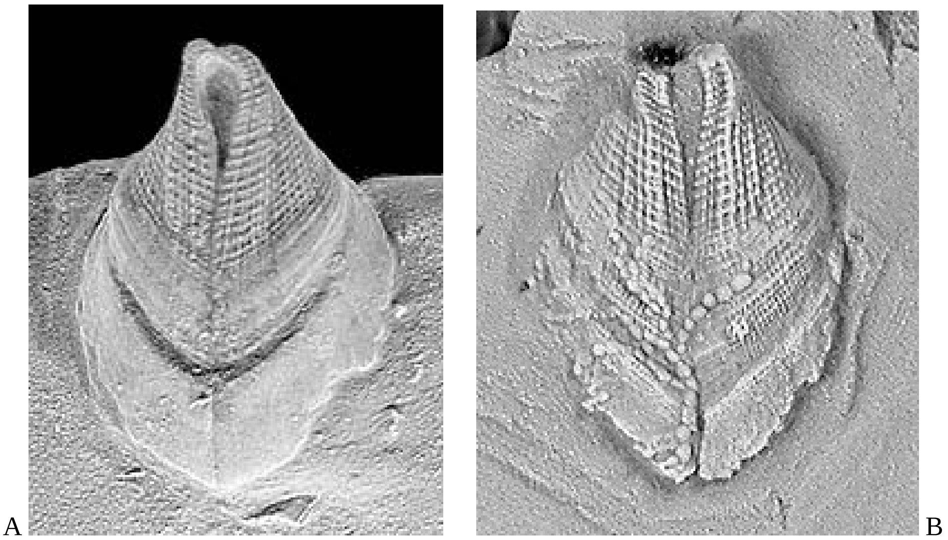
Derivation of name. From the Latin, *simus*, flat-nosed, alluding to the snout and body being flattened in lateral view.

Type material. BU 4355, from the Lower Elton Formation (?Wenlock-Ludlow) of Sedgley, near Dudley, England, is designated the holotype. Nine other specimens, six (BU 4351, 4352, 4357, 4360, 4361, 4363) from the same locality as the holotype, and three (BU 4358, 4359, 4362) from the Much Wenlock Limestone Formation (Wenlock) of Dudley, are designated paratypes.

Diagnosis. *Redstonia* with shell width approximately twice height. Snout short and slender, anteriorly constricted; body wide, flattened in lateral view. Anterior gape relatively small, with commissure occupying over half of ventral margin (only occupies one-third of margin in other species). Primary carina long, posteriorly curved, forming pronounced hood; secondary carina subdivided into three distinct ridges; sulcal field narrow.

Description. All ten specimens of *Redstonia sima* show the antero-ventral surface. BU 4355 (Text-fig. 5.8A) is the best-preserved example and one of only two specimens in which the dorsal part of the body and snout is exposed; it is therefore selected as the holotype. BU 4355 has a length of 12 mm, a height of 5 mm, and a width of 7 mm. The posterior of the shell, including the rostrum, is not visible in any specimen.

In antero-ventral view, three distinct regions can be defined by the type of ornament and the nature of the ventral margin (see e.g. Text-fig. 5.8B). The coarsest ornamentation is at the anterior, around the anterior gape, and demarcates the snout. Slightly posterior to where

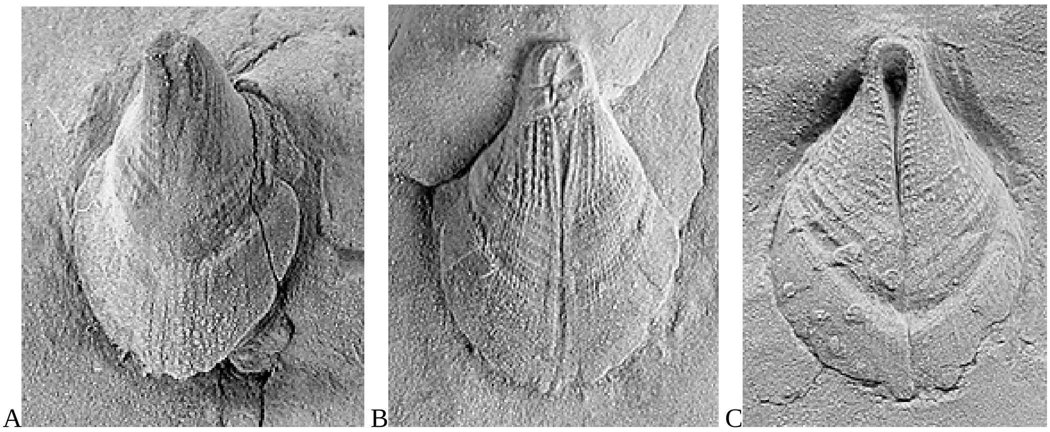


TEXT-FIG. 5.8. *Redstonia sima* sp. nov., Lower Elton Formation (?Wenlock-Ludlow), Sedgley, England. A, Antero-ventral view of holotype BU 4355, showing scarf-like structure around narrow anterior gape, secondary carina divided into three ridges, and large primary carina, separated from rest of body by narrow sulcus; x 6. B, Antero-dorsal view of paratype BU 4360, showing more pronounced reticulate ornament on body; overgrown by cyclostome bryozoan; x 6.

the anterior gape closes to form the commissure the ornament becomes notably finer. This marks the main body area, comprising the secondary carina, which forms three distinct ridges, and sulcus. The third, posteriormost, region is the primary carina, defined by a reopening of the commissure to form a long, slit-like ventral orifice, and by the ornamentation becoming even finer. Denticles are not seen in the anterior gape of *R. sima*, although there is an undulation to the margin of BU 4359 that suggests they may have been weakly developed in some specimens. The other distinctive anterior feature is a scarf-like structure around the anterior gape (see e.g. BU 4355, Text-fig. 5.8A). In dorsal view, the snout is almost triangular in shape, with the hinge forming a distinct cleft that widens anteriorly. Either side of the widest part of this longitudinal cleft are smaller, transverse clefts.

Remarks. *Redstonia sima* is larger than the three previously described species, with the holotype of *R. visbyensis* being approximately 9 mm long, that of *R. tercierae* 8 mm long, and that of *R. buskasi* approximately 6 mm long, in comparison with the 12 mm length of the holotype of *R. sima*.

Of the three other species of *Redstonia*, *R. sima* is most similar to the type species *R. tercierae*, particularly in the pattern of shell ornamentation (see Johnston and Chatterton



TEXT-FIG. 5.9. *Redstonia sima* sp. nov. A, Antero-ventral view of paratype BU 4357, Lower Elton Formation, Sedgley; x 5. B, Antero-ventral view of paratype BU 4358, Much Wenlock Limestone Formation, Dudley; x 5. C, Antero-ventral view of paratype BU 4359, same locality as B; x 5.

1983, pl. 4, figs 1, 6). However, *R. sima* is far more slender in lateral view, and the primary carina is much larger, being comparable to the hood present in many species of the genus *Hippocardia*. The primary carina of *R. sima* is also noticeably larger than those of *R. visbyensis* and *R. buskasi*, but the series of flanges that run along the ventral perimeter of the primary carina of *R. sima* are also seen in *R. buskasi* and *R. tercierae*. Following Caldwell and Chatterton (1995), these flanges are interpreted as original shell structures rather than artefacts of preservation.

The absence of denticles from the anterior gape is a feature common to *R. sima*, *R. tercierae* and *R. buskasi*. However, they are prominent in *R. visbyensis* (see Pojeta and Runnegar 1976, pl. 35, fig. 17), and more closely resemble the denticles seen in species of *Mulceodens*. The constriction of the snout seen in all species of *Redstonia* is also present in both *M. jaanussoni* and *M. latus*, although the scarf-like structure around the anterior gape of *R. sima* is more pronounced than in other forms of *Redstonia*, being closer to that seen in *M. latus* and paratype SMNH Mo.18546 of *M. jaanussoni*.

The longitudinal dorsal cleft and smaller, transverse clefts of *R. sima* are very similar to those of *R. buskasi* and *R. tercierae*, as illustrated by Johnston and Chatterton (1983, pl. 3, fig. 4; pl. 4, fig. 3). The clefts are not seen in specimens of *R. visbyensis*, but the preservation of the dorsal surface of the snout is incomplete.

As the rostrum is not visible in any specimen of *Redstonia sima*, BU 4360 (Text-fig. 5.8B) was sectioned longitudinally along the commissure to investigate whether the rostrum was present beneath the surface and whether its morphology could be determined. The results were inconclusive, and in the following section on palaeoecology, the rostrum of *R. sima* is inferred, based on the rostral morphology of *R. tercierae* and *R. buskasi*.

5.4 PALAEOECOLOGY

As noted in section 5.1, the rostrum of conocardiaceans is regarded as posterior and the largest shell opening (gape) as anterior. The functional interpretation of this orientation is that, during life, the anterior of the rostroconch was buried in the sediment with the foot able to protrude from the anterior gape, whilst the rostrum projected out above the sediment, acting as a siphon for the inhalation of clean water and expulsion of waste material (Pojeta and Runnegar 1976; Runnegar 1978; Pojeta 1987*a*; Hoare 1989).

It was argued by Pojeta and Runnegar (1976) that all conocardiaceans were deposit feeders, with modified muscles enabling a partial protrusion of the mantle out of the anterior gape (Runnegar 1978). Pojeta and Runnegar (1976) also hypothesized that filter-feeding rostroconchs became extinct at the end of the Ordovician, whilst the rostral orifice of conocardiaceans was ‘too narrow for suspension feeding’ (Runnegar 1978, p. 322). Whilst the hypothesis that conocardiaceans were deposit feeders is not questioned here, even a very narrow rostral orifice would have admitted microscopic nutrients suspended in the inhalant water current, and it is possible that at least some conocardiaceans were able to supplement their food intake in this way. In modern oceans, many deposit-feeding invertebrates display analogous behaviour, having the ability to use filter-feeding techniques under certain hydrodynamic conditions (Levinton 1996, p. 107).

The mobility of conocardiaceans is also contentious. Runnegar (1978) interpreted many rostroconchs as sessile, and argued that even the most mobile taxa ‘were sluggish burrowers that rarely moved about’ (Runnegar 1978, p. 327). Thus, they lived mainly in quiet, offshore environments, where the risk of being dislodged or exposed by storms was less (Runnegar 1978). The autecology of Wenlock taxa is discussed in detail below, but the hypothesis that most conocardiaceans were sessile or virtually immobile appears unlikely. If this were so, the rostroconchs would have been reliant on the same area of sediment being constantly restocked with nutrients, rather than being able to move within or upon the seafloor in search of food. Deposit feeders are primarily dependent on organic particles settling out of the water column (Levinton 1996) and thus exploit the same nutrient supply as filter-feeders. Since filter-feeding taxa extract food particles from the water before they settle on the substrate, immobile deposit feeders are vulnerable not only to temporal fluctuations in nutrient supply, but also to efficient suspension feeders capturing the nutrients before they become available to deposit feeders. As extant conchiferan molluscs with a wide variation in size of shell apertures (e.g. bivalves, scaphopods, gastropods) use the foot for locomotion and burrowing, it is probable that conocardiaceans, even those with a small anterior gape, were mobile.

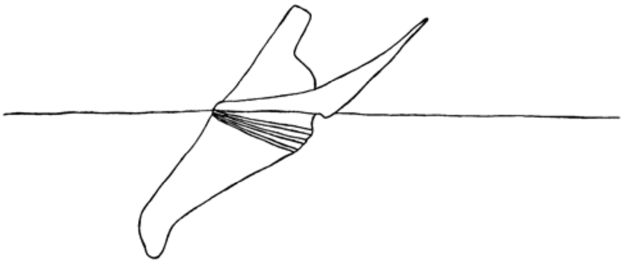
5.4.1 AUTECOLOGY OF WENLOCK ROSTROCONCHS

Although rostroconch palaeoecology has been examined in some detail at a general level (see e.g. Pojeta and Runnegar 1976; Runnegar 1978; Pojeta 1985, 1987*a*) there have been few autecological studies. Detailed investigations of Devonian species from North America were carried out by Bonem (1982) and Hoare (1989), but an equivalent analysis of Silurian taxa has never been attempted. The rostroconchs studied here are all from museum collections and lack precise information as to which stratigraphical horizon(s) they were collected from, but specimens of *Redstonia sima* and *Mulceodens aedicula* are preserved in matrix, and petrographical examination of these lithologies has enabled their likely provenance to be determined. By combining this palaeoenvironmental information with the shell morphology of the two species, the first detailed interpretation of rostroconch palaeoecology during the Silurian has been made.

5.4.1.1 Autecology of *Redstonia sima*

Redstonia sima is found in two distinct lithologies, one a grey, siliciclastic siltstone, the other an olive green, calcareous mudstone. Petrographical analysis (see Appendix) indicates that the siliciclastic siltstones are from the Nodular Beds Member of the Much Wenlock Limestone Formation (the interbedded limestone and silty mudstone lithofacies of Ratcliffe and Thomas 1999), and that the pale green, calcareous mudstone probably belongs to the overlying Lower Elton Formation (?Wenlock-Ludlow). Both lithologies are indicative of low energy depositional conditions, and their excellent preservation shows that the specimens of *R. sima* cannot have undergone much, if any, transportation. Additionally, all specimens are preserved the same way up, suggesting that they may be preserved in, or close to, life position (but see section 5.4.1.3). Thus, they are interpreted as autochthonous.

Ratcliffe and Thomas (1999) showed that the Nodular Beds Member was deposited below fair weather wave-base, and below storm wave-base in part. In comparison, environmental conditions during deposition of the Lower Elton Formation are less well-understood. It is probable that the environment was an offshore shelf setting similar to that of the Nodular Beds Member (A. T. Thomas, pers. comm. 2003; see Appendix for further discussion), but it is unclear whether the finer grain-size of the sediments indicates that they were laid down in lower energy conditions than those of the Nodular Beds Member, or



TEXT-FIG. 5.10. Proposed life position of *Redstonia sima*, with snout and body buried in substrate, and rostrum and primary carina projecting out into water column. See text for further details.

whether only fine sediments were being supplied to the area. Regardless of this uncertainty, *R. sima* evidently lived in low energy environments, and its functional morphology is interpreted in that context.

