Evolution and development of the brachiopod shell

Edited by *FERNANDO* **ALVAREZ** *and* **GORDON B. CURRY**

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Cover: *Argyrotheca* sp., dorsal view of a small punctate rhynchonelliformean brachiopod; Recent, Lara Beach, Akamas Peninsula, Cyprus, NHM ZB 4634 (from Taylor *et al.* in this volume).

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with 124 text-figures, 30 plates and 23 tables

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A REVIEW OF CRURAL TYPES, THEIR RELATIONSHIPS TO SHELL MICROSTRUCTURE, AND SIGNIFICANCE AMONG POST-PALAEOZOIC RHYNCHONELLIDA

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Abstract: This overview deals with a few key morphological features that appear crucial to the advancement of knowledge about relationships between macromorphology and micromorphology of the rhynchonellide brachiopod shell. Relevant aspects that may hinder description, comparison and/or interpretation of morphological skeletal structures of rhynchonellides when studied by means of serial grinding techniques are briefly reviewed. First, the types of crura, traditionally regarded of paramount taxonomic importance, are currently placed into four main cognate groups: septifal, arcual, raducal and ensimergal. Constituent types are characterized, and likely transformation series among them are also outlined. The value of crural types and their groupings within the systematic and evolutionary framework currently applied to post-Palaeozoic Rhynchonellida is corroborated, as is the significant role of heterochronic processes in the development of evolutionary novelties or in the recovery from a severe biotic crisis. Therefore, further studies of ontogenetic development of crura should be encouraged. Second, the main kinds of microstructural patterns of the secondary shell layer as seen in cross section are summarized and illustrated. The leptinoid pattern, typically displaying finer, anisometric fibres with anvil-like or halberd-like outline is contrasted with the eurinoid type, characteristically having coarser, isometric fibres with predominantly diamond-shaped cross section. A close correspondence established between leptinoid shell microstructure and superfamilies with crura of the raducal and ensimergal groups (such as hemithiridoids, rhynchonelloids, rhynchotrematoids, dimerelloids) on the one hand, and between eurinoid shell pattern and superfamilies with crura of the septifal and arcual groups (e.g. pugnacoids, wellerelloids, norelloids) on the other vindicates the prevailing classificatory scheme. Finally, some broad variations of the basic configurations in mantle canal patterns are outlined, confirming the merit of jointly analysing multiple morphological characters and of applying a variety of techniques. All these may lead towards a stronger, more stable and predictive classification of Rhynchonellida in which there is potential for reconsidering the suitability of proper subordinal divisions.

Key words: Brachiopoda, Rhynchonellida, crura, shell microstructure, mantle canals, systematics, heterochrony.

THIS review stems from the long-term involvement of one of us (MOM) with the revision of the 'Treatise on invertebrate paleontology, Part H' as well as from collaborative work between both authors that synergistically sprung from International Brachiopod Congresses (especially The Millennium Congress, in London).

The main objective of this essay is to explore in more detail some of our lines of research on various shell characters which have important implications for improving current views on the basic evolutionary stocks and high-level systematic arrangement of post-Palaeozoic Rhynchonellida. For that purpose, our respective experiences on Mesozoic–Cainozoic representatives of the order are merged in order to shed new light on the choice of morphological features worthy of further investigation (Manceñido and Owen 2001, p. 197; Manceñido *et al.* 2007, pp. 2727–2730; Motchurova-Dekova *et al.* 2008, p. 231). Some of the most recent results obtained from samples prepared and examined by NMD are also incorporated.

MATERIAL AND TERMINOLOGY

Terminology herein adopted (basically in accordance with the 'Treatise' policies and recommendations) is

mnemonic, euphonious, and eschews terms with an implicit systematic label. Also, as the succinct format of the '*Treatise*' style did not allow for detailed etymological explanations, this seems a good place for including them, where appropriate. Although many of the ideas currently expressed may be traced to individual earlier papers by us, the particular blend and upgrading are certainly novel for the advancement of knowledge about relationships between macromorphology and micromorphology of the rhynchonellide shell.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; CGS, Czech Geological Survey, Prague, Czech Republic; GI BAS, Geological Institute, Bulgarian Academy of Sciences; IGiG, Institute of Geology and Geophysics, Siberian Branch, Academy of Science, Akademgorodok, Russia; NHMM, Geological Museum of Copenhagen University, Copenhagen, Denmark; NMNHS, National Museum of Natural History Sofia, Bulgaria; NRM, The Swedish Museum of Natural History, Stockholm; PMNUF, Paleontological Museum at the University of Naples Federico II; UMUT, University Museum of the University of Tokyo, Tokyo, Japan; USNM, United States National Museum, Washington DC, USA.

CONTEXT AND METHODOLOGICAL SETTING

Prior to the main discussion, it is appropriate to comment how certain factors arising from technical practices or preservational state may influence the proper description and interpretation of relevant morphological skeletal structures. In synonymizing various nominal genera, as also in oversplitting, a certain amount of subjectivity is always involved. Yet, it is still true that 'almost every morphological character, considered apart from [all the] others, can be shown to be unsatisfactory as a basis for classification in one or more groups' (Ager 1965a, p. H598). Thus, a combination of evidence from several key features is to be preferred for attaining a more objective taxonomy. Although the number of rhynchonellide genera which are fairly adequately described (both externally and internally) has increased tremendously over the last 30–40 years, the overall picture is not yet fully satisfactory and the number of Mesozoic species awaiting a reliable generic allocation is still excessive.

Access to morphological information about brachiopod shell interiors, in particular, differs depending upon whether one is dealing with internal moulds (natural, decalcified or burnt and scraped), carefully excavated valves, acid-developed silicified specimens, or serially sectioned shells. What is common for extant and Tertiary faunas may not be so for Mesozoic and even less for Palaeozoic forms, and data derived from different methods of examination are not always easy to interpret in mutually compatible terms (cf. Brunton *et al.* 1996, p. 10; Savage *et al.* 2002a, p. 1027; Alvarez and Brunton 2008, p. 59; Motchurova-Dekova *et al.* 2008, p. 238).

Moreover, information obtained from serial grinding techniques alone, reputedly yielding very accurate, quantifiable results amenable to computerized 3-D reconstructions, has been proven to pose certain difficulties when comparing independent sets of sections, particularly if prepared by different (but sometimes even by the same) practitioners (cf. Williams 2002, pp. xxvi–xxvii). One of the most frequent risks stems from the axial tilt effect, namely the appearance of internal structures in sections being highly dependent upon the relative orientation of the sectioning plane. Though development of apparatuses that ensure successive parallel grinding surfaces has been a fundamental breakthrough towards standardization, the sheer fact that the growth axis of each valve is a variation of a geometrical logarithmic spiral (McGhee 1980, pp. 58–64) implies that traditional 'transverse' sections cannot be strictly perpendicular to either valve growth axis, but rather to some conventional, roughly antero-posterior, straight line (cf. Burri 1957, fig. 12). At least two alternative recommended procedures are currently used: perpendicular to the posterior portion of the lateral commissure (Ager 1956, p. v, 1965b, p. 215) or to the maximum shell length (e.g. Sandy 1986, p. 144, 1989, p. 147). These are seldom coincident (save for low-gibbosity, equibiconvex, rectimarginate, lenticular shells), and even then there are often further accidental errors that may be inadvertently introduced during mounting.

As pointed out by Burri (1957, fig. 16), Rousselle (1965, figs B–C; 1973, fig. 2), Laurin (1984, fig. 39), and also Sulser and Calzada (1991, figs 2–3) for rhynchonellides, as well as by Barczyk (1969, pp. 10–11) and also Singeisen-Schneider (1976, pp. 93 and onward, 1979, pp. 13–23) for terebratulides, and by Alvarez (1990, p. 21) and Alvarez and Brunton (2008, pp. 59–60) for athyrides, the shape (both in sections and restorations) of internal structures such as dental plates, septalium, hinge plates, and crura may be seriously affected by axial tilt (and sectioning angle), being critical the more they depart from the truly transversal, to approaching a tangential, condition.

Certain symptomatic features can be recognized by a trained eye. For example, in shells sectioned with ventral axial tilt, dental plates tend to look more divergent, ventral shell wall thicker proximally but thinner distally, septalium 'shallower', moderately curved crura tending to appear 'longer', etc. In shells sectioned with dorsal axial tilt, the median septum and crura may appear 'higher' but 'shorter', septalial plates 'pendant', etc. Occurrence of lateral axial tilt is usually more obvious, for deviation from bilateral symmetry readily reveals skeletal features that consistently start and/or end faster on one side

relative to the other. Because axial tilt may also affect the general outline, its analysis may likewise yield important clues towards an accurate assessment of orientation.

What is more, a similar effect may result not only from extrinsic operational inaccuracies but from intrinsic shell growth peculiarities such as disposition within available internal space (with or without geometrical constraints). Thus, partial resemblance to ventral axial tilt may derive from strongly incurved ventral beaks, to dorsal axial tilt from very gibbous or cynocephalous dorsal valves, and to lateral axial tilt, from shell asymmetry because of crowding or post-depositional deformation. The last cause, of course, can also simulate any of the previous contingencies.

When preparing the compendium of generic diagnoses for the 'Treatise H (R)' project, axial tilt effects were taken into consideration (whenever possible), especially in the treatment of synonymies. This is not a trivial point, as it has been so often neglected or inappropriately interpreted in the past, thereby giving grounds occasionally for the erection of superfluous new nominal taxa. The example shown in Text-figure 1A–B is of particular relevance for the main subject of this paper. Resorting to standard graphical software, a digital representation of a single crus (canaliform type) has been cut using two different sectioning angles (approximately at 90 degrees to each other): for each sectioning angle, three parallel cuts have been made and the resultant cross sectional outlines displayed. Further implications of this insightful exercise will be discussed below.

Other sources of significant morphological changes that may affect internal skeletal structures are ontogenetic development as well as other intraspecific variation (cf. Manceñido and Walley 1979, pp. 326–328; Laurin 1984, p. 431; Motchurova-Dekova *et al.* 2002, pp. 303–315; Tomašových 2006, p. 220; Alvarez and Brunton 2008, pp. 63–67), degree of internal curvature of the crura (Nekvasilová 1973, p. 105), and incompleteness of grinding or preservation.