The most prominent feature of *R. sima* is the primary carina, which is larger than in any other species of *Redstonia*. Primary carinae formed via addition of shell material either side of the tubular ventral orifice, so rostroconchs with longer ventral orifices have larger primary carinae, the giant hood of some hippocardiids (e.g. *Hippocardia cunea*) being the most extreme example of this. Pojeta and Runnegar (1976, p. 22) suggested that the ventral orifice is the functionally significant structure, with the primary carina simply the resultant morphological expression of its development. The exact function of the ventral orifice is not known, but the most plausible explanation is that it served either as a second inhalant siphon or, more probably, as an outlet for the expulsion of waste material (Pojeta and Runnegar 1976; Runnegar 1978; Hoare 1989). Its development would thus relate to the separation of the inhalant and exhalant currents to avoid self-fouling, as seen in many other molluscs. Having only a single (rostral) orifice through which both inhalant and exhalant currents passed would have increased the likelihood of waste products mixing with clean water, whereas having two distinct orifices, one for taking in clean water, the other for expelling waste products, would have lessened that possibility. In high energy environments, where the water column was more constantly agitated and waste products quickly dispersed, the risk of re-inhaling expelled material may have been small, but for species like *R. sima* living in low energy conditions, it would have been beneficial to position the exhalant orifice as far from the inhalant orifice as possible, hence the development of a long ventral orifice and, consequently, a large primary carina.

Being so large, the primary carina would have had a profound effect upon the autecology of *R. sima*. Pojeta and Runnegar (1976) speculated that a large primary carina (hood) might have acted as shell support in soft substrates, or that it could have been used in the deflection of water currents. With regard to *R. sima*, both these hypotheses are plausible, but particularly the former. The anterior margin of the primary carina is demarcated by the sulcus, a narrow depression that runs between the primary and secondary carinae. The sulcus is asymmetrical, with the slope on the anterior side being gentler than that of the posterior side, such that the anterior margin of the primary carina forms a ridge. With the primary carina positioned above the substrate, this sulcal asymmetry would result in sediment being wedged beneath the primary carina (see Text-fig. 5.10), perhaps helping to keep the primary carina fixed in place. A lack of sulcus would have made the ventral margin a continuous slope in lateral view, with the risk either that the rostroconch would sink into the substrate, or that currents, even relatively low energy ones, might scour away sediment from around the shell.

The need to maintain a semi-infaunal life position and avoid being exposed by the scouring of sediment away from the buried anterior part of the shell might also explain the pattern of ornamentation seen in *R. sima*. The reticulate ornamentation is present across the snout, body and primary carina, but is noticeably coarser on the snout and body than it is on the primary carina (see e.g. Text-fig. 5.8B). Amongst living, infaunal and semi-infaunal bivalves, shell ornamentation plays an important role in maintaining the position of the mollusc within the sediment (Stanley 1981). The small, semi-infaunal venerid *Chione cancellata*, for example, has a shell ornament composed of symmetrical, concentric ridges intersected by low, radial ribs, and Stanley (1981) showed that the concentric ridges helped to reduce scour of sediment from around the shell. It is possible, therefore, that a similar, stabilizing function was served by the shell ornament of *R. sima* (see e.g. Text-figs 5.8A, B). The ridges of *C. cancellata* are much more pronounced than either the radial or comarginal ribs of *R. sima*, but this may reflect the fact that *C. cancellata* lives in intertidal and shallow subtidal conditions, where high energy currents are a frequent occurrence. Deposition of the Nodular Beds Member took place under much lower energy conditions, where currents of such strength were very much rarer, so the ornamentation of *R. sima* would not need to have been so pronounced.

The other notable morphological feature of *R. sima* is that its shell is extremely slender in lateral view, particularly in comparison with other species of *Redstonia*. Assuming the anterior-posterior orientation as outlined in section 5.1.1 is correct, and the foot provided mobility by protruding from the anterior gape, such a morphology would have made the shell ‘streamlined’, perhaps as an adaptation towards more efficient burrowing.

5.4.1.2 Autecology of *Mulceodens aedicula*

All examples of *Mulceodens aedicula* are found in bioclastic limestones, and are fragmented to some degree. Large, often angular bioclasts of various sizes indicate that the limestones were deposited relatively rapidly under high energy conditions, and petrographical examination (see Appendix) suggests that they come from either the upper part of the Nodular Beds Member or the overlying Upper Quarried Limestone Formation. If they derive from the Nodular Beds Member then they probably belong to the same interbedded limestone and silty mudstone lithofacies (Ratcliffe and Thomas 1999) as some specimens of *Redstonia sima*. However, whereas the silty mudstones containing *R. sima* are autochthonous, the interbedded limestones containing skeletal debris are allochthonous event beds, probably transported by storms (Ratcliffe and Thomas 1999). Thus, although the two species may have been present in the same lithofacies, they were living in quite different environments. The limestones of the Upper Quarried Limestone Formation were laid down in shallow-water conditions, so, irrespective of which lithology *M. aedicula* derives from, it evidently inhabited a higher energy environment than that of *R. sima*.

This is reflected in the shell morphology of *M. aedicula*. The reticulate ornamentation (see e.g. Text-fig. 5.3A) is much more pronounced than in *R. sima,* and there are prominent denticles in the anterior gape, both of which serve to thicken the shell, making it more robust. The posterior of the shell is imperfectly preserved in specimens of *M. aedicula*, and the rostrum is not seen, but by comparison with other species of *Mulceodens*, it was shorter than that of *R. sima*, and a primary carina was absent or only weakly developed. In higher energy environments, separation of inhalant and exhalant currents would not have been as important as in low energy conditions, because expelled material would have been more rapidly dispersed into the water. Additionally, a shorter rostrum and primary carina would have been less vulnerable to damage from suspended particles.

The more pronounced shell ornamentation of *M. aedicula*, compared with that of *R. sima*, may also reflect the higher energy conditions it lived in, with the radial and comarginal ribs helping to stabilize its position in the sediment, the risk of being exposed by scouring being greater in an environment where strong currents were more frequent.

5.4.1.3 Epifauna

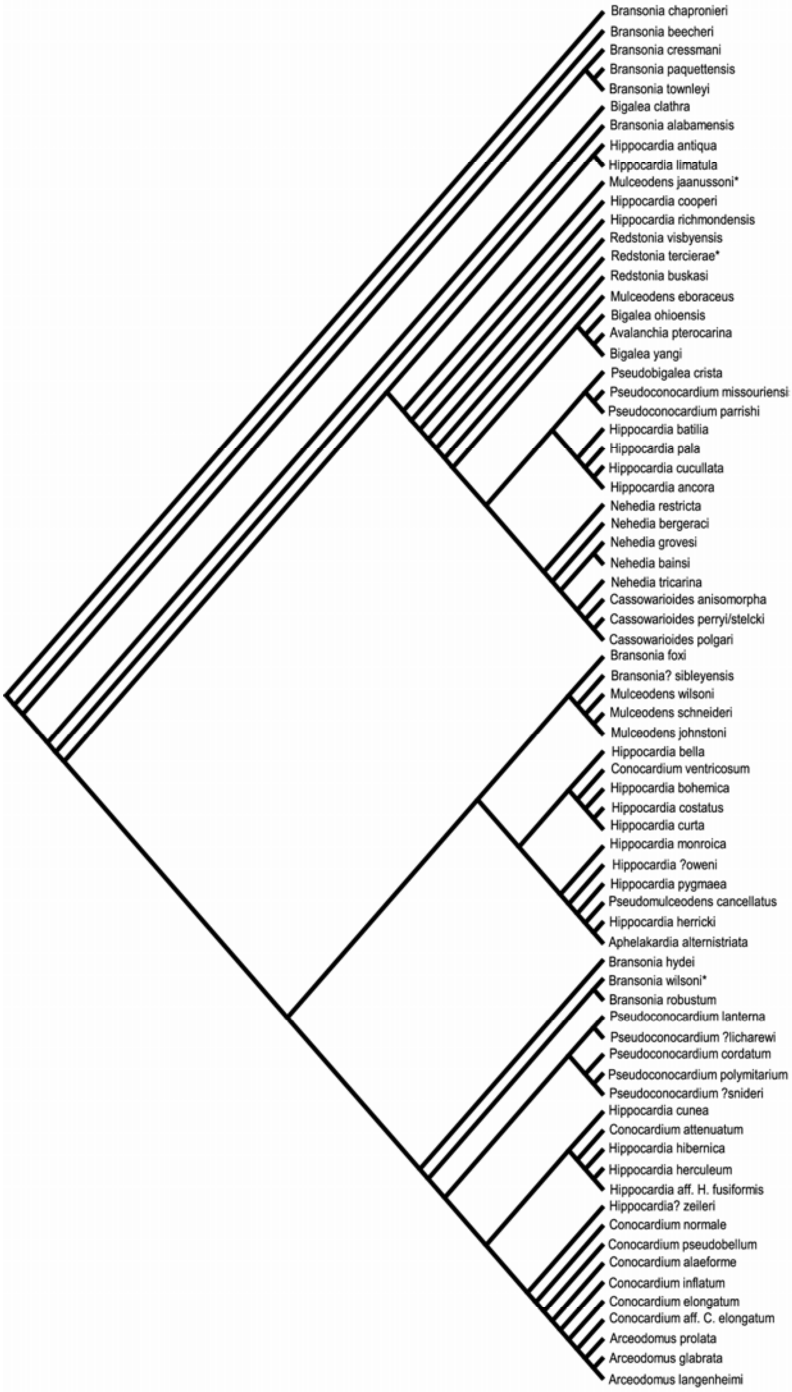
Although the specimens of *Redstonia sima* are well-preserved, evidence from epizoans indicates that at least some were overturned prior to burial. BU 4360 is encrusted by a cyclostome bryozoan that grew from a point on the primary carina close to the ventral orifice across much of the ventral surface, including the commissure (Text-fig. 5.8B). Given the likely life position of *R. sima,* and since shell growth was accommodated by the addition of increments either side of the commissure (Pojeta and Runnegar 1976), the encrustation must have been post-mortem. The dead rostroconch may have provided an island of hard substrate in a sea of muddy sediment, and was probably lying on the seabed for some time prior to burial. It is thus possible that the consistent orientation of *R. sima* specimens simply reflects preservation of the most stable resting position of empty shells.

5.4.1.4 Summary

If the provenance of *Redstonia sima* and *Mulceodens aedicula* as interpreted above is correct, the two species coexisted temporally but not spatially, with *R. sima* occurring both above and below *M. aedicula* in the Silurian stratigraphy of the West Midlands. Both taxa were ecologically specialized, with *M. aedicula* living in high energy, near-shore environments, and *R. sima* inhabiting quieter, offshore environments. Thus, in the deeper water sediments of the Nodular Beds Member, *R. sima* is present, before being replaced by *M. aedicula* as water levels dropped and deposition of the Upper Quarried Limestone Member began. When quieter, deeper water conditions returned, and the Lower Elton Formation started being deposited, so did *R. sima*.

5.5 CONCLUSIONS AND PHYLOGENETIC IMPLICATIONS

Under the classification of Pojeta and Runnegar (1976), *Mulceodens* and *Redstonia* were placed in separate conocardiacean families. However, the phylogenetic analysis of Wagner (1997) did not support this and suggested instead that the two genera belonged to the same clade (see Text-fig. 5.11). Wagner also showed that hoodless and hooded conocardiaceans do not fall into separate, monophyletic clades, leading to the abolition here of the family Bransoniidae, and the recognition of just two conocardiacean families – Hippocardiidae and Conocardiidae. Clearly, further work is required to provide a better understanding of the phylogeny and systematic classification of conocardiaceans, but *R. sima* and *M. aedicula* inhabited very different niches, and their disparity of form probably reflects adaptation to life in these separate environments, rather than their being only distantly related. Similarly, *M. latus* shows differences in coarseness of shell ornamentation and development of primary carina from *R. sima*, but the two species are the same size, pronouncedly flattened in lateral view, have downturned snouts, and a scarf-like constriction around the anterior gape. By including species from other Silurian localities, the hypothesis that the two genera are closely related gains further support. The Gotland species *Redstonia visbyensis* has denticles in the ventral part of the anterior gape that almost touch, exactly like those of *Mulceodens*, but is otherwise very similar to the other species of *Redstonia*. Conversely, Johnston and Chatterton (1983) and Caldwell and Chatterton (1995) interpreted three species from the Wenlock of Canada as examples of *Mulceodens*, despite the taxa having pronounced primary carinae.



TEXT-FIG. 5.11. Phylogenetic tree of conocardiacean relationships (Wagner 1997)

This generic placement was not supported by Wagner (1997), whose analysis placed them in a separate clade to *M. jaanussoni* (see Text-fig. 5.11), but this only serves to highlight the problem in determining which rostroconch shell features are phylogenetically significant. It is highly probable that some characters (e.g. presence/absence (strength/weakness) of the primary carina) are homoplastic, such that unrelated taxa look similar, whereas other, homologous characters vary in degree of expression according to ecological function, and can thus make closely related taxa appear wholly dissimilar.

CHAPTER SIX

MACHAERIDIANS

ABSTRACT. The problematical Palaeozoic group Machaeridia consists of elongate, slug- or worm-shaped animals with a dorsal skeleton of imbricating calcite plates. Machaeridians have been placed in a variety of phyla by previous authors, but their systematic position has never been firmly determined. Many of the best-preserved specimens are from the Much Wenlock Limestone Formation (Silurian) of England, in which three species are recognized here: *Turrilepas wrightiana* (de Koninck, 1857), *Lepidocoleus ketleyanus* (Reed, 1901) and *Lepidocoleus*? *extraplax* sp. nov. With at least 65 sets of inner and outer sclerites, *L*? *extraplax* has the largest number of skeletal elements seen in any machaeridian taxon, and shows that not all lepidocoleids had biseriate scleritomes. An individual sclerite of *T. wrightiana* was sectioned to investigate skeletal microstructure, supporting previous observations of a two-layered structure, with growth by marginal accretion. Based on the sclerite microstructure and overall scleritome morphology, it is argued here that machaeridians are stem-group molluscs, probably the sister group of Polyplacophora + Conchifera.

The taxon Machaeridia was erected by Withers (1926) to include four genera of Palaeozoic problematica – *Turrilepas* Woodward, 1865, *Plumulites* Barrande, 1872, *Lepidocoleus* Faber, 1886, and *Deltacoleus* Withers, 1926. Deriving the name from the Greek, *machairidion*, meaning ‘little sabre’, Withers (1926) defined machaeridians as metazoans with elongate bodies covered by two or four longitudinal rows of imbricated, calcite plates (sclerites). Articulated sclerite assemblages, representing original machaeridian scleritomes, are extremely rare in the fossil record, though individual sclerites are abundant at many localities. However, as it is often difficult to ascertain exactly where in the scleritome, and in some cases to which species, a disarticulated sclerite belongs, horizons preserving complete or near-complete machaeridians are vital to our understanding of these animals. One of the best examples is the Much Wenlock Limestone Formation (Silurian: Wenlock) of the English Midlands and Welsh Borderlands, where storm-generated obrution deposits smothered a diverse reef and inter-reef fauna, including machaeridians, a significant number of which are at least partly articulated. Two species – *Turrilepas wrightiana* (de Koninck, 1857) and *Lepidocoleus ketleyanus* (Reed, 1901) – have previously been described from outcrops in and around Dudley, West Midlands, but the diversity of the machaeridian fauna has been little studied and the taxa were previously relatively poorly understood.

The taxonomy and morphology of machaeridians from the Much Wenlock Limestone Formation are here re-assessed, with the sclerite microstructure of *Turrilepas wrightiana* described for the first time, and the presence of outer sclerites in lepidocoleids confirmed. These data not only enable a greater understanding of the palaeobiology and palaeoecology of Silurian machaeridians, but also shed light on the affinities of the group as a whole.

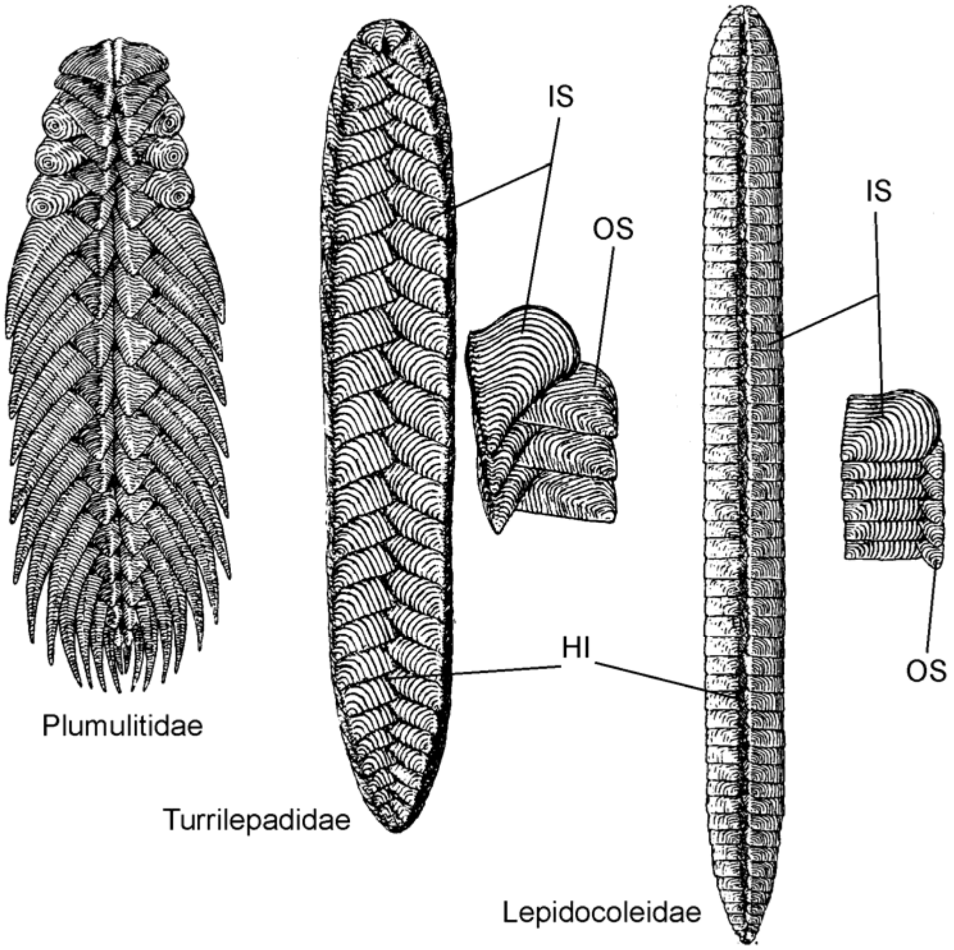
6.1 PREVIOUS WORK ON THE MACHAERIDIA

With plates arranged in series along an elongate body, machaeridians look at first glance rather like armoured 'worms' (see Text-fig 6.1). However, a variety of interpretations of their affinity have been made since their first description almost 150 years ago. That first species, now identified as *Turrilepas wrightiana* (de Koninck, 1857), was originally classified by de Koninck as belonging to the polyplacophoran mollusc genus *Chiton*. This was contested by Woodward (1865), who reinterpreted the animal as an early form of cirripede and transferred it to his new genus, *Turrilepas*, although in later publications (e.g. Woodward 1871, 1880) he raised the possibility of *T. wrightiana* being the stem of the anomalocystid carpoid *Placocystites forbesianus*. Despite the subsequent misgivings of Woodward, the hypothesis that *Turrilepas* belonged to the Arthropoda was accepted by most authors for the next 60 years (see Withers 1926, pp. 76-80 for summary), though a dissenting voice was provided by Salter (1873), who placed *Turrilepas* in the Annelida. One of the few researchers to follow Woodward's (1871, 1880) alternative interpretation was Reed (1901, p. 109), who found 'much probability' in the notion that the species he described as '*Turrilepas*?? *ketleyanus*' was part of a carpoid stem.

By the 1920s, there was reasonable agreement that *Turrilepas*, *Plumulites* and *Lepidocoleus* were related, but it was clear that the systematics of the group were in need of revision. Through detailed study of material from the UK, Europe and North America, housed mainly in the Natural History Museum, Withers (1926) was able to produce the first comprehensive taxonomy. He divided machaeridians into two families – Lepidocoleidae with two rows of sclerites along the body, and Turrilepadidae with four – and 43 species were diagnosed, collectively ranging from the Lower Ordovician to the Middle Devonian. Withers (1926) also re-examined previous workers' thoughts on the biological affinities of the group, beginning with their putative relationship to cirripedes. Gruvel (1905), Clarke (1918) and Ruedemann (1924) had strongly supported that hypothesis but, after assessing their main lines of reasoning, Withers (1926, pp. 77–82) dismantled it. Firstly, he pointed out that Woodward (1865) and Gruvel (1905), amongst others, had based their comparison of *T. wrightiana* with Mesozoic cirripedes on incomplete specimens that were not fully representative of *Turrilepas*.

Thus, although there were apparent similarities in the ornamentation and imbrication of *Turrilepas* sclerites and cirripede plates, as identified by Woodward (1865), these alone could not be considered as convincing evidence that machaeridians were arthropods. Withers argued that the capability of machaeridian sclerites to slide over one another gave a flexibility to the scleritome that was quite unlike the relatively rigidly plated shell of cirripedes, whilst neither the imbrication nor patterns of plate ornamentation were features unique to the Arthropoda. Furthermore, the growth pattern and musculature of machaeridian sclerites, as well as the number of sclerites present in a single scleritome, were characters not shared by cirripedes, requiring ‘vast structural changes’ (Withers 1926, p. 81) to have occurred for the earliest (Triassic) cirripedes to be the sister group of machaeridians. This combination of functional and structural evidence, coupled with his knowledge of cirripede phylogeny, led Withers (1926) to conclude that machaeridians could not belong to that order, or indeed any other group of arthropods. Neither, he contended, could *Turrilepas* be a polyplacophoran, having as it did four rows of up to thirty sclerites rather than a single row of eight plates, whilst lacking the ability to flatten its body in the manner typical of *Chiton* and relatives, and it seemed ‘impossible’ (Withers 1926, p. 82) to recognize the machaeridians as members of any other molluscan class. As for them being members of the Annelida he reached similar conclusions, admitting the broad morphological resemblance but emphasizing the lack of a terminal opening, the presence of muscle scars on the inner surface of every sclerite that showed the animal could not have moved freely inside its shell, the structure of the sclerites, and the fact that it was unknown for annelids to form shells of such distinct, individual plates. With arthropods, molluscs and annelids excluded, only the relationship to echinoderms remained to be investigated.

Contrary to the claims of some authors (e.g. Newman *et al*. 1969; Pope 1975), Withers (1926) did not refer machaeridians to the Echinodermata. He did note (Withers 1926, p. 83, 84) that sectioned sclerites of some species of *Lepidocoleus* showed some mineralogical and optical features similar to those of echinoderm ossicles, particularly in their apparently uniform extinction under cross-polarized light, but he emphasized the difficulty in referring machaeridians ‘to any single group of that or any other class’ (Withers 1926, p. 84). Withers did not place them in any existing phylum either then or in 1933, when he mentioned only that a new specimen of *L. ketleyanus* further diminished the possibility that machaeridians were cirripedes. It was Bather, in his preface to Withers (1926), who concluded, originally with misgivings but later (Bather 1930) with greater certainty, that machaeridians were a class of Echinodermata. He suggested (Bather *in* Withers 1926, p. xi) that machaeridians were, along with carpoids, ‘among the earliest offshoots from the Echinoderm stem’ and had diverged prior to the acquisition of most of the features, such as pentameral symmetry, that were typical of later echinoderms.



TEXT-FIG. 6.1. General morphology of machaeridians, shown in dorsal view, with anterior of scleritome at top. Turrilepadidae and Lepidocoleidae also shown in right lateral view, with hinge (HI), inner sclerites (IS) and outer sclerites (OS) marked. From Dzik (1986).

Despite the inherent risk in accepting one character, in this case the optical properties of skeletal elements, as being of greater significance than all others, and the doubts raised by Withers, the interpretation of machaeridians as echinoderms held pre-eminence for over half a century. During that time, relatively little work on the group was done, but support for Bather's concept came from Whitehouse (1941) who erected a new echinoderm subphylum, Homalozoa, to include both carpoids and machaeridians. Not all authors, however, were convinced of that systematic assignation, with Ubaghs (1967, p. S52) describing it as 'an open question' whilst Fell and Moore (1966, p. U110) regarded it as 'very doubtful', though they had not examined the Machaeridia in detail themselves. Other workers were sure of its accuracy. Pope (1962, 1975) considered lepidocoleids to be the plate-covered spines of mitrates. Having apparently disregarded Withers' (1926, p. 83) assertion that they were entities in themselves, not part of another organism, Pope (1975, p. 395) identified the mineralogy of lepidocoleid plates as being 'clearly…holocrystalline' and therefore identical to echinoderm ossicles. Furthermore, he argued that the alliance of Lepidocoleidae and Turrilepadidae as families within the same higher order group of animals was unproven, with only the former unequivocally acceptable as belonging to the Machaeridia.

Evidence against an echinoderm affinity was provided by Bengtson (1970, 1977, 1978). He initially remarked (Bengtson 1970) upon the similarities between machaeridians and taxa of the problematical Cambrian order Mitrosagophora, tentatively suggesting that the two groups were related and that they perhaps represented early examples of the phylum Annelida. Later (Bengtson 1977, 1978), he was able to show convincingly that Pope's (1975) hypothesis was incorrect. Firstly, lepidocoleids could not be parts of mitrate carpoids, as there was no consistent co-occurrence of the two groups – many stratigraphical horizons with abundant lepidocoleids were devoid of carpoids, and articulated examples of one group were not found with articulated specimens of the other (Bengtson 1977, p. 34, 35). More significantly though, from re-investigation of Withers' (1926) material and by making thin sections of *Turrilepas* and *Lepidocoleus* sclerites from the Silurian of Gotland, Bengtson (1978) demonstrated that the calcite shell of machaeridians was unlike the stereom of echinoderms. A key observation was that neither the newly sectioned sclerites, nor those made by Withers (1926), truly displayed the uniform extinction under cross-polars that is characteristic of echinoderm hard tissues. In fact, the sclerites showed a two-layered structure that proved they could only belong to the Echinodermata if all previous diagnoses of the phylum were incorrect (see also section 6.7). With regard to the question of whether lepidocoleids and turrilepadids belonged together in the Machaeridia, Bengtson (1978) argued convincingly that their shared characters were far more numerous than their dissimilarities and that no compelling reasons could be found for removing either from the group.

Although having excluded echinoderms, Bengtson (1977, p. 36) did not wish 'to lock thoughts and colour future observations' by firmly placing machaeridians into any other higher taxon, although he did retain the earlier proposal (Bengtson 1970) of a relationship between machaeridians and mitrosagophorans. Jell (1979), however, concluded his review of *Plumulites* by arguing that machaeridians most likely belonged to the Annelida. This was partially supported by Dzik (1986), but he stated that ambiguity of available evidence made it possible to interpret them as either polychaete annelids or primitive molluscs related to polyplacophorans. A solution proposed by Bergström (1989) was to place machaeridians in a new phylum Procoelomata, ancestral to most metazoans including both molluscs and annelids, but this was not followed by subsequent workers (e.g. Adrain 1992; Högström 1997). On the basis of sclerite growth patterns (see section 6.6 for further details), Adrain (1992) compared machaeridians with molluscs and articulate brachiopods, but Dzik (1993) argued that the presence of 'tagma' in *Plumulites* might indicate a closer relationship to stem-group arthropods, such as *Anomalocaris*. Hoare *et al*. (1996) did not attempt to resolve the affinities of the group, but noted similarities in microstructure of machaeridian sclerites and mickwitziids, probable stem-group brachiopods (Holmer *et al*. 2002). Thus, the systematic position of Machaeridia has remained problematical, but, as noted by Högström and Taylor (2001), they are now almost universally accepted as being protostomes rather than deuterostomes.

6.2 SILURIAN MACHAERIDIANS

Machaeridians are known from Silurian rocks worldwide, with Withers (1926) having catalogued specimens from the Silurian of Britain, Europe, North America, Asia and Australia. Only in the last decade or so have any of these species been re-examined, and most work has concentrated on material from North America and Europe. The generic diagnosis of *Turrilepas* was revised by Adrain *et al*. (1991), with a new species – *T. modzalevskae* – described from the Ludlow of the Ukraine, whilst the faunal diversity of machaeridians from the Wenlock and Ludlow of Gotland was assessed in detail by Högström (1997, 2000; see also Bengtson 1979). Additionally, *Lepidocoleus sarlei* (Clarke, 1896) from the Rochester Shale (Wenlock) of New York State, USA, was re-described by Högström and Taylor (2001). However, other than the revision of *T. wrightiana* by Adrain *et al*. (1991), British Silurian machaeridians have been considered only briefly in the last three-quarters of a century.