By analogy, certain microstructure properties may be similarly influenced by comparable factors. Thus, when fibres of the secondary layer are spread laterally, or obliquely cut for any reason, such slanted sections usually differ in shape and/or proportions from truly perpendicular ones (cf. patterns of *Erymnaria* depicted in von Hagn *et al.* 1968, pl. 10, figs 1–2 *vs.* Motchurova-Dekova and Taddei-Ruggiero 2000, pl. 3, figs 2, 5). In addition, misleading conclusions may result from diagenetic phenomena such as silicified bands or recrystallized zones (with the latter being misidentified as an alleged 'tertiary' layer).

Bearing the above-mentioned cautionary statements in mind, this overview focuses on a few key morphological features, with greater emphasis on crural form, microstructural patterns recognizable in the secondary layer of the shell wall, and more subordinately, mantle canal markings.

CRURAL TYPES

Crura are varied and distinctive structures of the rhynchonellide cardinalia which have been regarded as one of the most valuable characters for classification and unravelling of main evolutionary lineages within the group
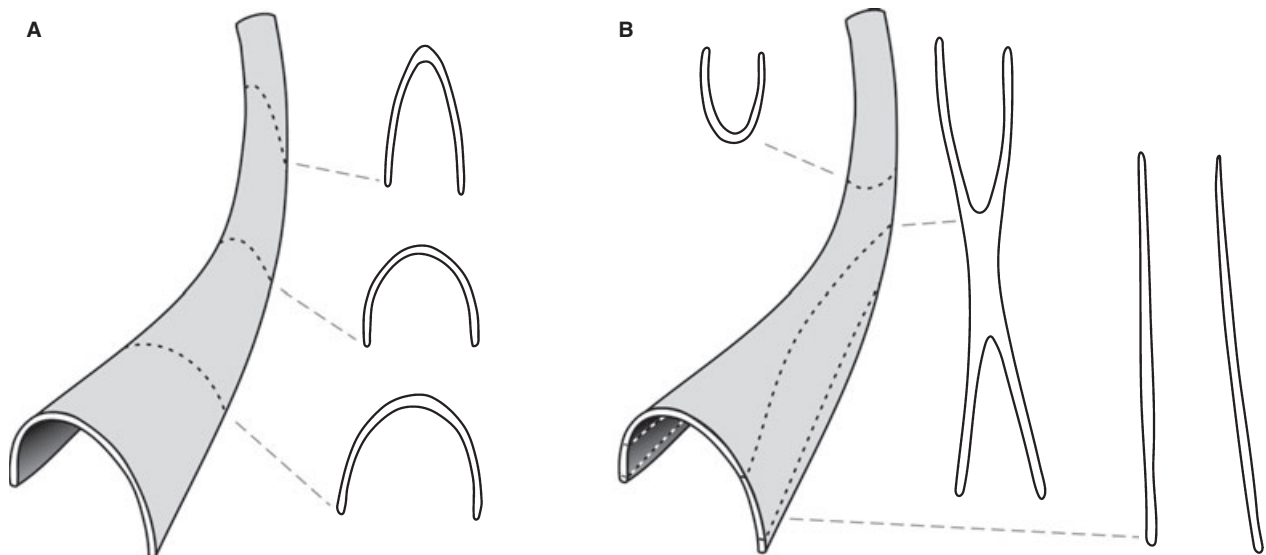
TEXT-FIG. 1. Effect of different sectioning angles on bidimensional morphology shown in successive cross sections. A, a distally expanded canaliform crus with three parallel sectioning planes fairly across its growth axis. B, exactly the same canaliform crus with three parallel sectioning planes oblique up to tangential to its growth axis. Notice substantial variation among resultant cross sections recorded.

(Ager 1965a, pp. H598–601; Ager et al. 1972, p. 161; Shi and Grant 1993, p. 4; Manceñido and Owen 1996, 2001, p. 197; Savage et al. 2002a, pp. 1036–1040, among others).

Inspired by the pioneering observations of Quenstedt and Davidson, Rothpletz (1886) was responsible for the introduction of three basic types of crura (raduliform, falciform and septiform). Incidentally, he named each distinctive type using the termination '-form' (= shaped as), while he employed the ending '-fer' (= bearer) to categorize the taxa having each kind of crura. Since then, a profuse and complex terminology comprising some twenty additional terms have been introduced (mostly by Wisniewska 1932; Muir-Wood 1934; Cooper 1959; Ager 1965a; Dagis 1968, 1974, among several others, cf. Table 1). Unfortunately, Wisniewska's misunderstanding (that misled her to pick the wrong ending) was adopted for some time thereafter. However, subsequent reversion to the original form has been advocated with sensible, solid arguments by Pearson (1977, p. 14) and has been adopted in the revised 'Treatise' (Manceñido and Owen 2001; Savage et al. 2002a; Manceñido et al. 2007).

A major rearrangement of crural types developed by one of us (MOM) is discussed in detail in this paper, having been only briefly outlined elsewhere (Manceñido 2000; Manceñido and Owen 2001; Manceñido et al. 2007). Four fundamental crural groups are recognized, namely septifal (a contraction from septi-form and fal-ciform); arcual (a contraction from arcui-form and al-lies); raducal (a contraction from radu-liform, ca-naliform and cal-cariform); and ensimergal (a contraction from ensi-form, merg-iform and al-lies).

Septifal group

The septifal group encompasses the following types:

Falciform crura. This term was introduced by Rothpletz (1886, p. 86), for 'sickle-shaped' crura, consisting of a

TABLE 1. Summary of crural terminology adopted herein and its approximate equivalence with previous usages.

TREATISE and THIS REVISION			According to previous authors	
Group	Types	Subtypes - variants		
ARCUAL	ARCUIFORM	flared	LUNIFER	Logan and Zibrowius 1994
ARCUAL	ARCUIFORM	spiculate	SPICULIFER	Dagis 1974
ARCUAL	ARCUIFORM		ARCUIFER	Wisniewska 1932
ARCUAL	SPINULIFORM	spatulate	SPINULIFER	Cooper 1959
ARCUAL	SPINULIFORM	narrow		
ARCUAL	CLIVULIFORM		CLIVULIFER	Dagis 1968 (1)
SEPTIFAL	SEPTIFORM	lyrate	PYGMAELLIFER	Baranov 1977
SEPTIFAL	SEPTIFORM		SEPTIFER	Rothpletz 1886
SEPTIFAL	SEPTIFORM	fulcral buttressed	PARASEPTIFER	Ching et al. 1979
SEPTIFAL	HAMIFORM		PREFALCIFER	Ager 1962
SEPTIFAL	HAMIFORM		"Subcilifer"	s. Ovcharenko 1983
SEPTIFAL	HAMIFORM	kinked	"Subfalcifer"	sensu Baranov 1980
SEPTIFAL	SUBFALCIFORM	smooth	SUBFALCIFER	Shi and Grant 1993
SEPTIFAL	SUBFALCIFORM	serrated edge		
SEPTIFAL	FALCIFORM	smooth	FALCIFER	Rothpletz 1886 (2)
SEPTIFAL	FALCIFORM	serrated edge		
RADUCAL	CALCARIFORM		CALCARIFER	Muir-Wood 1934-6
RADUCAL	CANALIFORM		CANALIFER	Ager 1965a
RADUCAL	RADULIFORM	channelled end	MUCRIFER	Cooper and Grant 1976
RADUCAL	RADULIFORM	serrated end	"Maniculifer"	sensu Jin 1989
RADUCAL	RADULIFORM	compressed	UNCINULIFER	Baranov 1980
RADUCAL	RADULIFORM	depressed	"Cilifer"	sensu Feldman 1987
RADUCAL	RADULIFORM	triangular	RADULIFER	Rothpletz 1886
RADUCAL	RADULIFORM	strongly incurved	PSEUDOCALCARIFER	Mitra and Ghosh 1973
RADUCAL	RADULIFORM	barbed end	HAMULIFER	Jin 1989
ENSIMERGAL	ENSIFORM		ENSIFORM	Savage et al. 2002a
ENSIMERGAL	SUBMERGIFORM		TEREBRATULIFER	Dagis 1968
ENSIMERGAL	MERGIFORM		MERGIFER	Ager 1965a
ENSIMERGAL	MANICULIFORM	smooth serrated edge	MANICULIFER	Cooper 1959
ENSIMERGAL	CILIFORM		CILIFER	Ager 1965a

[1]This may include 'preseptifer' sensu Jin (1989).
[2]This includes 'subfalcifer' sensu Ovcharenko (1983).

pair of subvertical blades that arise from the dorsal side of divided hinge plates, and extend further into the dorsal than the ventral valve cavity. Each broad blade is convex outward, has a sickle-shaped or sigmoidal cross section, and a scimitar-like lateral aspect; minor variants may have their frontal edge serrated or smooth (Text-figs 2E, 3). Typical examples are *Lacunosella* or *Orbirhynchia*, while so-called 'subfalcifer' crura (sensu Ovcharenko 1983) are reinterpreted as an axially tilted variant of falciform (see below).