Including *Turrilepas wrightiana* and *Lepidocoleus ketleyanus*, Withers (1926) listed seven machaeridian taxa as being present in the Silurian rocks of the UK. Two Scottish examples of *Plumulites*, one from the Llandovery of Girvan, the other from the Lower Silurian of the Pentland Hills (described by Withers (1926, p. 70) as from the Ludlow, but subsequently shown by Lamont (1952) and Robertson (1989) to be of Llandovery to Wenlock age), and a form of *Lepidocoleus* from the Ludlow of Shropshire, were insufficiently well preserved to be identified to species level. However, Withers (1926) did erect *L. turnbulli* from the Llandovery of Haverfordwest, Wales, and *L. britannicus* from the Wenlock of Malvern. This paper considers those species present in the Much Wenlock Limestone Formation of the West Midlands.

6.3 MATERIALS AND METHODS

The specimens described herein are in the collections of the Lapworth Museum, University of Birmingham (prefixed BU), the Natural History Museum, London (NHM), the Sedgwick

TEXT-FIG. 6.2. Cross-sectional body morphology of machaeridians, with dorsal surface at top. A, Lepidocoleidae; B, Turrilepadidae; C, Plumulitidae (from Högström 1997).

Museum, Cambridge (SM), and Wollaton Hall Museum of Natural History, Nottingham (NOTNH). All illustrated material is from the Lapworth Museum and was whitened with ammonium chloride prior to photography.

The mineralogy and structure of *Turrilepas wrightiana* was determined by longitudinally sectioning an isolated sclerite (BU 3769) from the Tilley Collection, Lapworth Museum. The thin section was examined petrographically using a Zeiss Axioskop microscope and under cathodoluminescence, then etched for three hours in a saturated solution of EDTA in deionized water before being studied under a Philips XL30 FEG environmental scanning electron microscope (ESEM).

6.4 TERMINOLOGY

There has been very little stability or consistency in the terms used to describe machaeridian morphology. This reflects the uncertainty over their affinity, with different authors using different terms for the same features. Machaeridian skeletons, for example, have been variously described as shells (Withers 1926), strobili (Pope 1975; Dzik 1986), sclerite assemblages (Jell 1979) and scleritomes (Adrain *et al.* 1991; Högström 1997), whilst the skeletal elements have been called plates (Withers 1926; Pope 1975), sclerites (Bengtson 1970; Jell 1979; Adrain *et al.* 1991) and elytra (Dzik 1986). Noting this problem, Adrain *et al.* (1991) proposed a standardized set of terms, originally devised for use in their reassessment of the family Turrilepadidae, but later (Adrain 1992) being extended to cover the entire taxon Machaeridia. With occasional minor modifications (see Högström 1997; Högström and Taylor 2001) this system has been accepted by subsequent researchers and is followed here, except for the use of *segment* to describe each series of inner and outer sclerites along the body. Although no functional interpretation was attached to its usage (Högström and Taylor 2001), segment implies an homology with the body divisions of organisms such as annelids, and its usage is best avoided (see section 6.8). Each transverse unit of outer left, inner left, inner right and outer right sclerites (or inner left and inner right in biseriate machaeridians) is here termed a *set*, with longitudinal, imbricated units of inner or outer sclerites a *series*.

The body orientation of machaeridians is uncertain, as no specimens with preserved soft-parts are known. However, the most plausible functional arrangement of the scleritome is with the sclerites covering the dorsal or dorso-lateral surfaces and imbricating from anterior to posterior, such that the posterior margin of one sclerite over-rides the anterior of the next.

6.5 SYSTEMATIC PALAEONTOLOGY

Order MACHAERIDIA Withers, 1926

Remarks. Withers (1926) erected Machaeridia as a group containing two families, Lepidocoleidae and Turrilepadidae, but did not give the level of the higher taxon. The interpretation of machaeridians as echinoderms led authors such as Bather (1930) and Whitehouse (1941) to place them at class level within that phylum. Following the rejection of echinoderm affinities by Bengtson (1977, 1978), Jell (1979) redefined Machaeridia as an order, of equivalent status to the Mitrosagophora Bengtson, 1970, and erected the family Plumulitidae in addition to the two defined by Withers (1926).

Dzik (1986) agreed that three families could be delineated, but placed them all in the Turrilepadida, one of four orders of a dramatically redefined class Machaeridia (see section 6.1). This revision was followed by Bergström (1989), but Adrain (1992) rejected the taxonomy and returned to a trifamilial Machaeridia. However, he did not revert to classifying machaeridians as an order, placing instead turrilepadids and plumulitids in the Order Turrilepadomorpha and lepidocoleids in the Order Lepidocoleomorpha, both belonging to the class Machaeridia. The basis for separating the two groups was that lepidocoleids were biseriate, had a distinct tongue-and-groove dorsal hinge, and could fully close their scleritome, whereas the quadriseriate turrilepadids and plumulitids had a much simpler hinge and could not bring their outer sclerites into contact ventrally (Adrain 1992).

This classification was followed by Högström (1997) and Högström and Taylor (2001), but with some reservations. Firstly, Högström (1997, p. 819) cast doubt on the biseriate diagnosis of Lepidocoleomorpha, noting that outer sclerites were present in *Lepidocoleus* sp. A (Högström 1997) from the Upper Wenlock of Gotland, and that Dzik (1986) had documented the same feature in specimen BU 2804 (transferred herein to *Lepidocoleus*? *extraplax* sp. nov.) from the Much Wenlock Limestone Formation. Detailed examination of BU 2804 (see below) confirms Dzik’s observation and shows that outer sclerites were retained, albeit in reduced form, in at least some species of lepidocoleid. Secondly, Högström (1997) and Högström and Taylor (2001) showed that the tongue-and-groove hinge system was not present in all lepidocoleids, with some taxa having a simple dorsal overlap of sclerites. It is thus difficult to justify interpreting plumulitids and turrilepadids as being more closely related to one another than either is to lepidocoleids, and, until further analysis resolves this argument, the most logical approach is to revert to the classification of Jell (1979). Thereby, the Machaeridia are reinstated as an ordinal-level clade containing three family groups, Plumulitidae, Turrilepadidae, and Lepidocoleidae.

Family TURRILEPADIDAE Clarke, 1896

Genus TURRILEPAS Woodward, 1865

Type species. *Chiton wrightianus* de Koninck, 1857 from the Much Wenlock Limestone Formation (Homerian, Silurian) of Dudley, England. By monotypy.

Diagnosis (after Adrain *et al*. 1991). Quadriseriate machaeridians with large, thick sclerites, bearing coarse rugae. Inner sclerites of mid-region with pronounced longitudinal fold of approximately 90 degrees, becoming flattened at anterior and posterior of scleritome; dorsal and lateral parts of inner sclerites of similar size. Outer sclerites flat, somewhat triangular in shape, but with rounded accreting margin. Apical and marginal spines present in well-preserved specimens.

Turrilepas wrightiana (de Koninck, 1857)

Text-figs 6.3A-D

v*	1857	*Chiton Wrightianus* de Koninck, p. 199, pl. 1, fig. 2.
v	1865	*Turrilepas* (*Chiton*) *Wrightii* H. W. [sic]; Woodward, p. 486, pl. 14, figs 1a-l [specimens in figs 1d-f and 1k cannot be traced].
	1873	*Turrilepas Wrightianus*, De Kon.; Salter, p. 129.
	1875	*Turrilepis* [sic] *Wrightianus*; Baily, p. xliv.
v	1926	*Turrilepas wrightiana* (de Koninck); Withers, p. 33 [with detailed synonymy list covering 1873 to 1926].
v	*1933*	*Turrilepas wrightiana* (de Koninck); Withers, p. 162.

1970 *Turrilepas wrightiana*; Bengtson, p. 385.

1978 *Turrilepas wrightiana*; Bengtson, p. 7.

1986 *Turrilepas wrightiana* (Koninck); Dzik, p. 117.

v 1991 *Turrilepas wrightiana* (de Koninck); Adrain, Chatterton and Cocks, p. 637, pl. 1, figs 4, 5, 7, 8, 10-12; pl. 2, figs 6-9, 11-14.

1995 *Turrilepas wrightiana*; Adrain, Chatterton and Blodgett, p. 734.

1996 *Turrilepas wrightiana* (de Koninck); Hoare *et al*., p. 129 [but type species of *Turrilepas* described on p. 130 as '*Turrilepas wrighti* Woodward 1865'].

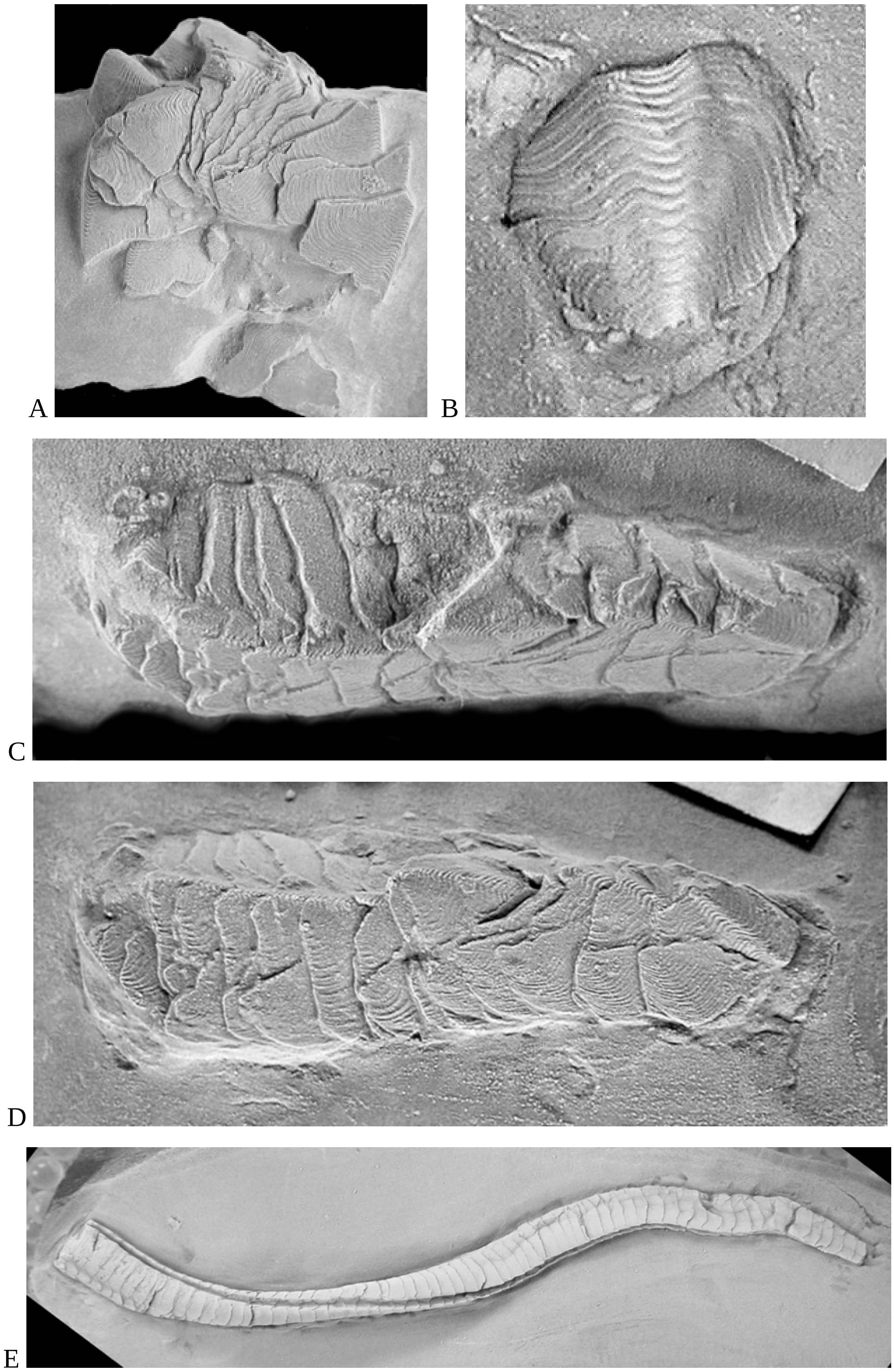
1997 *Turrilepas wrightiana* (de Koninck); Högström, p. 818.

Holotype. NHM I16283 from the Much Wenlock Limestone Formation (Silurian, Homerian) of Dudley, England.

Other material studied. NHM 46429, 46433, 47871, 59056-7, 59164, 59406, I1569, I4420, I16254, I16272-3, I16275-82, I16284-92, I16302-3, I16305-6, I16308, In25812-5; BU 375, 3768-70, 3772-3, 3775-6; NOTNH FS04221.

Diagnosis (after Adrain *et al*. 1991). Species of *Turrilepas* with at least 26 sets of sclerites, each sclerite having at least 25 rugae when mature. Outer sclerites have accreting margin of same length as length of longitudinal angle of inner sclerites. Apical and marginal spines very small.

Remarks. Specimens of *Turrilepas wrightiana* in the Natural History Museum were described and figured by Withers (1926) and Adrain *et al*. (1991). Material in the Lapworth Museum was listed by Withers (1933) and BU 375 was originally figured by Woodward (1865, pl. 14, fig 1c), but none of the specimens have ever been discussed in detail. Of the eight specimens, BU 375 (Text-fig. 6.3A) and BU 3776 (Text-figs 6.3C, D) are the best preserved, the former showing the right lateral and dorsal surfaces of an enrolled specimen, the latter showing the dorsal surface of a specimen in which the modified anterior sclerites are clearly seen (e.g. Text-fig. 6.3D). Individual sclerite BU 3769 (Text-fig. 6.3B) has a slightly flattened longitudinal fold, a modification that indicates it is an inner sclerite from close to the anterior of the scleritome. It was sectioned longitudinally to investigate sclerite microstructure (see section 6.7 for detailed description).



TEXT-FIG. 6.3. A-D, *Turrilepas wrightiana* (de Koninck, 1857), Much Wenlock Limestone Formation, Dudley; A, BU 375, right lateral surface, x 2; B, BU 3769, inner sclerite from anterior of scleritome, showing concentric rugae; accreting margin towards top of image, x 7; C, dorsal, and D, right lateral surface of BU 3776, showing modified anterior sclerites (right), x 3.5; E, *Lepidocoleus*? *extraplax* sp. nov., Lower Elton Formation, Sedgley; BU 2804, left lateral, dorsal, and right lateral surfaces of holotype, x 1.75.

T. wrightiana was the only species of *Turrilepas* until Adrain et al. (1991) recognized *T. modzalevskae* from the Ludlow of the Ukraine. It was distinguished from *T. wrightiana* on the grounds of having smaller, more closely spaced marginal spines, and outer sclerites in which the accreting margin was two-thirds to three-quarters the length of the longitudinal angle of the inner sclerites.

Family LEPIDOCOLEIDAE Clarke, 1896

Genus LEPIDOCOLEUS Faber, 1886

Type species. *Plumulites jamesi* Hall and Whitfield, 1875 from the Upper Ordovician of Ohio. By monotypy.

Diagnosis. Machaeridians with dorso-ventrally elongated inner sclerites, normally convex in transverse section across the scleritome; outer sclerites small or absent. Dorsal part of inner sclerites normally much reduced, forming narrow, sunken hinge line. Rugae much less coarse than those of turrilepadids.

Remarks. Withers (1926) identified 16 species of *Lepidocoleus*, ranging in age from the Middle Ordovician to the Middle Devonian. Dzik (1986), however, interpreted the genus as monospecific on the grounds that only the type species, *L. jamesi*, had elongated dorsal sclerites with prominent rugae and transferred all other species to the genus *Aulakolepos* Wolburg, 1938. Högström (1997, p. 820) agreed that there were taxonomic problems, with ‘several’ types of lepidocoleids being classified together, but, having assessed only Silurian species from Gotland, did not attempt to differentiate them. Thus, there are inherent problems in simply assigning species to *Lepidocoleus*, but prior to a comprehensive re-examination of all lepidocoleid taxa, the approach of Högström (1997, 2000) and Högström and Taylor (2001) is followed, and *L. ketleyanus* is retained in the genus *Lepidocoleus*.

Lepidocoleus ketleyanus (Reed, 1901)

Text-fig. 6.4

1873 *Turrilepas Ketleyanus* Salter, p. 129 [without description or illustration].
* 1901 *Turrilepas* ?? *ketleyanus*, Salter; Reed, p. 108 [description, without illustration, of specimens listed by Salter (1873)].

v	1926	*Lepidocoleus ketleyanus* (Reed *ex* Salter MS.); Withers, p. 20, pl. iii, figs. 1-10 [first comprehensive description and diagnosis].
?	1997	*Lepidocoleus ketleyanus* (Reed); Högström, p. 819, 820, 823.
?	2000	*Lepidocoleus ketleyanus* (Reed); Högström, p. 224.
?	2001	*Lepidocoleus ketleyanus* (Reed); Högström and Taylor, p. 122.

Type material. SM A54086 and SM A54087 from the Much Wenlock Limestone Formation (Homerian, Silurian) of Dudley, England. SM A54086 designated as lectotype by Withers (1926, p. 20; pl. 3, fig. 1).

Other material. NHM 59058, I540, I16255-68, I16270-1, I16293-4, I16296-301, I16307, In17508-9, In61500; BU 3767, 3771, 3774, all from same locality as type specimens.

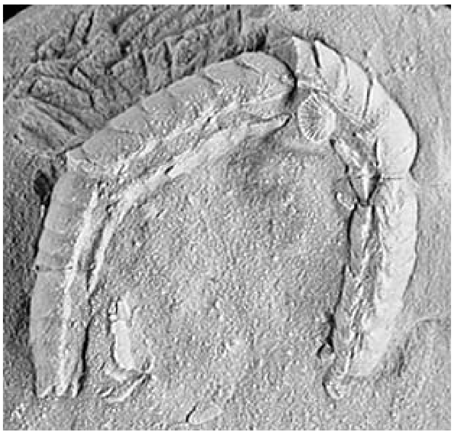
Emended diagnosis (after Withers 1926). Biseriate species of *Lepidocoleus* with up to around 35 sets of inner sclerites; sclerites almost three times high as wide. Posterior margin of sclerites with slight sigmoidal curve, ventral margin rounded. Rugae extremely fine, very closely spaced.

Remarks. The diagnosis of *Lepidocoleus ketleyanus* published by Withers (1926) was revised by him (Withers 1933) on the basis that BU 2804 was an exceptional example of the species. As described below, the presence of outer sclerites and the extremely high number of sclerite sets in BU 2804 indicates that it belongs to a separate taxon and thus this study follows Withers' (1926) diagnosis of *L. ketleyanus*.

Lepidocoleus? *extraplax* sp. nov.

Text-fig. 6.3E, 6.5A-D

v.	1933	*Lepidocoleus ketleyanus* (Reed *ex* Salter MS.); Withers, p. 162, pl. iv, fig. 4.
v.	1977	*Lepidocoleus ketleyanus* (Reed); Bengtson, p. 29, fig. 3.
?	1986	*Aulakolepos ketleyanum* (Reed); Dzik, p. 117, fig 1c.
	1986	*Aulakolepos ketleyanum* (Reed); Dzik, p. 122.
?	1997	*Lepidocoleus ketleyanus* (Reed); Högström, p. 819, 820, 823.
	1997	*Lepidocoleus ketleyanus* (Reed); Högström, p. 824.
?	2000	*Lepidocoleus ketleyanus* (Reed); Högström, p. 224.



TEXT-FIG. 6.4. *Lepidocoleus ketleyanus* (Reed, 1901), Much Wenlock Limestone Formation, Dudley. Dorsal view of BU 3771, showing left lateral series of inner sclerites, hinge line, and dorsal part of right lateral sclerite series, x 3.5.

? 2001 *Lepidocoleus ketleyanus* (Reed); Högström and Taylor, p. 122.

2001 *Lepidocoleus ketleyanus* (Reed); Högström and Taylor, p. 122.

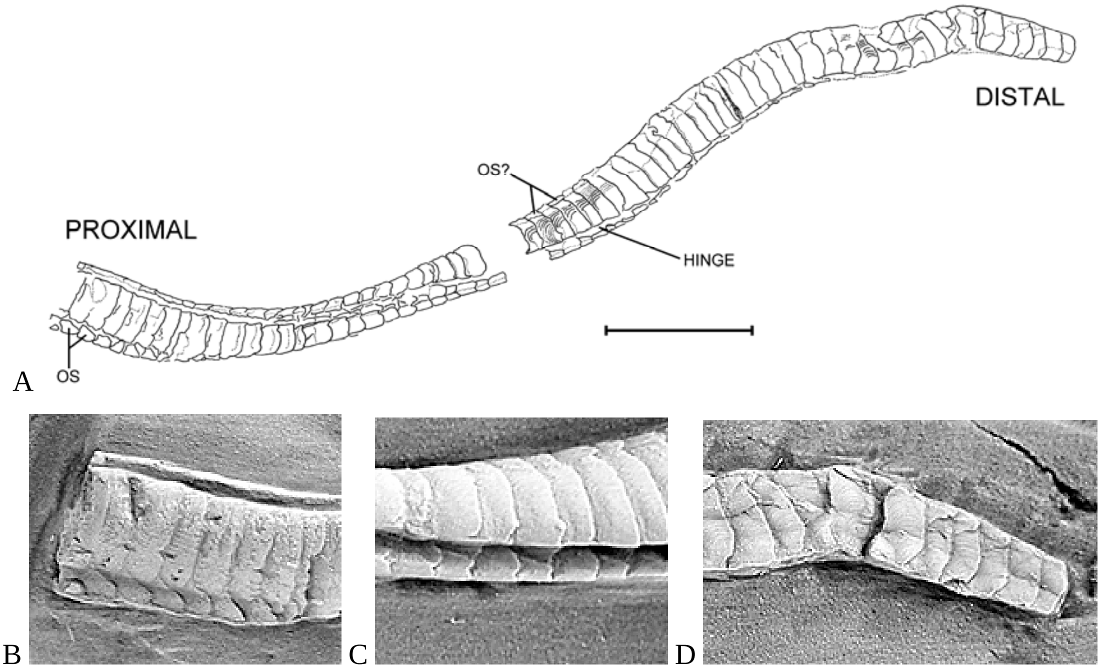
Derivation of name. From the Latin, *extra*, outside, and the Greek, *plax*, plate, in reference to the distinctive outer sclerites.

Holotype. BU 2804, the only known specimen, from the Lower Elton Formation (?Wenlock-Ludlow) of Sedgley, near Dudley, England.

Diagnosis. Species of *Lepidocoleus* with at least 65 sets of sclerites along body; small but distinct outer sclerites present, approximately triangular in shape.

Description. Holotype articulated, but with anteriormost part of scleritome missing. Sclerites directly oppose across hinge, rather than alternating, as seen in *Lepidocoleus sarlei* (Högström and Taylor 2001); inner sclerites having short dorsal flange, forming narrow dorsal depression along hinge line. Inner sclerites approximately 3 mm high, 1 mm wide; outer sclerites of roughly same width as height, width being same as width of inner sclerites; rugae fine, often indistinct. Posterior margins of inner sclerites parallel and almost straight, giving sclerites rectangular shape; ventral margins straight.

Remarks. In all previous descriptions, the holotype of *Lepidocoleus*? *extraplax* has been interpreted as an exceptionally well-preserved example of *L. ketleyanus*. However, *L*?



TEXT-FIG. 6.5. *Lepidocoleus*? *extraplax* sp. nov., BU 2804, Lower Elton Formation, Sedgley. A, *camera lucida* drawing of specimen, showing outer sclerites (OS), scale bar = 10 mm; B, incomplete anterior end of specimen, showing outer sclerites, x 8; C, mid-region of scleritome, showing hinge line with opposing inner sclerites, x 9; D, posterior of scleritome, x 7.5.

extraplax shows two characters that, even allowing for differences in preservation, indicate that it belongs to a separate taxon. Firstly, although most specimens of *L. ketleyanus*, including the type material, are incomplete or disarticulated, there is no evidence of outer sclerites having been present, whereas they are clearly seen in *L*? *extraplax* (Text-figs 6.3E, 6.5). Since lepidocoleids are normally biseriate, the presence of outer sclerites in *L*? *extraplax* is both distinctive and significant. Secondly, the number of sclerite series in *L*? *extraplax* is at least 65, the highest number known in any machaeridian. The growth of machaeridian scleritomes is discussed in detail below, but Adrain *et al*. (1991), Högström (1997) and Högström and Taylor (2001) all provided evidence to suggest that the number of series in a scleritome was fixed relatively early in ontogeny. Thus, if *L*? *extraplax* was conspecific with *L. ketleyanus*, one would expect the number of sclerite series in articulated specimens to be very similar, which is not the case. Additionally, the posterior margins of the inner sclerites of *L*? *extraplax* are almost straight, whereas those of *L. ketleyanus* are sigmoidal. Thus, *L*? *extraplax* is here interpreted as a different species, and, given the absence of outer sclerites in the type species of *Lepidocoleus*, may even belong to another genus.

6.6 MACHAERIDIAN AUTECOLOGY

Withers (1926) regarded machaeridians as sessile organisms, attached to the substrate by modified sclerites at the anterior end of the scleritome. However, much of the material he examined was incomplete, and it is now known that both anterior and posterior ends of the scleritome had modified sclerites. Thus, all recent workers (e.g. Jell 1979; Dzik 1986; Adrain et al. 1991; Högström and Taylor 2001) have interpreted machaeridians as unattached, vagile organisms, with the separate, imbricating sclerites protecting the dorsal surface whilst providing the flexibility required for multi-directional movement. The distinct differences between plumulitids, turrilepadids, and lepidocoleids in terms of the morphology and relative size of inner and outer sclerites (see Text-figs 6.1, 6.2) suggests that the three groups were ecologically distinct. Turrilepadids, for example, could not entirely close their scleritome (Adrain 1992; Högström 1997), whereas lepidocoleids were capable of bringing the ventral margins of opposing sclerites into contact with one another (Text-fig. 6.2). It is probable that machaeridians were primarily epifaunal, but the laterally flattened, flexible scleritome of taxa such as *Lepidocoleus*? *extraplax* suggests that some lepidocoleids may have been capable of ploughing through or burrowing into the sediment (Högström and Taylor 2001).

6.7 SCLERITE MORPHOLOGY AND GROWTH

Since no examples of machaeridian soft-tissue preservation are known, sclerite and scleritome morphology provide the only direct information on body shape and pattern of growth of the animals, and thus the sole means of investigating their biological affinities.

6.7.1 SURFACE STRUCTURE OF SCLERITES

The primary morphological features of the external surface of the sclerites are the rugae. These are raised linear structures that run sinuously from the medial to the lateral margin, concentric with the umbo (see e.g. Text-fig. 6.3B). Between the prominent rugae, smaller parallel striations may be visible also (see e.g. Adrain *et al*. 1991, pl. 2, fig. 10). On the medial and lateral margins of turrilepadid sclerites small spines are normally developed, but in many specimens they have been broken off (Adrain *et al*. 1991).

By comparison, the internal sclerite surface is relatively smooth. A narrow depression, termed the inner groove by Adrain *et al*. (1991), runs diagonally from the apex to the anterior margin, and a large muscle scar is visible in the centre of the anterior side of well-preserved sclerites (e.g. Högström 1997, text figs 4G, H). The topology of the internal surface varies between species, but this and other aspects of the external morphology cannot be properly understood without examination of the internal sclerite structure.

6.7.2 INTERNAL STRUCTURE OF SCLERITES

Withers (1926) was the first to examine the internal structure of machaeridian sclerites. He described the inner surface of all forms as having a reticular ornament and noted that, when broken, some lepidocoleid sclerites showed a 'distinct crystalline cleavage' (Withers 1926, p. 83). However, *Turrilepas wrightiana* and *Lepidocoleus ketleyanus* did not, having instead a granular structure in which patches of calcite went into extinction simultaneously. His sections were not figured and it was not until Bengtson (1977, 1978) that sclerite microstructure was described in detail.

By re-examination of some of Withers' (1926) material, along with investigation of new specimens from the Silurian of Gotland, Bengtson (1978) showed that machaeridian sclerites were two-layered. The inner layer comprised small, densely packed calcite elements arranged in undulating stacks parallel to the inner surface of the sclerite. The undulations within the inner layer corresponded to the surface texture (see Bengtson 1978, pl. 1, figs 2, 3, 14), which he described as granular rather than reticular. The structure of the outer layer was not identical in all material, but normally consisted of dense, apparently homogenous calcite with uniformly aligned crystals.

Dzik (1986, p. 124) described the granulated inner surfaces figured by Bengtson (1978) as representing 'tubercles and depressions' and suggested a relationship to the pseudoporous plate structure of the putative machaeridian *Carnicoleus gadzickii* Dzik, 1986. He also interpreted plumulitids as having different sclerite structure and growth pattern to turrilepadids and lepidocoleids, but did not include any supporting illustrations.