Subfalciform crura. Redefined by Shi and Grant (1993, pp. 11–14) as 'almost sickle-shaped', they are regarded as transitional in development from 'prefalcifer' to 'falcifer';

TEXT-FIG. 2. Examples of taxa with septifal (A–E, G) and arcual (F, H–Q) crura. A–B, *Acanthobasiliola doederleini* (Davidson), subfalciform crura with serrated edge, Recent. A, juvenile; B, adult; C, *Basiliola lucida* (Gould), subfalciform crura, Recent (Tokyo Univ. Mus., to be catalogued). D, *Homaletarhynchia limbata* (Schlotheim), subfalciform crura with serrated edge, Upper Cretaceous, NMNHS F-31299. E, *Orbirhynchia* sp., falciform crura with serrated edge, Upper Cretaceous, Turonian, BMNH B 85944. F, *Hispanirhynchia cornea* (Fischer *in* Davidson), narrow spinuliform crura, Recent, BMNH ZB 281. G, *Aphelesia bipartita* (Brocchi), subfalciform crura smooth anteriorly, Miocene, USNM 549380. H, *Veghirhynchia arpadica* (Bittner), hamiform crura, Upper Triassic, IGiG 394/200. I, *Ptilotorhynchus delicatus* Cooper and Grant, hamiform crura, Permian, USNM 154710a. J, *Grammetaria bartschi* (Dall), narrow spinuliform crura, Recent, USNM 239269. K, *Compsothyris racovitzae* (Joubin), spatulate spinuliform crura, Recent, USNM 549343. L–M, *Parasphenarina cavernicola* (Motchurova-Dekova, Saito and Endo), narrow spinuliform crura, Recent. L, juvenile, UMUT RB 28220-R5-4; M, adult, UMUT RB 28220-R1-12. N–Q, *Tethyrhynchia mediterranea* (Logan *in* Logan and Zibrowius), flared acuiform crura (= 'luniform' of some authors), ontogenetic development, Recent. N, juvenile, O–Q, adults in ventral (O), subanterior (P) and lateral (Q) views. Adapted from: Cooper 1959 (G, J, K), Cooper and Grant 1976 (I) (courtesy of Smithsonian Institution), Zezina 1981 (A, B, courtesy of O. Zezina), Savage et al. 2002b (H, courtesy of the GSA and The University of Kansas © 2002), Motchurova-Dekova et al. 2002 (L, M), courtesy of E. Simon (N–Q), courtesy of M. Saito (C), new (D, E, F).

a slightly different definition from earlier usages of 'sub-falcifer' (e.g. Baranov 1980, p. 83; Ovcharenko 1983, p. 49). Subfalciform crura are very similar to falciform, but with outwardly convex blades that are compressed, elongate to crescent-like in section (instead of falcoid), and

may or may not also show a serrated distal edge (Text-figs 2A–D, G, 3). Good examples are seen in *Acanthoba-siliola* or *Homaletarhynchia*. This term cannot be applied to Ovcharenko's 'subfalcifer' (1983, p. 49, footnote) which was based independently on her new genus
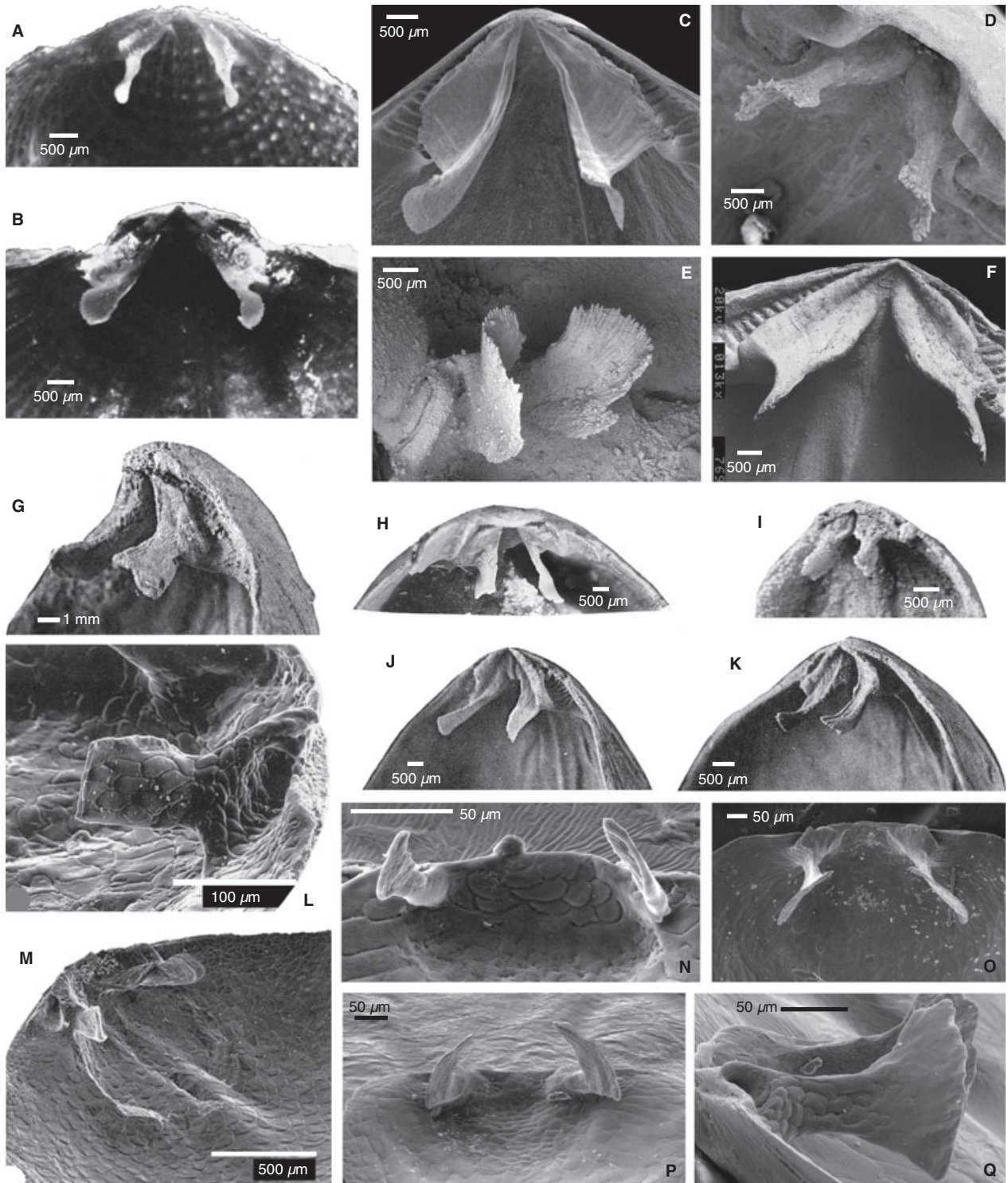
Dzanghirhynchia (distinguished from the main 'falcifer' type only by strong dorsal growth of its distal tips). However, as differences alleged by Ovcharenko appear to be artefacts owing to sectioning angle, her genus has now been placed in synonymy with the genuine falcifer *Stolmorhynchia* (Savage *et al.* 2002*b*, p. 1210).

Hamiform crura. Named by Pearson (1977, p. 14) for crura which are 'fish-hook-shaped' in cross section, replacing the unsuitable 'pre-falcifer' of Ager (1962, p. 109, 1965*a*, p. H600). Hamiform crura differ from falciform in that each blade is considerably narrower and straighter, with an arcuate, comma-like or kinked cross section (Text-figs 2H–I, 3). *Pseudogibbirhynchia* or *Cirpa* provide characteristic examples of the 'normal' hamiform crura, and *Yakutijaella,* of the occasional midway- kinked variant, which has also been figured in some *Euxinella* (Dagis 1968, text-fig. 29). Ovcharenko (1983, p. 49, foot-note) introduced the term 'subcilifer', taking her new genus *Aidynkulirhynchia* as reference, stressing its dorsally

grown distal tips as the main distinction from 'cilifer'. Here, too, the effect of sectioning angle seems responsible of the alleged differences, and Ovcharennko's term 'subci-lifer' is considered a superfluous equivalent to hamiform and the genus, a subjective synonym of *Pamirorhynchia* (Savage *et al.* 2002*b*, p. 1204).

Septiform crura. Another of the original triad established by Rothpletz (1886, p. 86), for crura that are 'shaped like a septum', and consisting of short, subvertical, crural plates that connect the dorsal, inner edge of narrow, sub-horizontal hinge plates directly to the floor of the dorsal valve, and extend forward for about one-fifth to one-third of that valve length (Text-fig. 3). When viewed through the translucent shell (or on internal moulds), the crural and fulcral plates appear as four radiating dark lines (the central pair being longer than the two flanking laterals). Typically exhibited by *Septocrurella*, though a couple of main variants are also known: (1) *lyrate septiform*, so-called by their lyre-shaped distal cross section, as in
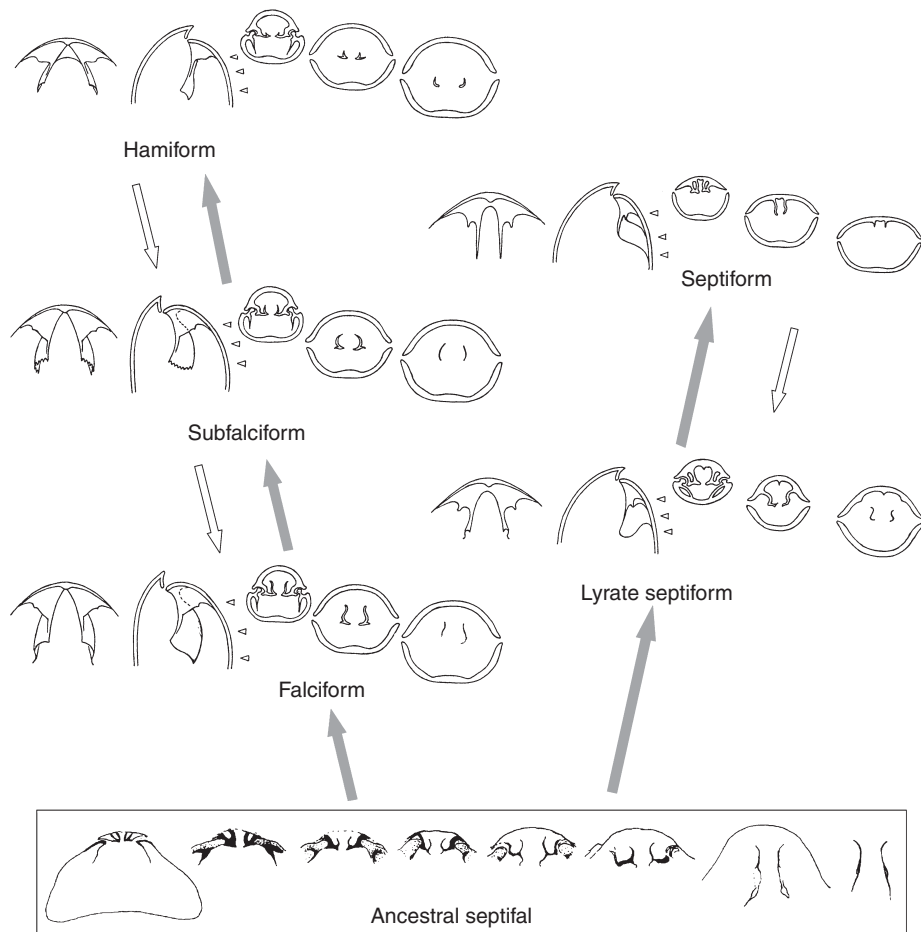
TEXT-FIG. 3. Septifal group crura, some hypothetical relationships. See text for details (possibility of heterochronic reversals in trends denoted by blank arrows).