In their revision of the Turrilepadidae, Adrain *et al*. (1991) repeated most of Bengtson's (1977, 1978) findings, but also noted that some turrilepadid sclerites showed the same granular texture between the rugae on the exterior surface as on the internal surface. This led them to conclude that those sclerites were composed almost entirely of the inner layer, with the outer layer restricted to the rugae. This was seen only in silicified specimens, and the fine lines between the rugae of *Turrilepas modzalevskae* (Adrain *et al*. 1991, pl. 2, fig. 10) were interpreted by Adrain (1992) as part of the outer layer.

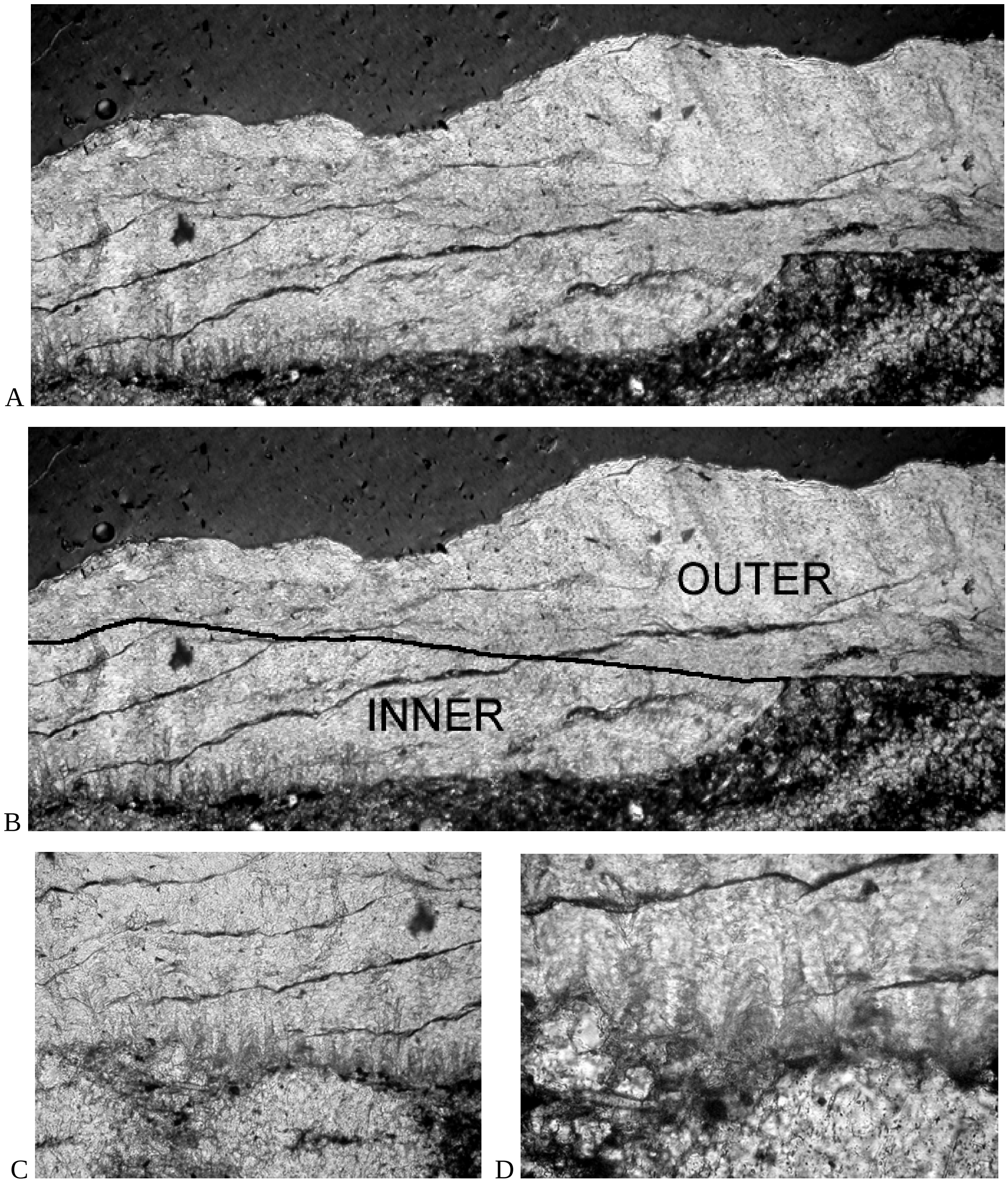
Hoare *et al*. (1996, fig. 2) showed the inner sclerite surface of some Permo-Carboniferous turrilepadids to be covered with tiny, rounded protuberances arranged in radial series across the sclerite. The pattern produced resembles the granular inner surface texture depicted by Bengtson (1978, pl. 1, figs 2, 3), but was termed papillate rather than granular by

Hoare *et al*. (1996). They also described vertical, tubular structures within the inner layer as possible canals connected to the papillae. Similar structures are seen in the inner layer of Silurian machaeridians (e.g. Bengtson 1978, pl. 2, fig. 9; also see below).

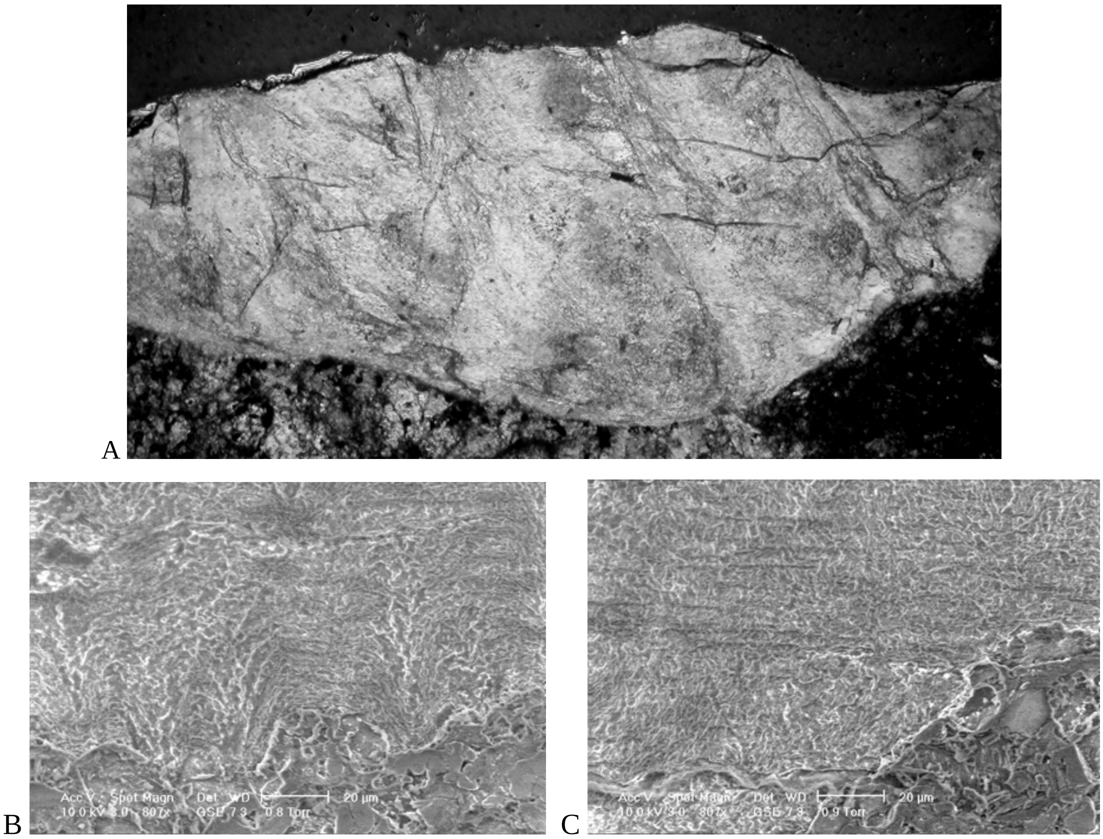
For this study, a disarticulated inner right sclerite (BU 3769; Text-fig. 6.3B) from the anterior of *Turrilepas wrightiana* was sectioned parallel to the longitudinal fold. The section confirms that the internal structure consists of two distinct layers, resembling the sections figured by Bengtson (1978), particularly the section of *Lepidocoleus* sp. a (Bengtson 1978, pl. 1, fig. 12). The inner layer of *T. wrightiana* is relatively thin, but shows stacked lamellae of small calcite crystals that undulate in a relatively angular fashion, giving the inner surface of the inner layer a herringbone pattern (Text-fig. 6.6B-D). Between the stacked, undulating elements of the inner layer are narrow, tubular structures that begin at, and run upwards perpendicular to, the inner surface (Text-figs 6.6C, D). They are seen most prominently at the posterior end of the inner layer, becoming less distinct towards the anterior, and appear to correspond to the canals of the inner layer described by Hoare *et al*. (1996). The outer layer of *T. wrightiana* is thicker than the inner layer, much more homogenous, and split by very thin, arcuate, sub-vertical increments of calcite (Text-fig. 6.7A), which divide it into separate, evenly spaced ‘blocks’. The calcite in each block shows a posterior-to-anterior extinction, with the equivalent regions of adjacent blocks going into extinction at the same time.

The sclerite is not entirely two-layered – the stacked, undulating lamellae of the inner layer are present only at the posterior of the sclerite before terminating abruptly approximately halfway along the inner surface (Text-figs 6.6A, B, 6.7C). A very similar morphology is seen in the section views of *Clarkeolepis clarkei* and *Turrilepas lepros*, as figured by Hoare *et al*. (1996, figs 2E, G), although the orientation of those sections was not specified, making direct comparison difficult. The outer layer of *T. wrightiana* is continuous across the sclerite, but thickens considerably towards the anterior, where the blocks of calcite are most clearly developed (Text-fig. 6.7A). This may, however, be an artefact of incomplete preservation – the outer layer appears to be at least partly broken off at the anterior end of the sclerite.

The contact between the inner and outer layers of *T. wrightiana* is transitional, with the stacked, undulating lamellae of the inner layer merging vertically into the more homogenous outer layer. However, the thin calcite increments that lie between each block of the outer layer are also present beneath the blocks, and coalesce to form a thin unit between the inner and outer layers. This unit continues beyond the termination of the inner layer before pinching out close to the anterior margin (see Text-figs 6.7A, 6.8). Again, the pattern is similar to that seen in *Lepidocoleus* sp. a (Bengtson 1978, pl. 1, fig. 12), where the strong undulation of the inner layer is restricted to the posterior of the sclerite, and the outer layer is underlain by a much more gently undulating series of lamellae towards the anterior.



TEXT-FIG. 6.6. BU 3769, *Turrilepas wrightiana* (de Koninck, 1857), Much Wenlock Limestone Formation, Dudley. A, Photomicrograph, and B, annotated photomicrograph of sclerite microstructure from posterior (left) towards anterior (right) of sclerite, showing inner layer overlain by outer layer and terminating towards anterior, outer layer developing calcite 'blocks' towards anterior, x 20; C, D, photomicrographs of narrow, tubular structures at interior surface of inner layer, C x 25, D x 40; All images oriented with exterior surface of sclerite towards top; taken using Nikon Coolpix digital camera attached to Zeiss Axioskop microscope with Nomarski prism.



TEXT-FIG. 6.7. BU 3769, *Turrilepas wrightiana* (de Koninck, 1857), Much Wenlock Limestone Formation, Dudley. A, Photomicrograph of sclerite structure at anterior region of sclerite, showing distinct 'blocks' of calcite; exterior surface at top of image, x 20; B, ESEM image of narrow, tubular structures at interior surface of inner layer; C, ESEM image of termination of inner layer beneath outer layer, outer layer having prominent parallel laminations.

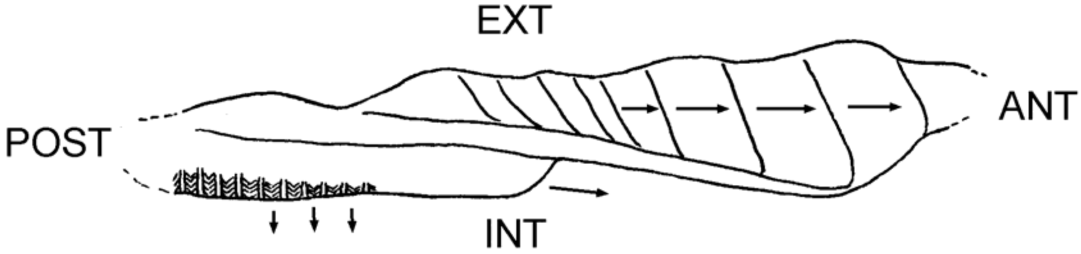
Examination of the sclerite of *T. wrightiana* under cathodoluminescence suggests that it was originally composed of low-magnesium calcite. Like all other groups from the Much Wenlock Limestone Formation that had originally low-magnesium calcite skeletons (e.g. brachiopods, bryozoans, trilobites), highly luminescent microdolomite inclusions are lacking.

These do, however, occur in the originally high-magnesium calcite echinoderm ossicles from the same formation (Wilmot and Fallick 1989). The original sclerite mineralogy cannot have been aragonite either, as there are no inclusion trails diagnostic of alteration from aragonite to low-magnesium calcite, and because originally aragonitic fossils in the Much Wenlock Limestone Formation are preserved in clear, neomorphic calcite.

6.7.3 SCLERITE GROWTH

The layered structure of machaeridian sclerites was used by Bengtson (1977, 1978) to propose the first hypothesis on how they grew. Using *Lepidocoleus* sp. a of Bengtson (1978) as an illustrative example, Bengtson (1977) showed that, at the contact between them, the inner and outer layers had an interfingering relationship. This led him to interpret the sclerites as having grown by accretion on the inside of the sclerite (forming the inner layer) and at the anterior margin (forming the outer layer) in a pattern of 'stepwise deposition of mineralized substance from an epithelium' (Bengtson 1978, p. 8), and that this pattern was directly analogous to the growth of skeletal elements in many invertebrates. Dzik (1986) agreed with this model in regard to the growth of turrilepadid and lepidocoleid sclerites, but suggested that sclerite mineralization in *Plumulites* 'probably occurred instantaneously over the entire [sclerite] surface' (Dzik 1986, p. 116). However, he reached this conclusion solely on the grounds that plumulutid sclerites were always thin-walled, and it was not accompanied by any images of microstructure.

The most detailed hypothesis of sclerite growth was produced by Adrain (1992), but his conclusions were reached through studies of surface morphology, coupled with the structural information provided by Bengtson (1977, 1978), and no sections of internal structure were described or illustrated. Fine lines radiating from the umbo on the external surface of some sclerites (e.g. Adrain 1992, figs 4A, F) led him to interpret the inner layer as having been laid down as distinct elements in a radial pattern rather than as lamellae. Thus, the rugae (and parallel striations running between them) represented the growth stages of the outer layer, whilst the series of fine lines cutting obliquely or perpendicularly across them were the surface expression of the elements of the inner layer. He rejected Dzik's (1986) hypothesis that plumulitid sclerites were mineralized in a single event, arguing instead that larger sclerites had a larger number of rugae, indicating a similar process of incremental growth to that seen in turrilepadids and lepidocoleids. That process was described by Adrain (1992, p. 26) as follows: the outer layer was deposited at the same time as the inner layer, forming the external sclerite surface and then being separated from the secreting tissue. The inner layer, meanwhile, remained in contact with the soft-parts and could be reshaped by 'further deposition and possibly resorption of calcite elements' (Adrain 1992, p. 26). This later deposition on, or resorption of, the inner layer was proposed because the inner surface of some lepidocoleid sclerites (see e.g. Adrain 1992, fig. 4G) was not entirely covered by the characteristic granular/papillate texture. The anterior portion of the sclerites showed only the muscle scar and a series of lines running parallel to the anterior, accreting margin, and Adrain (1992) regarded the inner layer as having been deposited there but then obscured. The preservation of the inner layer on the posterior part of the sclerite was the result of that end being 'shifted atop the anterior portion of the next sclerite in the series' (Adrain 1992, p. 26)



TEXT-FIG. 6.8. Growth model of machaeridian sclerites, based upon BU 3769, *Turrilepas wrightiana* (de Koninck, 1857); ANT, anterior of sclerite; EXT, external sclerite surface; INT, internal sclerite surface; POST, posterior of sclerite. The calcite ‘blocks’ of the outer layer are added at the sclerite anterior, giving the anterior-to-posterior growth direction indicated by the horizontal arrows, with the stacked, undulating elements of the inner layer accreting on the internal surface.

as the machaeridian grew, and the sclerites began to imbricate. Once the posterior margin was resting on top of the adjacent sclerite it was not connected to any soft tissue and its structure could not be altered. A tripartite pattern of growth was thus outlined – a fixed outer layer, an original inner layer of radiating elements, and a later inner layer of non-radiating or resorbed radiating elements restricted to the anterior of the sclerite.

This is not supported by the internal structures seen in *Turrilepas wrightiana*. The distinct inner layer of tubes and stacked calcite elements is absent from the anterior of the sclerite (see Text-figs 6.6, 6.7) and, rather than having been entirely resorbed, it is more parsimonious to regard it as never having been deposited. The anterior of the inner surface bears the muscle scar in well-preserved sclerites (see e.g. Högström 1997, text figs 4G, H) and would have been in contact with the soft tissue. Rather than the inner and outer layers being deposited synchronously, only for the inner layer to be resorbed at the anterior of the sclerite, it is more plausible that the outer layer was deposited first and the inner layer later (Text-fig. 6.8). This would explain the larger increments of homogenous calcite separated by linear structures (?growth lines) in the outer layer as having been deposited in ‘blocks’, whereas the series of stacked, undulating elements that form the inner layer were added in much smaller increments (Text-fig. 6.8).

The overall growth pattern of an individual sclerite was thus one of increments being added around the anterior and ventral margins of the sclerite, giving a posterior to anterior direction of growth (Text-fig. 6.8). The outer layer was deposited at the sclerite perimeter as a continuous block underlain by a thin lamella of calcite, and the inner layer as radiating series of calcite elements separated by thin tubes, the external expression of which is the granular/papillate texture of the inner surface. The inner layer was not deposited beneath the most recent block of the outer layer, however, but under older blocks towards the centre of the sclerite.

6.7.4 SCLERITOME GROWTH

Each machaeridian sclerite grew by marginal accretion, with rugae deposited at regular intervals. Thus, in articulated sclerite assemblages representing the original scleritome, the number and spacing of rugae enables the overall growth pattern of the animal to be determined. Adrain *et al*. (1991) noted that, in specimens of *Turrilepas wrightiana*, every sclerite in an assemblage had a similar number of rugae, leading them to conclude that 'the scleritome very likely had a fixed number of segments…with rugae deposited one at a time, at the same time for all sclerites in the assemblage' (Adrain *et al*. 1991, p. 648). The specimens of *T. wrightiana* examined in this study support that hypothesis – BU 375 (Text-fig. 6.3A), for example, has approximately 28 rugae per sclerite – although Högström (1997) added the qualification that aberrant growth patterns on some sclerites (e.g. *Turrilepas* sp. A, Högström 1997, pl. 1, figs 5, 6) indicated that later interpolation of sclerites might have been possible.

More recently, both Högström (2000) and Högström and Taylor (2001) provided evidence that the synchronous deposition of rugae across the entire scleritome also occurred in lepidocoleids. Firstly, it was observed in *Lepidocoleus* cf. *britannicus* (Högström 2000, fig. 2F) that the rugae of adjacent sclerites all showed a pattern of becoming crowded close to the accreting margin, which was interpreted as a feature of maturity seen in other taxa that grew skeletons by marginal accretion, such as gastropods and ammonites. Secondly, in their study of *L. sarlei*, Högström and Taylor (2001) were able to trace distinctive rugae across some scleritomes, showing that they occurred at the same position in different sclerites (see e.g. Högström and Taylor 2001, pl. 2, fig. 3). Although it was not possible to identify the same increment across an entire scleritome (they tended to be clearly identifiable only on sclerites of the mid-body region), Högström and Taylor (2001) also thought it probable that the number of sclerite sets within a scleritome was fixed early in ontogeny. However, although complete specimens of *L. sarlei* normally have 14 sclerite sets, an example with only 13 sets was described, leading Högström and Taylor (2001, p. 126) to suggest that the number of sets might vary intraspecifically, or that extra sclerite sets could have been added during ontogeny. By way of comparison, seven of the eight shell plates of polyplacophorans form simultaneously, and are present two days after metamorphosis (Wanninger and Haszprunar 2002*a*, fig. 1D), whereas the final plate is added separately a short time later. However, in adult chitons, the eighth plate cannot be readily distinguished as having fewer growth increments present. It is thus possible that sclerites added later in machaeridian ontogeny would not have noticeably fewer rugae.

In machaeridians with a high number of sclerite sets, it becomes less probable that all were generated simultaneously. At least sixty-five sets, the largest number known in any machaeridian, are present in BU 2804, the only specimen of *Lepidocoleus*? *extraplax* (Text-figs 6.3E, 6.5) If all sclerites – inner and outer series on both sides of the scleritome – began growing synchronously, the juvenile machaeridian would have had a minimum of 260 tiny plates arranged along an extremely slender, elongate body. It is more likely that the original number of sets was less than 65, with later addition of sets as the machaeridian grew. However, although the rugae of BU 2804 are far less prominent than in *T. wrightiana* and *L. sarlei*, making correlation of increments across the scleritome difficult, none of the sclerites have an obviously reduced number of rugae that could be taken as evidence of their having been added later in ontogeny.

The evidence outlined above supports the hypothesis that the number of sclerite sets in taxa such as *T. wrightiana* was fixed relatively early in development. Whether the markedly larger number of sclerite sets in some lepidocoleids is indicative of a slightly different developmental pattern, with the number being fixed later in ontogeny, remains to be answered. The correlation of growth increments in *L. sarlei* by Högström and Taylor (2001), however, shows that the pattern of scleritome growth is closely similar in both turrilepadids and lepidocoleids, although in the latter family the full growth history may only be traceable in the sclerites of the mid-body region.

6.7.5 MACHAERIDIAN SOFT-PARTS

The muscle scar present on well-preserved sclerites provides the only unequivocal information on the arrangement of machaeridian soft tissues. Withers (1926) was the first author to examine the musculature, showing that it was probable every sclerite had a scar, indicating that the muscles were serially repeated into the same number of sets as the sclerites. Jell (1979, p. 256), however, thought that ‘attachment of the sclerites to the soft parts of [*Plumulites*]…was probably not by muscles’, which would suggest a different soft-tissue arrangement to that of turrilepadids and lepidocoleids. This was not followed by Dzik (1986, fig. 1), whose reconstruction of *Plumulites* showed muscles as having been present, although it is unclear what evidence this was based upon. Adrain *et al*. (1991) regarded plumulitid sclerites as having muscle scars, but stated that they were rarely preserved.

The most detailed appraisal of machaeridian soft-parts was by Högström (1997) and Högström and Taylor (2001). Högström (1997) thought it likely that the sclerite muscles were adductors, used to partly or fully enclose the animal within its scleritome. The absence of a set of counteractive muscles to open the scleritome led her to suggest (Högström 1997, pp. 825, 826) that hydrostatic pressure was probably used instead, and that the machaeridian soft body might have been divided into segments, giving greater control over the opening and closing of the scleritome. This was developed by Högström and Taylor (2001), who compared lepidocoleids with millipedes and chitons in terms of the musculature and soft-part organization required for enrolment, concluding that they were more like the former than the latter. Thus, they argued that there were ‘strong reasons for regarding lepidocoleids as ‘segmented’, with muscle attachments at segment boundaries or on structures similar to the tendons of millipedes’ (Högström and Taylor 2001, p. 125).

6.8 BIOLOGICAL AFFINITIES

Machaeridians are extinct and problematical. However, as with all Palaeozoic Problematica, they must be more closely related to some extant taxa than others and should not simply be placed in an extinct ‘phylum’ without consideration of their relationship to living organisms (Budd and Jensen 2000). As outlined in section 6.1, there have been numerous suggestions concerning the affinities of machaeridians, but many were based on general, often superficial, morphological similarities with extant or other fossil taxa, rather than on an understanding of machaeridian biology. The morphology, structure and growth of sclerites described above, coupled with their arrangement within the scleritome, enables a more comprehensive assessment of the systematic position of machaeridians to be made.

6.8.1 COMPARISONS WITH OTHER TAXA

Machaeridians were bilaterally symmetrical metazoans with elongate bodies covered by serially repeated sets of sclerites. This serialization of the sclerites has led to machaeridians being referred to as ‘strictly metameric’ (Adrain 1992, p. 20) and ‘segmented’ (Högström and Taylor 2001, p. 125). A distinction must be made however between metameric segmentation of the body, as seen in annelids and arthropods, and serial repetition of external hard parts. Serialization of skeletal elements does not by definition mean that the animal was metameric, and applying such terms to machaeridians without precise knowledge of the organization of soft tissues should be avoided. The machaeridian body could have been metamerically segmented, but until specimens with preserved soft-parts resolve that question, the pattern of sclerite arrangement should be referred to as serialization or serial repetition.

6.8.1.1 Deuterostomes

Machaeridians had a soft body enclosed by a skeleton formed of interconnected calcitic elements. Within the deuterostomes, the only group with a similar suite of characters is the echinoderms. However, echinoderm ossicles are composed of high-magnesium calcite and have a characteristic stereom structure, and new increments of calcite are deposited in optical continuity with existing ones, giving the ossicles the optical properties of single calcite crystals (Smith 1990). Additionally, the echinoderm skeleton is mesodermal – the ossicles originate from, and are embedded within, the dermis – rather than being ectodermal. Machaeridian sclerites were not formed of high-magnesium calcite, have a heterogenous, layered crystallographic structure, and appear to have been deposited ectodermally, with soft tissue only present beneath the sclerite. Thus, as originally identified by Bengtson (1977, 1978), they are fundamentally unlike echinoderms and must belong to the protostomes.

6.8.1.2 Protostomes

Based on morphological and molecular data, most recent authors (e.g. Aguinaldo and Lake 1998; Gavey and Schmidt-Rhaesa 1998; Peterson and Eernisse 2001; Balavoine *et al*. 2002; Mallatt and Winchell 2002; but see Schram 1991; Neilsen *et al*. 1996; Scholtz 2002 for alternative views) divide protostomes into two main clades. The Ecdysozoa include all taxa that accommodate increases in body size by moulting (e.g. arthropods, priapulids and nematodes), whereas the Lophotrochozoa unite non-moulting forms with spiral cleavage (e.g. annelids, molluscs and brachiopods). The exact relationships of organisms within each clade remain contentious, but the most comprehensive phylogenetic analysis, combining morphological, developmental and molecular (18S rDNA) data, was produced by Peterson and Eernisse (2001) and is followed here.

The structure of *Turrilepas wrightiana*, coupled with the evidence of previous workers, confirms that the machaeridian scleritome grew by the marginal addition of calcite increments to pre-existing plates (Bengtson 1977, 1978; Adrain 1992). It is likely that the number of sclerites was fixed early in ontogeny (Adrain *et al*. 1991; Högström and Taylor 2001), although some machaeridians may have added sclerites later in growth (see Högström and Taylor 2001, pp. 125, 126; section 6.7.4). Nonetheless, there is no evidence that machaeridians moulted. All arthropods, including forms such as cirripedes and ostracodes that are entirely enclosed by calcitic valves, shed their exoskeletons periodically rather than growing by marginal accretion (Dalingwater *et al*. 1993), so machaeridians cannot belong to the Arthropoda. Interpretations of their being closely related either to cirripedes (Woodward 1865) or *Anomalocaris* (Dzik 1993) can thus be discounted as, for the same reasons, can the possibility that they belong to any other group of ecdysozoans.

Of the taxa placed in the Lophotrochozoa by the phylogenetic analysis of Peterson and Eernisse (2001), molluscs and annelids are the two with which machaeridians have been most persistently allied. Adrain (1992) also compared the marginal accretion of machaeridian sclerites with that of brachiopods, whilst Hoare *et al*. (1996) noted that the tubular morphology of the inner layer shared some similarities with structures seen in mickwitziids, probable stem-group brachiopods (McMenamin 1992; Skovsted and Holmer 2003). There are many other lophotrochozoan groups, however, that have elongate or vermiform bodies with distinct skeletal elements and these must also be considered. Phoronids (horseshoe worms) are the sister-group of brachiopods (Peterson and Eernisse 2001), but have tubes formed of chitin, not separate calcite plates, and their bodies are not entirely enclosed – the mouth remains open at one end of the body. Ectoprocts and entoprocts are colonial, sessile and their skeletons are not formed of separate plates, whilst nemerteans are entirely soft-bodied except for oral barbs (stylets) of calcium phosphate. Some sipunculids have a calcified anal plate, and it has been suggested that the problematical Palaeozoic organisms hyoliths are sipunculids in which the soft body was entirely covered by a calcite shell. This relationship is doubtful however (see Pojeta 1987*b*, pp. 436–444), and no sipunculids are known that have skeletons of separate sclerites. Other lophotrochozoan groups that contain vermiform taxa, such as echiurans, rotifers and gnathostomulids, are entirely soft-bodied and thus cannot be directly compared with machaeridians.