Erymnaria or *Costerymnaria*, and even in Devonian *Pygmaella*, hence equivalent to Baranov's (1977, p. 325, 330; 1980, p. 83) 'pygmaellifer' (but this variant is not restricted to a genus in particular, as implied by such term); (2) *fulcral butressed septiform*, which is unusual because the crural plate is buttressed against the fulcral plate and more or less intimately fused to it, thus equivalent to the term 'paraseptifer' as used by Ching, Sun and Ye (*in* Ching *et al*. 1979, pp. 62–63, 132), litterally 'beside septifer', as applied to *Crurirhynchia*.

Relationships and trends. Crura of the septifal group are known in the Superfamilies Pugnacoidea and Wellerelloidea: septiform crura are confined to Erymnariidae (with fulcral butressing in cryptorhynchiines), while falciform, subfalciform and hamiform crura occur within Basiliolidae, and hamiform also in Wellerellidae, Pontisiidae and Allorhynchidae. They are linked with a spirolophous lophophore in all adult living basiliolids (Savage *et al*. 2002*b*, p. 1199), though some of the smaller fossil erymnariids may have not developed much beyond a schizolophous stage.

Initially, Rothpletz (1886, p. 86) implied that septiform crura might have arisen from falciform crura, by means of the crural plates coming into contact with the dorsal valve floor. Ager (1965*a*, p. H598) thought the reverse more likely, envisaging a passage from raduliform to (para)septiform and thence to falciform. A modified view (invoking median migration of septa) was later favoured by Ager *et al*. (1972, p. 221). Our understanding of crural morphology in this group is enhanced when the peculiar structure exhibited by early Carboniferous *Pugnax* is taken into account, whereby the apical portion is septiform but the subvertical crural plates become gradually detached anteriorly. As depicted in Text-figure 3, this may be considered as an unspecialized ancestral septifal condition (the genus is known since Devonian times) from which two main evolutionary trends may be derived (Manceñido and Owen 2001, p. 198): (1) One trend involves the persistence of the early fusion of crural plates to the dorsal valve floor and their overall simplification, giving rise to septiform crura (and hence to the erymnariid branch). This may represent a paedomorphocline, indeed many Jurassic septocrurellines (and Devonian plectorhynchellids, too) are small sized, yet in view of the extended time gap it is not certain if such an evolutionary event could have happened more than once. The possibility of reversion (or iteration) within septiform – from normal to lyrate – is also hinted at (blank arrow in Text-fig. 3), to account for the occurrence of the latter in early Devonian *Pygmaella* as well as in late Cretaceous to Tertiary erymnariines. (2) The other trend entails progressively earlier detachment of crural plates from the dorsal valve floor (until fusion is lost), accompanied by

forward extension of the falcoid blades, thus peramorphically originating the falciform crura. In fact, such a trend may be continued and exaggerated until the development of very narrow blades, comma-like in section; passage from subfalciform to hamiform would mark that progression. There is enough circumstantial evidence within the mainstream pugnacid-basiliolid stock to suggest that afterwards, such progression could easily have been changed heterochronically (back and forth) several times (even in different branches).

Arcual group

The arcual group comprises a number of main types plus several variants:

Arcuiform crura. First described by Wisniewska (1932, p. 6) as 'arcuifer', arcuiform crura ('arc-shaped'), are crura with separate crural bases, which are widely divergent and projecting along commissural plane, and which become hammer-shaped in cross section and dorsoventrally subparallel distally, and resemble a pair of parentheses '()' (cf. Text-fig. 4). *Monticlarella* has been taken as a model for arcuiform crura (see also Ager 1965*a*, p. H599; Dagis 1968, p. 35, 1974, p. 37; Savage *et al*. 2002*a*, p. 1036), yet they may even appear inclined medially and flattened instead of arcuate, to end truncated beyond the articulation zone (as in *Pseudomonticlarella*).

Flared Arcuiform crura. This variation was called 'lunifer' (from the Latin word for moon) by Logan and Zibrowius (1994, pp. 80–81); these crura are very close to the basic arcuiform, except for being longer (up to one-third of valve length), distally much expanded dorsoventrally, and flared crescent-shaped in lateral view (Text-fig. 4), with their curved extremities pointed and inwardly directed to face each other. Those features are well displayed in *Tethyrhynchia* (Text-fig. 2N–Q), which was originally compared to the calcariform type (but in the latter the most acuminate end of the broad lamina would tend to point antero-ventrally, instead of postero-ventrally as in the former).

Spiculate Arcuiform crura. This variation was called 'spiculifer' by Dagis (1974, p. 35), meaning 'spicule-bearing', being like the basic arcuiform, save for having the distal ends connected by a bridging arc of tightly packed calcitic spicules, as in *Laevirhynchia*. It is merely regarded as a subordinate variant, because the presence of spiculation in the fossil state is considered to yield information more relevant to taphonomic conditions (linked to the chance preservation inherent to such brittle structures) rather than to taxonomic relationships.
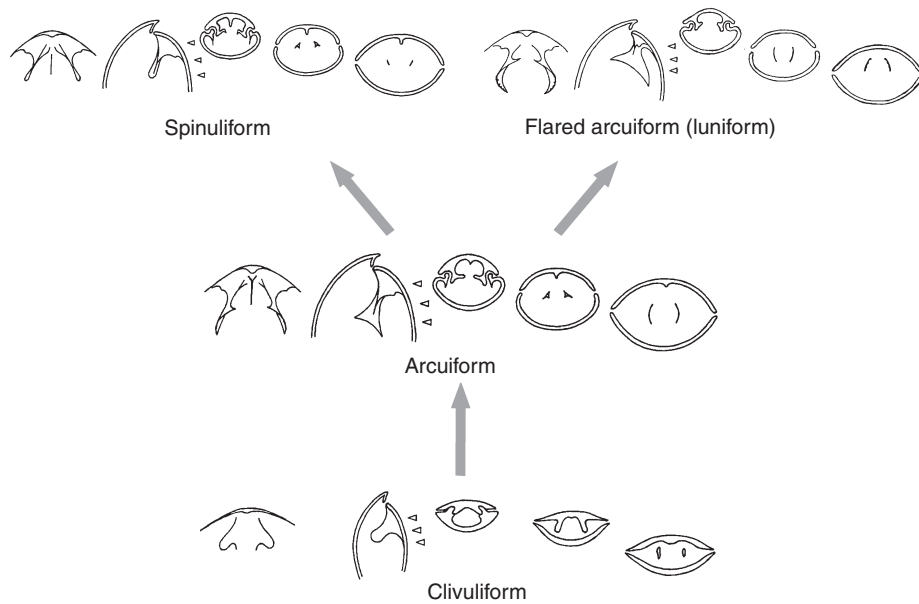
TEXT-FIG. 4. Arcual group crura, some hypothetical relationships. See text for details.

Spinuliform crura. Coined as 'spinulifer' by Cooper (1959, p. 9), each spinuliform crus (litterally 'shaped like a small spike'), is short, narrow, compressed, nearly straight, divergently projecting subparallel to sagittal plane, and with distal end blunt and unflared. Characteristic examples are *Frieleia* or *Parasphenarina*: both a narrow and a spatulate variant can be recognized (Text-figs 2J–M, 4).

Clivuliform crura. Introduced by Dagis (1968, p. 40), meaning 'knoll-shaped', based upon early Jurassic *Ochotorhynchia* (Text-fig. 4) these crura are short, massive, knob-like, and arise from the inner socket ridges and project as laterally compressed subvertical plates, which straighten ventrally and divergently. 'Preseptifer' crura described by Jin (1989, pp. 27, 107–112) in the Silurian leptocoeliid *Platytrochalos* are strongly reminiscent of (if not synonymous with) the Mesozoic clivuliform.

Relationships and trends. Crura of the arcual group are typical of the Superfamily Norelloidea: with normal arcuiform in most Norellidae and neorhynchiine Frieleiidae, spinuliform in most Frieleiidae and paranorellinine Norellidae, flared arcuiform in Tethyrhynchiidae and some diholkorhynchiine Norellidae, spiculate arcuiform in laevirhynchiine Norellidae and clivuliform in Ochotorhynchiidae. They are accompanied by a spirolophous lophophore among extant frieleiids, and by a bell-shaped trocholophe in living tethyrhynchiids (Logan and Zibrowius 1994, pp. 80–81; Manceñido and Owen 2001, p. 193). Inferred basic relationships among crura belonging to this group are outlined in Text-figure 4. The clivuliform type is regarded as generalized and ancestral (a con-

clusion which would be reinforced by a close match already known in an early Silurian leptocoeliid), thus providing a good starting point for the normal arcuiform type to develop (this seems fully attained by the early Carboniferous, as in *Iowarhynchus*). From this eclectic type, a couple of divergent trends appear likely: (1) A trend towards narrowing (and distal elongation) which would end up in the spinuliform kind (via spatulate to narrow), and some support for this contention comes from what little is known about the ontogenetic development in cave-dwelling *Parasphenarina* (Motchurova-Dekova *et al.* 2002, herein Text-fig. 2L–M). (2) Conversely, a trend to maximize dorsoventral flaring distally would yield the flared arcuiform (or 'luniform' of some authors) variant. Crural morphology of extant micromorphic cave-dweller *Tethyrhynchia* provides some insight into its ontogeny (Text-fig. 2N–Q), and as fossil counterparts are known among Triassic diholkorhynchiines, evolutionary iteration looks feasible. Such a parsimonious scenario of simple derivation is logically sound and does accommodate the occurrence of heterochronic reversals from time to time (although not indicated by any blank arrow on Text-fig. 4); nevertheless, an alternative possibility of putative links between hamiform crura and arcuiform-spinuliform (in either direction) cannot yet be totally dismissed.