6.8.1.3 Machaeridians as brachiopods

Skeletons composed of individual calcite plates that grew by marginal accretion are known in two major groups of extant lophotrochozoans – molluscs and brachiopods. All crown-group brachiopods have two valves, normally composed of calcium carbonate, that entirely enclose the soft parts, with the valves normally described as covering the dorsal and ventral surfaces of the brachiopod. The hinge is thus posterior and the commissure anterior. Recent work by Cohen *et al*. (2003), however, has indicated that the valves are better interpreted as anterior and posterior, thus making the hinge dorsal and the commissure ventral. Irrespective of which hypothesis is correct, the orientation is quite unlike that seen in the machaeridian scleritome. There, the median line along which opposing series of sclerites meet is dorsal and the margin opposite ventral, with the sclerites imbricating posteriorly in lateral rows. Even allowing for the disparity in number of skeletal elements, the plane running from the dorsal to the ventral surface of machaeridians, parallel to the sclerite margins, is at 90º to the equivalent plane in brachiopods. Additionally, the lophopohorate feeding system of brachiopods is incompatible with a vagile mode of life. Machaeridians cannot therefore be regarded as closely related to crown-group brachiopods. The possibility of them being members of the stem-group Brachiopoda is discussed below.

6.8.1.4 Machaeridians as annelids

By virtue of their vermiform shape and serially repeated sclerites, it is easy to imagine machaeridians as armoured annelids. Within the Annelida, dorsal elytra are present in the polychaetes and have been interpreted as analogous or homologous to the sclerites of machaeridians (see e.g. Jell 1979; Dzik 1986). However, polychaete elytra are not mineralized and do not grow by marginal accretion (Sutton *et al.*, in press), and never form a skeleton that wholly encloses the body. Since machaeridian sclerites are biomineralized and grew by marginal accretion, only the serialization of the scleritome is comparable with annelids. As noted above, the nature of machaeridian serialization is not known and cannot be regarded as metameric without knowledge of soft-parts. Moreover, the scleritome of lepidocoleids, for example, is functionally incompatible with the parapodial locomotion of polychaetes (Dzik 1986, p. 129). Combined with the differences in structure, morphology and growth of machaeridian sclerites and polychaete elytra, this indicates that a close relationship between the two groups is improbable.

6.8.2 COMPARISONS WITH OTHER PROBLEMATICA

In addition to machaeridians, numerous groups of problematical organisms with elongate, scale-, spicule- or plate-covered bodies have been described from the Palaeozoic. A review of all such taxa is beyond the scope of this study, but certain groups have been proposed as closely related to machaeridians. For example, Bengtson (1970) discussed the similarities between machaeridians and mitrosagophorans (tommotiids and tannuolinids), leading Jell (1979) to conclude that they were probably more closely related to each other than any other group, whilst Dzik (1986) united the five families included in those two groups with hercolepadids, lapworthellids, siphogonuchitids and wiwaxiids in a radically amended Machaeridia. Adrain (1992) rejected the possibility that machaeridians were closely related to any of the other groups suggested by Bengtson (1970), Jell (1979) and Dzik (1986), but, in the light of subsequent work, those conclusions need to be reassessed.

Few of the other Problematica are known from articulated material, but two exceptions are the Cambrian genera *Halkieria* and *Wiwaxia*. Both taxa are broadly morphologically similar to machaeridians, being elongate organisms with a dorsal skeleton composed of sclerites arranged in rows down the body. However, wiwaxiid sclerites were hollow and unmineralized, and were probably moulted periodically (Bengtson and Conway Morris 1984), making them quite unlike those of machaeridians. Structural similarities between wiwaxiid sclerites and the dorsal setae of polychaete annelids (Butterfield 1990; Conway Morris and Peel 1995), led Butterfield (1990, 1994) to interpret *Wiwaxia* as a member of the extant order Phyllodocida, and although this has been questioned (see e.g. Conway Morris and Peel 1995), a close relationship between machaeridians and wiwaxiids cannot be supported.

Bengtson and Conway Morris (1984) showed that the sclerites of *Halkieria* were mineralized, but otherwise of similar morphology, structure and arrangement to those of *Wiwaxia*, and that they were ‘rigid structures which could not grow once formed’ (Bengtson and Conway Morris 1984, p. 318; see also Conway Morris and Peel 1995). As with wiwaxiids, this makes the sclerites quite unlike those of machaeridians, but halkieriids also have two shells on the dorsal, sclerite-bearing surface, one at the posterior and one at the anterior of the body. These shells grew by marginal accretion (Conway Morris and Peel 1995) and are thus at least broadly comparable with machaeridian sclerites. However, the presence of just two marginally accreting skeletal elements in halkieriids is fundamentally dissimilar to the multi-element skeleton of machaeridians, whilst the line of symmetry separating the halkieriid shells, which are positioned at the anterior and posterior of the scleritome, is at 90 degrees to separating the series in a machaeridian scleritome. Many authors (e.g. Conway Morris and Peel 1995; Williams and Holmer 2002; Holmer *et al*. 2002; Cohen *et al*. 2003) regard *Halkieria* as a stem-group brachiopod, giving rise to taxa such as *Micrina* and *Mickwitzia* through a reduction of the dorsal skeleton to just the marginally accreting shells, and a transverse folding of the central body region (Williams and Holmer 2002). If this phylogenetic hypothesis is correct, it is difficult to support a close relationship of machaeridians to halkieriids, but some authors (e.g. Bengtson 1992; Runnegar 2002) have argued that *Halkieria* is more closely related to polyplacophoran molluscs, with an implied increase in the number of marginally accreting shell plates. On that basis, machaeridians could be derived from halkieriids, although the dramatic transformation required in number and arrangement of accreting skeletal elements makes it improbable.

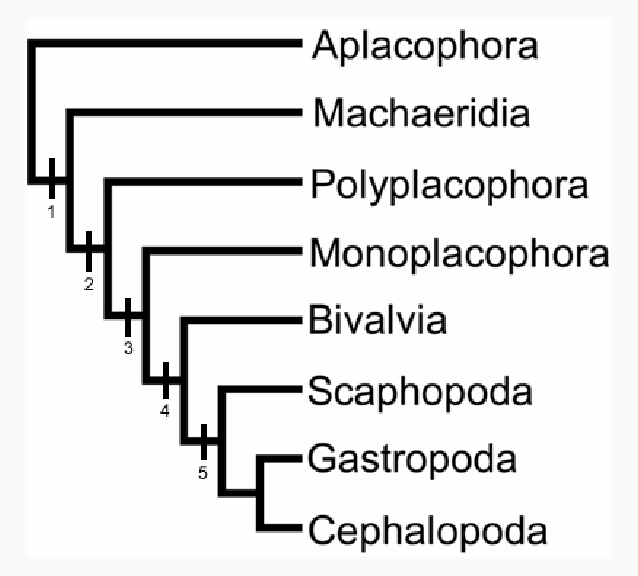
Other problematical taxa in which marginally accreting skeletal elements are known include tommotiids and tannuolinids (Bengtson 1970), *Maikhanella* (Bengtson 1992) and *Ocruranus* and *Eohalobia* (Siegmund 1997). An absence of articulated material makes it difficult to compare them with machaeridians, but Bengtson (1970) described tommotiids and tannuolinids as occurring in symmetrical pairs of sclerites of two types, possibly homologous to the inner and outer sclerites of quadriseriate machaeridians. However, their lamellar structure and phosphatic composition makes them quite unlike machaeridian sclerites (Bengtson 1970; Adrain 1992), and Williams and Holmer (2002) suggested that the different symmetries of tannuolinid sclerites might represent sexual dimorphism, rather than a biseriate or quadriseriate scleritome.

A closer comparison can be made with *Acaenoplax hayae* Sutton *et al*., 2001*a*, from the Herefordshire Lagerstätte (Silurian: Wenlock) of England. Exceptionally preserved, articulated specimens show that *Acaenoplax* was a small, elongate, worm-like organism with an external skeleton of serially repeated elements. The most prominent of these are the seven dorsal valves. Growth lines led Sutton *et al*. (2001*a*) to interpret the valves as having grown by marginal accretion, and, although the fossils are preserved in void-filling calcite, the original valve mineralogy was inferred to have been aragonite. *Acaenoplax* was diagnosed as a plated aplacophoran mollusc (Sutton *et al*. 2001*a*), but Steiner and Salvini-Plawen (2001, p. 601) argued that there was 'no evidence' the valves of *Acaenoplax* were mineralized, and concluded that the animal was an aberrant polychaete annelid. Sutton *et al*. (2001*b*, in press) rejected this, stating that the valves were undoubtedly aragonitic and grew by marginal accretion, and that *Acaenoplax* was a mollusc with both aplacophoran and polyplacophoran characters. There are distinct differences between *Acaenoplax* and machaeridians, notably that the dorsal valves of *Acaenoplax* are arranged in a single row and are not imbricated, and that spicules were also present, but if Sutton *et al*. (2001*a*, *b*, in press) are correct and the valves grew by marginal accretion of calcium carbonate, then there are closer similarities between the two groups than between machaeridians and any of the other Problematica discussed above.

6.8.3 MACHAERIDIANS AS MOLLUSCS

Extant molluscs display a highly diverse range of morphologies, but are the only crown-group lophotrochozoans to contain elongate, slug-like animals with a dorsal skeleton of serially repeated, imbricating calcitic skeletal elements that grow by marginal accretion – the Polyplacophora, or chitons. The possibility that they are the closest living relatives of machaeridians has been considered ever since the first species of machaeridian was described as *Chiton wrightianus* by de Koninck (1857).

Extant polyplacophorans have eight shell plates arranged in a single row along the body, rather than the two or four series of up to sixty or more sclerites present in machaeridians. However, the (dorsoventral) shell muscles of polyplacophorans are arranged in two sets, one on each side of every plate, giving a layout similar to that of biseriate machaeridians. Furthermore, the series of eight single plates, each with two sets of muscles, is 'clearly a secondary condition' (Wanninger and Haszprunar 2002*a*, p. 111), deriving from an originally much higher number of series. Aplacophorans are the most primitive living molluscs, and Solenogastres, one of the two extant classes, show an 'indefinitely serial arrangement' of their dorsoventral musculature (Salvini-Plawen 1985, p. 121), whilst recent ontogenetic studies (e.g. Haszprunar and Wanninger 2000, Wanninger and Haszprunar 2002*a*; Friedrich *et al*. 2002) have shown that, up to the completion of metamorphosis, polyplacophorans also possess a much larger number of sets of shell muscles. Only after metamorphosis do they reduce to seven (subsequently eight) sets attaching to either side of each plate. Thus, the high number of serially repeated machaeridian sclerites and muscle sets could represent a molluscan symplesiomorphy.



TEXT-FIG. 6.9. Probable phylogenetic position of machaeridians with respect to extant molluscan clades. The primitive state, represented by the Aplacophora, is a spicule-bearing, worm-like body shape, with numerous, serially repeated dorso-ventral muscle sets. Derived character states are as follows: 1, acquisition of mineralized sclerites; 2, sclerites and dorso-ventral muscle sets reduced to eight; 3, reduction of sclerites to single shell; 4, reduction of dorso-ventral muscle sets to fewer than eight (with autapomorphic development of bivalved shell in Bivalvia); 5, reduction of dorso-ventral muscle sets to one or two, with acquisition of cephalic retractor muscles.

Aplacophorans do not have shells, their skeleton being composed solely of spicules, and this is also regarded as the primitive state in molluscs (Text-fig. 6.9). The most advanced molluscs, including bivalves, cephalopods and gastropods, belong to the Conchifera, in which the soft parts are enclosed in a single shell (the two shells of bivalves being a later apomorphy). The simplest conchiferans are the Monoplacophora, which retain the eight-part shell musculature of polyplacophorans, attached to a single cap-shaped valve. This retention of serially repeated shell muscles in monoplacophorans suggests that the evolutionary history of molluscs is one of spicule-bearing forms (aplacophorans) giving rise to plated forms (polyplacophorans), which in turn gave rise to single-shelled taxa (conchiferans), accompanied by a gradual reduction in the number of sets of dorsoventral shell muscles, from greater than eight in aplacophorans, to eight in polyplacophorans and monoplacophorans, between three and eight in bivalves, and down to one or two in scaphopods, gastropods and cephalopods (Wanninger and Haszprunar 2002*b*, fig. 5; see Text-fig. 6.9).

Machaeridian sclerites increased in size by the addition of calcite to the antero-lateral accreting margin, giving an overall pattern of posterior-to-anterior growth. Baxter and Jones (1981) showed that polyplacophoran valves grow in the same way, with increments of calcium carbonate being added to the anterior and lateral edges, except for the tail plate, which adds new shell material ‘around the entire [valve] perimeter’ (Baxter and Jones 1981, p. 74). Furthermore, the ventral surface of polyplacophoran valves is ‘penetrated by numerous holes…which are the openings of the aesthete channels’ (Baxter and Jones 1981, p. 69). Aesthetes have a sensory and secretory function (Reindl *et al*. 1997) and form a system unique within the Mollusca (Baxter and Jones 1981). Although their function is unknown, the tubular structures seen in the inner layer of machaeridian sclerites bear a notable morphological similarity to the aesthete channels, raising the possibility that they are homologous.

Regardless of the precise systematic position of *Acaenoplax hayae* and its relationship to machaeridians, discussed above, there is no doubt that the serially repeated sclerites of machaeridians were mineralized and grew by marginal accretion, suggesting a much stronger affinity to molluscs than any other extant invertebrate group. Whether machaeridians are to be regarded as stem-group or crown-group molluscs hinges on whether aplacophorans represent the basal molluscan clade, or whether their lack of plates or shells is a secondary feature. If aplacophorans are basal, followed by polyplacophorans, and the acquisition of a dorsal skeleton of individual plates of calcium carbonate growing by marginal accretion is the step that derives the latter from the former, then machaeridians can be considered as crown-group molluscs, derived relative to the aplacophorans, but primitive with respect to the polyplacophorans. If aplacophorans have secondarily lost their skeletal plates, however, then the machaeridians must be primitive relative to both groups, making them stem-group molluscs. The more parsimonious model is the former, with aplacophorans as primitively shell-less, such that machaeridians are interpreted here as the sister group of Polyplacophora + Conchifera (Text-fig. 6.9).