The rôle of heterochronic processes has been emphasized by Manceñido and Owen (1996, p. 368, 2001, pp. 197–198), who cited 'the importance of minute, spinulifer, paranorellinines from the earliest Triassic as a likely source for the post-Palaeozoic radiation of norelloids' as an exemplifying case for the recovery of lineages after

mass extinctions from relatively few paedomorphic survivors. In fact, the above statement was based entirely on direct examination of well-preserved specimens of *Paranorellina*? *changxingensis,* kindly shown to one of us (MOM) in Nanjing by Dr. Liao (back in 1999). Subsequently and independently, very similar conclusions were reached by Chen *et al.* (2002, pp. 158–159), from a painstaking study on abundant material from the Yikeng Formation, based upon SEM analysis and serial sections (albeit somewhat disguised under the new denomination *Meishanorhynchia meishanensis,* misassigned by them to Tetrarhynchiinae). Detailed additional support like this is highly desirable.

Raducal group

The radical group constitutes a closely knit assemblage of crural types:

Raduliform crura. First recognized by Rothpletz (1886, p. 86), meaning 'shaped like a Greek-athlete's hook (or scraper)', represents the most frequent and fundamental type of crura. Each crus is relatively long, simple, divergent, rod-like, arises from the inner side of the hinge plate, and curves symmetrically forward and ventrally, in a hook-like fashion (Text-figs 5C–D, 6). This type of crura is well demonstrated in *Rhynchonella* or *Notosaria,* yet may show a number of variants affecting either the cross sections (e.g. subtriangular, compressed, depressed, subquadrate, elliptical) or the distal ends. The latter, in particular, exhibit variability in crural form: some may end distally with a concave surface facing dorsally, and terminate like a lozenge-shaped trowel, as in *Cretirhynchia* (Motchurova-Dekova *et al.* 2008, figs 2C, D *vs.* 3A, C); others may be rather more spoon-shaped. Some Palaeozoic examples similar to these (as in *Bryorhynchus*), have been called 'mucrifer' by Cooper and Grant (1976, p. 1928), meaning 'bearing a sharp point', yet it is more informative to refer to them as *raduliform with canaliform distal end* or *incipiently canaliform* (Text-figs 5A–B, 6).

A much depressed, flat (almost ribbon-like) distal end to the raduliform crura, as known in Callovian *Septirhynchia,* has been misinterpreted by Feldman (1987, pp. 1165–1166, figs 9–11) as 'cilifer', but to use the latter in such a sense would deviate significantly from Ager's original meaning (see below, and Text-fig. 5G). Similarly, Jin (1989, pp. 27, 47, 89) employed the term 'maniculifer' for crura of single species of Silurian *Rhynchotrema* and *Hercotrema* and further questioned the taxonomic value of Cooper's crural type because he found that of two conspecific specimens sectioned by him (Jin 1989, text-figs 18–20), one had 'radulifer' but the other had the alleged

'maniculifer' kind. However, the genuine maniculiform type has its digitations subparallel to the sagittal plane (i.e. roughly perpendicular to those recorded by him); it is thus more likely (and parsimonious) to interpret that he was just dealing with two intraspecific variants of the same type of crura, one with serrated distal edge (probably occurring in Triassic *Yidunella* as well), the other without. On the other hand, the apparently barbed distal end that characterizes the 'hamulifer' type (meaning 'bearing a small hook'), observed by Jin (1989, pp. 27, 47, 89) in one species of *Rhynchotrema* and one of *Fenestrirostra,* suggests that it, too, may be prudently regarded as a distal end variant (or subtype) of the well-known raduliform. Besides, a 'pseudocalcarifer' type (meaning 'false calcarifer') was coined by Mitra and Ghosh (1973, p. 178, fig. 1) to suit *Kutchirhynchia,* but it seems merely a strongly curved variant of radulifer, as pointed out by Shi and Grant (1993, p. 5, their fig. 1A–F depicts a range of other terminal variations).

Further cross-sectional variants have generated further nomenclature that are considered unacceptable in this paper and best abandoned in favour of self-explanatory expressions, such as *raduliform, triangular in section* for 'Septalirhynchia-type' [*sic*] (Xu and Liu 1980, p. 37; 1983, p. 68, text-fig. 4.5) as in *Triasorhynchia,* or *compressed raduliform* for 'uncinulifer' (Baranov 1980, p. 83), of Devonian *Pseudouncinulus* (which is said to precede during ontogeny the normal raduliform of adult *Eoglossinotoechia*).

Canaliform crura. First discriminated by Ager (1965*a,* p. H600), as 'canalifer' (i.e. 'channel-bearing', or 'channel-shaped' as in this paper), because they are anteriorly curved and longitudinally folded all along their length, and are shaped like a channel or gutter that faces dorsally (Text-figs 5F, 6). These are typical of *Cyclothyris* and allied genera and, because of the strong dorsal concavity, usually most cross sections look 'U' or 'V' shaped, though actually a variety of morphologies may result (cf. Shi and Grant 1993, fig. 5A–E). This would include 'diabolo shaped' or 'paired subvertical plates', depending on the angle between the folded lamellae, the gutter depth, and the incidence of sectioning angle, as clearly demonstrated herein in Text-figure 1A–B. This shows beyond doubt that what in the literature has sometimes been ascribed to 'distal splitting of crura into parallel plates' is just an artefact, as it is to be expected distally in a canaliform crura beyond a 'diabolo shaped' cross-section. Significantly, genera quoted by Radulović *et al.* (2007, p. 764) possess deeper, rather globose dorsal valves.

Calcariform crura. Proposed by Muir-Wood (1934, p. 525), meaning 'spur-bearing', here 'spur-shaped', on the
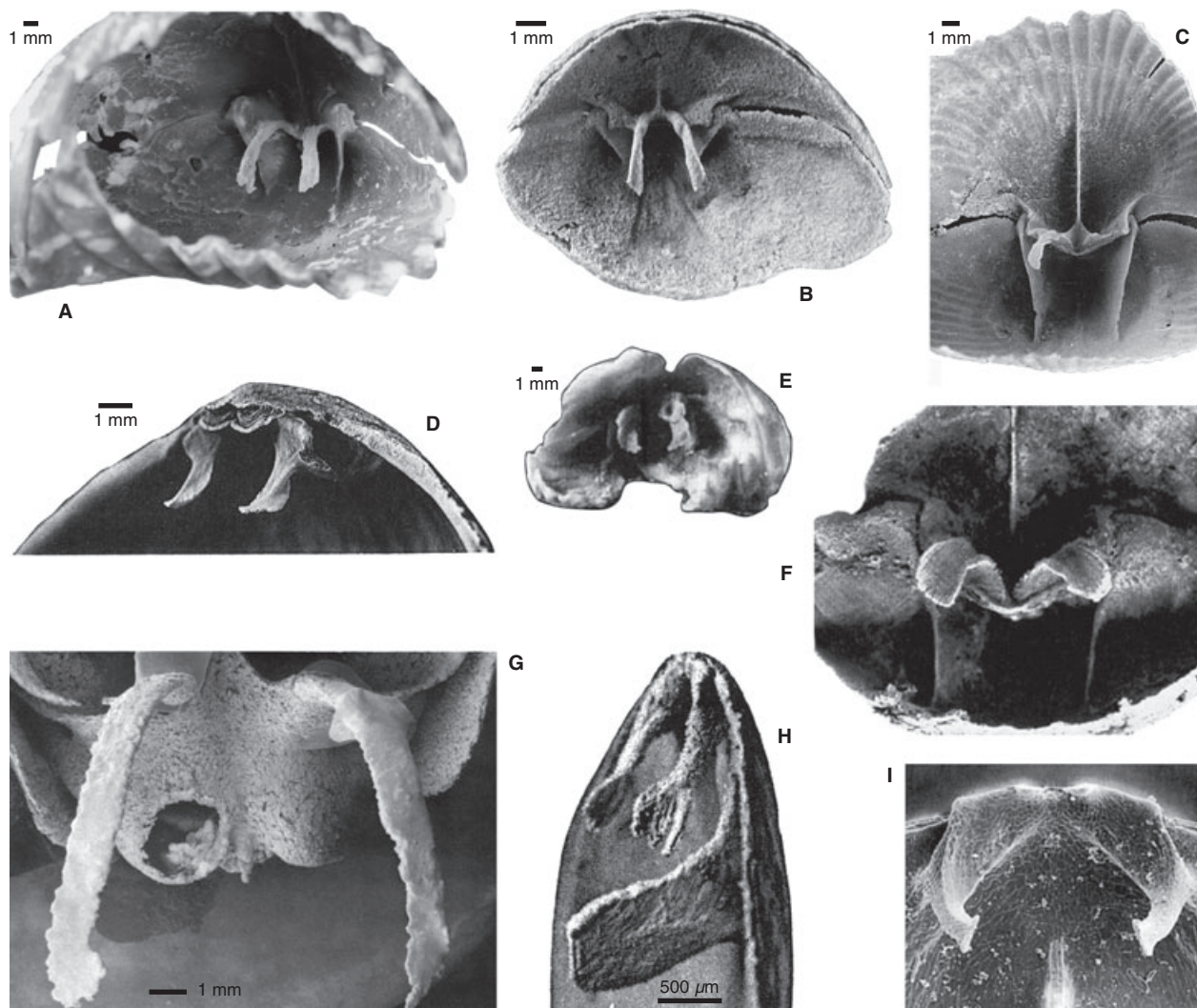
TEXT-FIG. 5. Examples of taxa with raducal (A–G) and ensimergal (H–I) crura. A, *Cymatorhynchia quadriplicata* (Zieten), raduliform crura with concave (incipiently canaliform) distal ends, Middle Jurassic, BMNH B.66919. B, *Bryorhynchus bisulcatus* (Shumard), raduliform crura with concave (incipiently canaliform) distal ends (= 'mucriform'), Upper Permian, USNM 154906e. C, *Somalirhynchia arabica* Cooper, raduliform crura (broadened distally), Upper Jurassic, USNM 380514. D, *Notosaria nigricans* (Sowerby), raduliform crura, Recent, USNM 111018a. E, *Thurmannella obtrita* (Defrance), calcariform crura, Upper Jurassic, USNM 306011g. F, *Cyclothyris* aff. *difformis* (Valenciennes *in* Lamarck), canaliform crura, Upper Cretaceous (Cenomanian), CGS ON16/690. G, *Septirhynchia hirschi* Feldman, raduliform crura (with depressed crossed section), Middle Jurassic; AMNH 42923a. H, *Cryptopora gnomon* (Jeffreys), maniculiform crura with serrated anterior edge, Recent, USNM 94367. I, *Aulites brazieri* (Crane), maniculiform crura smooth anteriorly, Recent. Adapted from: Cooper 1959 (D, H), Cooper and Grant 1976 (B), Cooper 1989 (C), Shi and Grant 1993 (E) (courtesy of Smithsonian Institution), Feldman 1987 (G, courtesy of H. Feldman), Nekvasilová 1973 (F, courtesy of O. Nekvasilová), Richardson 1987 (I, courtesy of The Royal Society of Victoria), Manceñido *et al.* 2002 (A, courtesy of the GSA and The University of Kansas © 2002).

basis of appearance on a longitudinal section from a species of *Kallirhynchia*. Later Muir-Wood (1936, p. 14), considered this kind of crura was also represented in her newly erected genus *Rhynchonelloidella* (in fact, it served to accommodate several species that were formerly assigned to *Kallirhynchia* by Buckman). Modern authors (e.g. Dagis 1974, pp. 35–36; Laurin 1984, p. 76; Shi and Grant 1993, pp. 6–7; Savage *et al.* 2002a, p. 2040) have

agreed that this crural form is well exemplified in species of *Rhynchonelloidella* and *Thurmannella* (but not in *Kallirhynchia* as presently understood). These crura are initially subhorizontal but become strongly bent ventrally and lengthened along the vertical plane; in so doing, each develops forward a wide, web-like lamina, which may be twisted distally (Text-figs 5E, 6; cf. also Shi and Grant 1993, fig. 4A–E). It may be recalled that this type of crura

was not distinguished from falciform originally (cf. Roth-pletz 1886, pl. 8, figs 41–45).

Relationships and trends. Crura of the radical group are typically present in the Superfamilies Rhynchonelloidea and Hemithyridoidea, occurring also in Rhynchotetradoidea: with normal raduliform being the most widespread, canaliform is distinctive for Cyclothyrididae, while calcariform characterizes the ivanoviellines, some other Rhynchonellidae (bilaminellines, striirhynchiines) and a few (mostly acanthorynchiine) Acanthothirididae. In all adult living members, they are associated with advanced conoidal spirolophes possessing apices directed dorsally and inwards (Manceñido and Owen 2001, p. 197; Manceñido *et al.* 2002, pp. 1326, 1367).

Possible mutual interrelations within the group are illustrated in Text-figure 6. There is ample consensus in considering the raduliform as the fundamental type from which others were derived (e.g. Ager 1965a, p. H598; Dagis 1968, p. 41, 1974, p. 37; Ager *et al.* 1972, pp. 189–213; Shi and Grant 1993, p. 4; Manceñido and Owen 2001, pp. 195–197); actually it is already recognizable from Ordovician times in many Rhynchotrematoids. As for the origins of the raduliform crura themselves, they could be sought directly from clivuliform on the basis of the remarkable similarity with sections of early juveniles of mid Jurassic forms with raduliform adult crura (unless the spinuliform alternative is preferred, as

carried out by Ager, Dagis, and others). Stemming from generalized, rod-like raduliform crura a basic dichotomy is evident: (1) A trend towards developing longitudinally a channel or gutter facing dorsally leads to the canaliform type. This was achieved over the full length of each crus in cyclothyridids, probably via a gradual process, passing through an intermediate stage that is incipiently canaliform distally. The latter may be just a transient step along a rather protracted peramorphocline (noticeable within the genus *Cyclothyris* itself), or may constitute an adult stage on its own, often somewhat broadly expanded distally, as in some Palaeozoic leiorhynchiids or petasmariids and Mesozoic cyclothyridids or even tetrarhynchiids (cf. Text-fig. 5A–B, F herein *vs.* Motchurova-Dekova *et al.* 2008, fig. 1A–B). (2) The second off-shoot would require development of a web-like laminar extension to turn into calcariform. Such a novel acquisition could be achieved by a minor adjustment in the secretory regime, whereby the tip of an ordinary raduliform crus grows anteriorly and ventrally while curving away from the commissural plane (in the usual way). If the forward growing secretion surface of the crus is not subject to resorption, a trailing calcareous web could be easily generated. Alternatively, it might be envisaged as a very asymmetrical and oversized development of a single convergent lamella from a normal canaliform crus (Shi and Grant 1993, p. 7). One rhynchonellid subfamily (Ivanoviellinae) seems to have
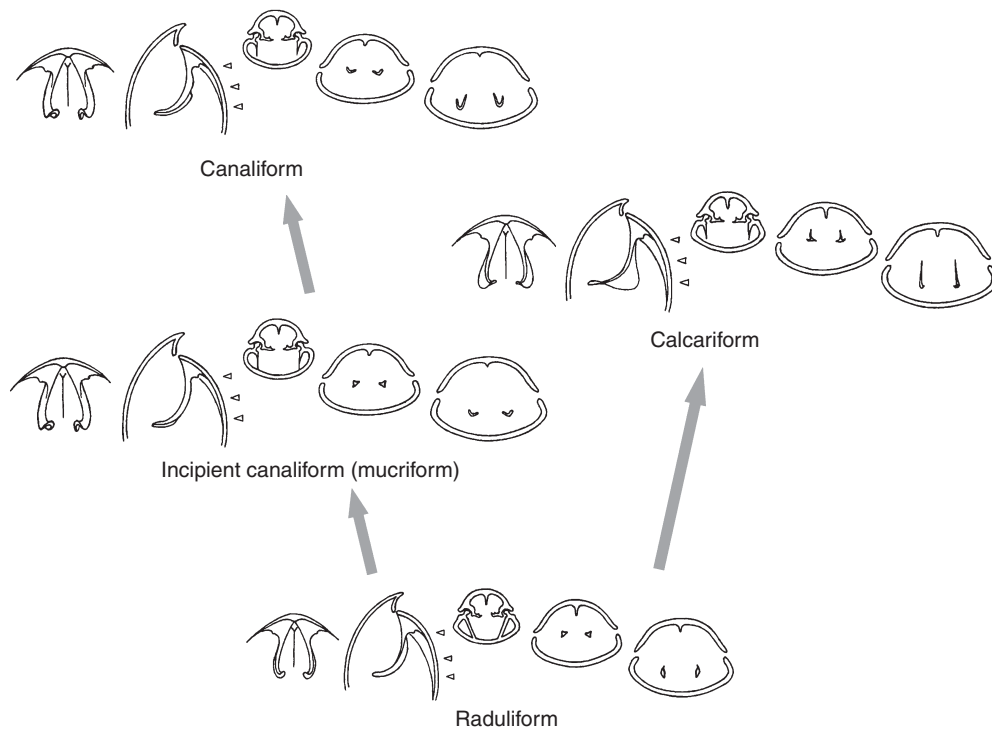
TEXT-FIG. 6. Radical group crura, some hypothetical relationships. See text for details.
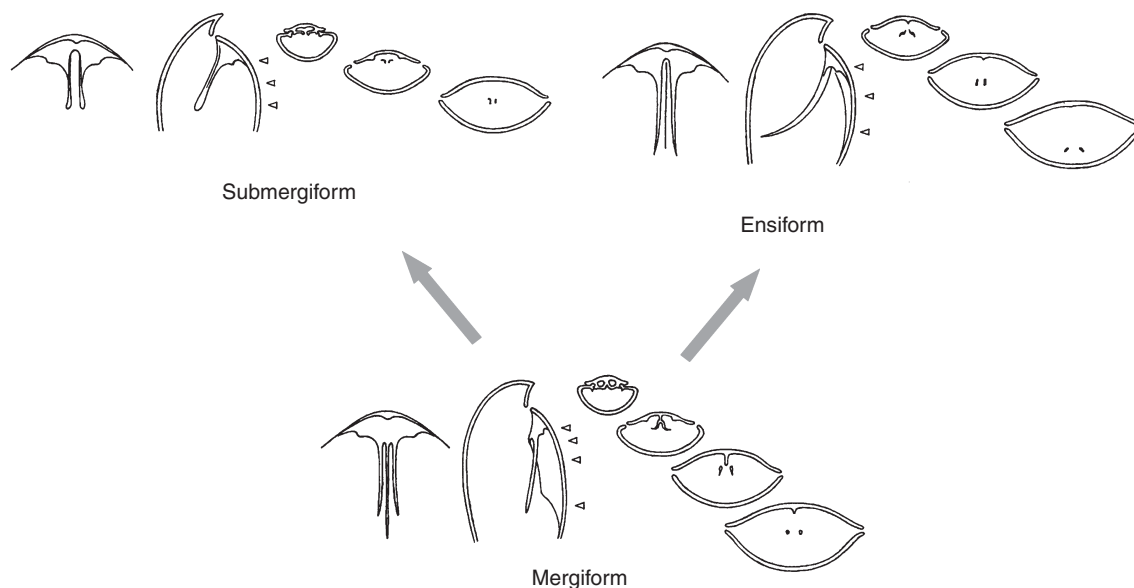
TEXT-FIG. 7. Ensimergal group crura, some hypothetical relationships. See text for details.

exploited this evolutionary novelty, but without precluding the occasional independent, iterative appearance in other related lineages (cf. Manceñido and Owen 2001, fig. 20.2).

Ensimergal group

Contains the ensuing types:

Mergiform crura. Denominated by Ager (1965a, p. H600), as 'mergifer' (meaning 'pitchfork-bearing', here 'pitchfork -shaped'), they are very long, closely subparallel and gently curved ventrally, arising from a lobate swelling at the junction of the dorsal median septum with the dorsally bent edge of a thin hinge plate. They are best characterized in the genus *Peregrinella* (Text-fig. 7).

Submergiform crura. Introduced in Savage et al. (2002a, p. 1040) to replace 'terebratulifer' of Dagis (1968, p. 39) for carrying undesirable implicit connotations, meaning 'almost pitchfork-shaped', are similar to the previous, though shorter and blunter, arising from the ventrally bent edge of a thin hinge plate, and unrelated to the dorsal median septum (typically absent). Their description has been based on structures in the genus *Peregrinelloidea* (Text-fig. 7).

Ensiform crura. First described in Savage et al. (2002a, p. 1040), from the Latin *ensis* = sword, sabre, thus meaning 'sabre-shaped'; generally subparallel, compressed, resem-

bling a pair of sabre blades, curving away from the dorsal valve and are barely divergent anteriorly (Text-fig. 7). It has been modelled after *Rhynchonellina* (yet it may occur with or without a dorsal median septum).

Maniculiform crura. Recognized by Cooper (1959, p. 9), as 'maniculifer' (meaning 'bearing a little hand', here 'shaped like a little hand'), these crura are moderately elongate, laterally compressed, gently divergent, with each crus ending in a subvertical flattened expansion (cf. Savage et al. 2002a, fig. 702.4). Two main variants are known, the more typical with a digitate distal edge to each crus (suggesting small fingers on a hand), as in *Cryptopora*, or with a smooth frontal edge (and somewhat bowed inwards anteriorly, rather than straight), as in *Aulites* (Text-fig. 5H–I). As explained above, this term should not be applied to certain early Palaeozoic rhynchotrematoids.

Ciliform crura. Distinguished by Ager (1965a, p. H600), as 'cilifer' (meaning 'chisel-bearing', here 'chisel-shaped'), proximally flattened parallel to the commissural plane, as a prolongation of subhorizontal hinge plates; the cross section starts chisel-like, and then becomes geniculated (cf. Savage et al. 2002a, fig. 702.5). Exemplified by Triassic *Halorella*, minor variations involve a greater or lesser development of such lateral flanges. Excessive emphasis on a chisel-like appearance in isolated sections has led certain authors to mistakenly refer 'cilifer' to other unrelated crura (e.g. Ovcharenko 1983, p. 49; Feldman 1987, p. 1165); so, use of this qualifier for septirhynchiids is best avoided.

Relationships and trends. Crura of the Ensimergal group characterize the Superfamily Dimerelloidea: with mergiform in most Peregrinellidae, submergiform in Peregrinelloideinae, ensiform in Dimerellidae, ciliform in Hallorellidae, and maniculiform in Cryptoporidae. They are combined with a simple circinate spirolophe in extant cryptoporids, but in extinct large ventribiconvex taxa perhaps a special outwardly coiling spirolophe may have been present, with the apices of wide-angled cones directed either laterally, or even ventrally (Ager *et al.* 1972, p. 164; Manceñido and Owen 2001, p. 192).

Although this group is less well understood than the others, some hypothetical links among crura assigned to it are tentatively sketched in Text-figure 7. Evidence from stratigraphical occurrence suggests that mergiform crural types are primitive (being the earliest recorded, since the Devonian), from which, two early Mesozoic derivatives may have arisen: (1) a shortening trend with loss of any connection with the dorsal median septum (and loss of the septum itself, for that matter) would lead to submergiform, (2) whereas transformation into ensiform could follow a trend to a sabre-like shape with increased curvature, and independence from the septum (however, the possibility of an independent derivation from raduliform, or even from as yet unknown ensiform Palaeozoic ancestors cannot be ruled out, cf. Ager *et al.* 1972, pp. 170–174; Manceñido and Owen 2001, p. 190).

Maniculiform and ciliform crura were deliberately excluded from the diagram because their derivation is still blurred by uncertainties (Manceñido and Owen 2001, p. 190); for instance, Ager (1965a, p. H600) considered ciliform more related to raduliform, Dagis (1974, p. 37) to septiform, and yet even proposing certain affinities to canaliform might not be out of place.

According to the integrative, comprehensive scheme presented above (see also Table 1), the four main groups exhibit a long history (dating back even to the Palaeozoic). Fortunately, at least some members of each group are extant, albeit at times in quite modified form (Manceñido 2000; Manceñido and Owen 2001; Manceñido *et al.* 2007). In the particular case of norelloids and basiliolids, ghost lineages have been invoked to bridge their respective gaps between their latest records in the Mesozoic and their earliest in the Cainozoic, thus reinforcing the idea of phylogenetic continuity for arcualbearers and septifal-bearers (see Vörös 2005, fig. 3).

SHELL MICROSTRUCTURE PATTERNS

At an early stage, Leidhold (1921, pp. 346–350) and Ager (1957, p. 7, 1965a, p. H601) drew attention to the possible taxonomic importance of the so-called shell mosaic (*Schalenmosaik* or *Schuppenpanzerstruktur*) observable on the inner surface of either valve and on internal moulds of exceptionally well-preserved material. With the advent of SEM studies, it was noticed that such characteristic, stable, geometrical patterns on the inner valve floor were also matched in the fabric of stacked fibres seen in cross sections of the shell wall (e.g. Williams 1968, figs 4–6, 1997, figs 242, 245; MacKinnon 1974, figs 3, 13). Concerning the order Rhynchonellida in particular, pioneering studies by Russian authors (such as Kamyshan 1977, 1986; Smirnova 1984 and others), have recently triggered a renewed interest in shell-wall microstructure (cf. Radulović *et al.* 2007, table 1). Although not specifically included (because of normal publishing delays) in vol. 4 of the '*Treatise*' (Savage *et al.* 2002a), the potential value of this feature for post-Palaeozoic rhynchonellides has been duly stressed elsewhere (Manceñido and Owen 2001, p. 197; Manceñido *et al.* 2007, p. 2727, fig. 1818; Radulović *et al.* 2007, p. 776, fig. 13). Incidentally, it has been likewise shown for certain Palaeozoic strophomenate groups that shell structure may be conservative, irreversible and thus bearing a strong phylogenetic signal (Dewing 2004, pp. 275, 281).

We consider that the impunctate post-Palaeozoic rhynchonellide shell is composed of only two layers: primary and secondary. Unlike some incorrect records in previous literature (Dagis 1974, pp. 55–56; Smirnova 1984, p. 55; Radulović 1991, p. 15, 18; Motchurova-Dekova 1994, p. 88), we consider there is no evidence for the presence of a tertiary prismatic layer in post-Palaeozoic rhynchonellides. We will not comment on localised fabric changes of the secondary layer often observed in muscle fields (myotest), the apical part of valves and cardinalia. These fabric changes may give rise to a distinct sublayer that sometimes could be misidentified as a tertiary layer.

As the primary shell layer is thinner and most frequently recrystallized (or not preserved) in fossil rhynchonellides, it is the thicker, secondary fibrous layer that holds much greater taxonomical potential. The size and orientation of the calcite fibres in the mosaic of the secondary shell are subject to changes according to their location in the thickness of the shell and according to their position in relation to the internal morphological features. Hence, for uniformity of comparisons, it is better whenever possible to consider only adult shells. The shell thickness and fibres of the secondary layer should be measured and described at the maximum shell width, close to the plane of symmetry, where the sections of fibres are closest to perpendicular to their long axes. In such a way, one can compare shells that are theoretically similar in their ontogenetic stage, topological position and cross sections. In order to find out if the size of fibres depends on the age of the specimen concerned, we

analysed ontogenetic series of two micromorphic species (*Parasphenarina cavernicola* and *Probolarina faxensis*). Our pilot studies revealed that fibre size is independent from the age of the individual, at least in those taxa.

Manceñido *et al.* (2007, p. 2727) have recently referred to the two main shell microstructure patterns recognized in cross section as: (1) leptinoid (from the Greek: *leptos* = fine, thin, slender + *inos* = fibre), and (2) eurinoid (from the Greek: *eurys* = wide, coarse, broad + *inos* = fibre). These two terms are largely equivalent in scope and meaning to previous terminology, respectively: (1) 'rhynchonellidine' or 'fine fibrous' and (2) 'basiliolidine' or 'coarse fibrous' used by other authors (e.g. Motchurova-Dekova and Simon 2007, p. 121; Radulović *et al.* 2007, p. 771; Lee and Motchurova-Dekova 2008, p. 359). The earliest published compilation and analysis of available data on post-Palaeozoic rhynchonellide shell microstructure was advanced in Radulović *et al.* (2007, table 2, fig. 13). Herein we upgrade the existing data with further references and with the most recent SEM results obtained by NMD.

The Leptinoid pattern

This type is characterized by finer fibres, 5–40 (exceptionally up to 50) *μ*m wide, and 2–10 *μ*m thick, that are rather anisometric, having an anvil-like or halberd-like outline in cross section (though rhombic or subhexagonal may also occur). This pattern has been extensively documented among hemithiridoid taxa (Motchurova-Dekova 2001; Manceñido *et al.* 2007; Radulović *et al.* 2007; Lee and Motchurova-Dekova 2008; Motchurova-Dekova *et al.* 2008, with further references, and herein see Text-fig. 8C–E). These encompass many Triassic–Cretaceous cyclothyridids like *Cyclothyris*, *Almerarhynchia*, *Fissirhynchia*, *Lamellaerhynchia*, *Septaliphoria*, *Torquirhynchia* as well as Jurassic–Cretaceous tetrarhynchiids including tetrarhynchiines (*Tetrarhynchia*, *Goniorhynchia*, ?*Belbekella*), gibbirhynchiines (*Burmirhynchia*), kallirhynchiines (*Rhactorhynchia*), isjuminellines (*Isjuminella*, *Mosquella*, *Russirhynchia*), viarhynchiines (*Viarhynchia*, *Septatoechia*,

Antulanella) and cretirhynchiines (*Cretirhynchia*, *Burrirhynchia*), plus Recent notosariids (*Notosaria*). It has been further recorded in a Cretaceous form of uncertain systematic position (*Chathamirhynchia*), in several Jurassic–Cretaceous rhynchonelloid genera (e.g. Text-fig. 8A–B), both rhynchonellids (*Homoeorhynchia*, *Ivanoviella*, *Grasirhynchia*) and acanthothiridids (*Acanthothiris*), in a few Jurassic–Cretaceous dimerellid dimerelloids, both rhynchonellinines (*Sulcirostra*) and peregrinellines (*Peregrinella*, Taddei-Ruggiero 1994, and herein Text-fig. 8F) and even among early Palaeozoic rhynchotrematoids (*Rostricellula*, *Rhynchotreta*, *Stegerhynchus*, Williams 1997, and herein). In the case of recent cryptoporid dimerelloids, the average width of individual fibres in the mosaic of *Cryptopora* seems to be in the order of 10 *μ*m (cf. Curry 1983, pl. 2, fig. F; Alvarez *et al.* 2005, fig. 33), which would be consistent with this pattern (though additional evidence on that peculiar group is needed).

The Eurinoid pattern

This type is distinguished by its coarser fibres, 30–150 (exceptionally up to 175) *μ*m wide, and 10–70 *μ*m thick, which are more isometric in shape, showing a typically rhombic (to subquadrate or subrectangular and subpolygonal) outline in cross section.

The pattern has been widely recorded among pugnacoid genera (von Hagn *et al.* 1968; Smirnova 1984; Motchurova-Dekova and Taddei-Ruggiero 2000; Motchurova-Dekova 2001; Graziano *et al.* 2006; Tomašových 2006; Manceñido *et al.* 2007; Motchurova-Dekova and Simon 2007; Radulović *et al.* 2007; Dulai *et al.* 2008; Motchurova-Dekova *et al.* 2008, 2009, and herein see Text-fig. 9A–D). These comprise many Jurassic–Tertiary basiliolids, including lacunosellines (*Lacunosella*), pamirorhynchiines (*Pseudogibbirhynchia*, *Orbirhynchia*, *Basiliocostella*, *Jakubirhynchia*), basiliolines (*Soaresirhinchia*, *Probolarina*), as well as some Jurassic–Cretaceous erymnariids, both erymnariines (*Erymnaria*, *Costerymnaria*) and septocrurellines (*Septocrurella*). The eurinoid pattern also occurs in Triassic–Jurassic wellerelloids (Dagis 1974; Radulović 2008,

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TEXT-FIG. 8. Examples of taxa with homogeneous leptinoid microstructure. A, *Homoeorhynchia cynocephala meridionalis* (Eudes-Deslongchamps) *sensu* Ager 1967, NMNHS F-31475-1 (SEM #C), Yeovil, UK, level with *Dumortieria*, Upper Toarcian? Dorsal valve, primary layer and external surface below. B, *Acanthothiris* sp., NMNHS F-31484 (SEM #E), Burton cliff, Burton Bradstock, S England, UK, Bajocian. Ventral valve, rib, whole shell thickness, note the thick primary layer. C, *Torquirhynchia inconstans* (J. Sowerby), NMNHS F-31480 (SEM #F), Black Heads, Osmington, S England, UK, Lower Kimmeridgian. Dorsal valve, fragment from of a rib, note portion of the primary layer in the lower left corner. D, *Goniorhynchia boueti* (Davidson), NMNHS F-31489 (SEM #D), Burton cliff, Burton Bradstock, S England, UK,'*boueti* bed', Bathonian. Dorsal valve, sulcus, thick primary layer below. E, *Rhactorhynchia* sp., NMNHS F-31447-1 (SEM #A), Gloucester, Leckhampton Hill, UK, Inferior Oolite, Upper *Trigonia* Grit, Upper Bajocian. Dorsal valve, fragment from of a rib, internal surface of the shell above. F, *Peregrinella multicarinata* (Lamarck), NRM Br 70383, Chatillion, Drôme, France, Lower Neocomian (Hauterivian?). Portion from supposedly transverse section of a shell from rhynchonellide coquina.

and herein Text-fig. 9E), both cirpine wellerellid (*Cirpa*, *Euxinella*) and allorhynchid? (*Livarirhynchia*) genera; also in several Jurassic–Recent norelloids (Smirnova 1984; Motchurova-Dekova *et al.* 2002; Radulović *et al.* 2007, and herein Text-fig. 9F), including monticlarelline (*Monti-clarella*) and praemonticlarelline (*Scalpellirhynchia*) norel-lids, plus frieleiids (*Parasphenarina*, and possibly *Frieleia*, *Manithyris*, *Compsothyris*).
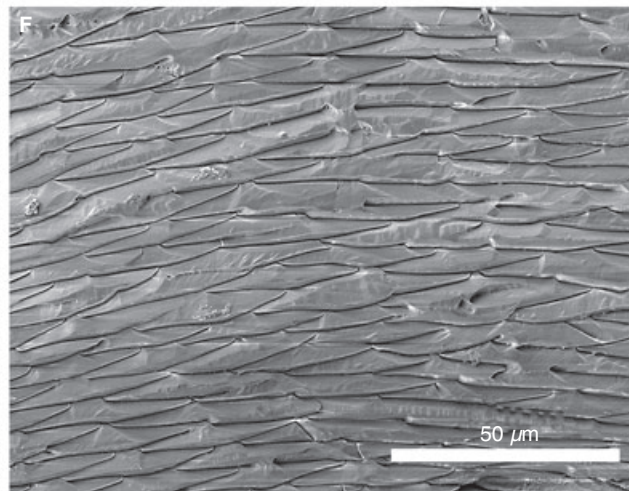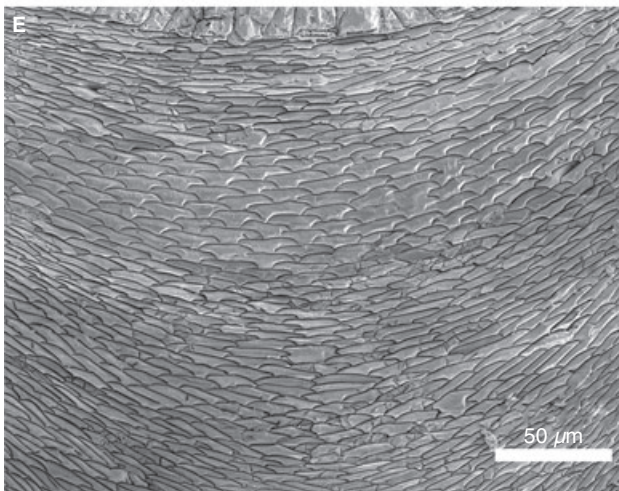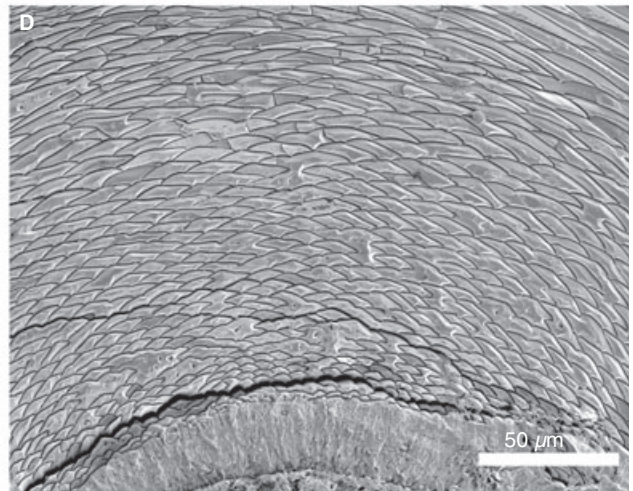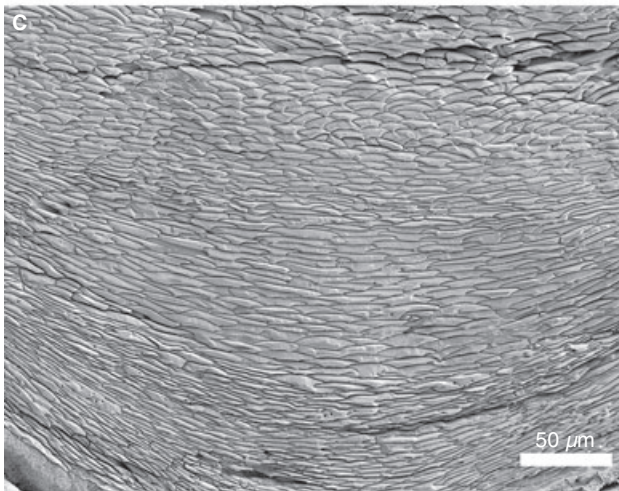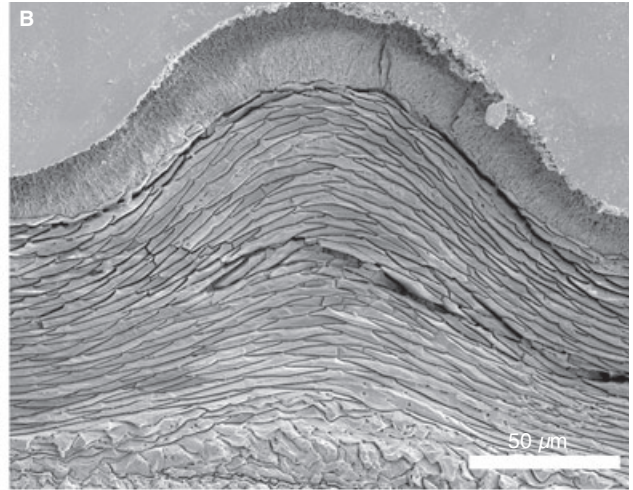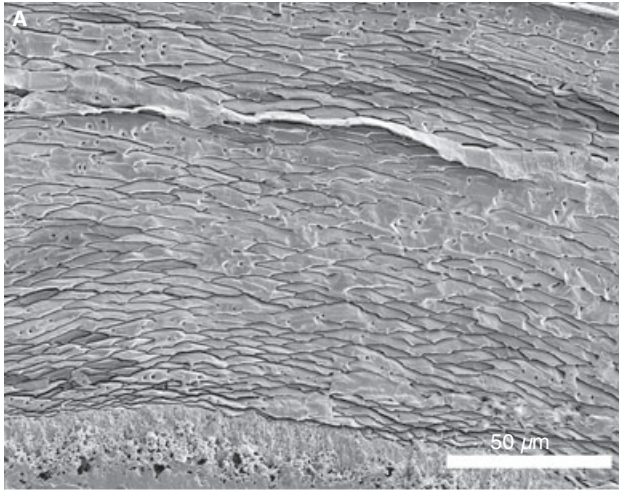
SUMMARIZED DISCUSSION

Text-figure 10 summarizes the perceived empirical correlation, at the present stage of knowledge, between those secondary layer microstructural patterns and the crural types and groups discussed above, as they are known to occur in various rhynchonellide superfamilies. Our working hypothesis, as presented in this figure (upgraded from fig. 13 in Radulović *et al.* 2007), is based mainly on post-Palaeozoic taxa, and awaits fur-
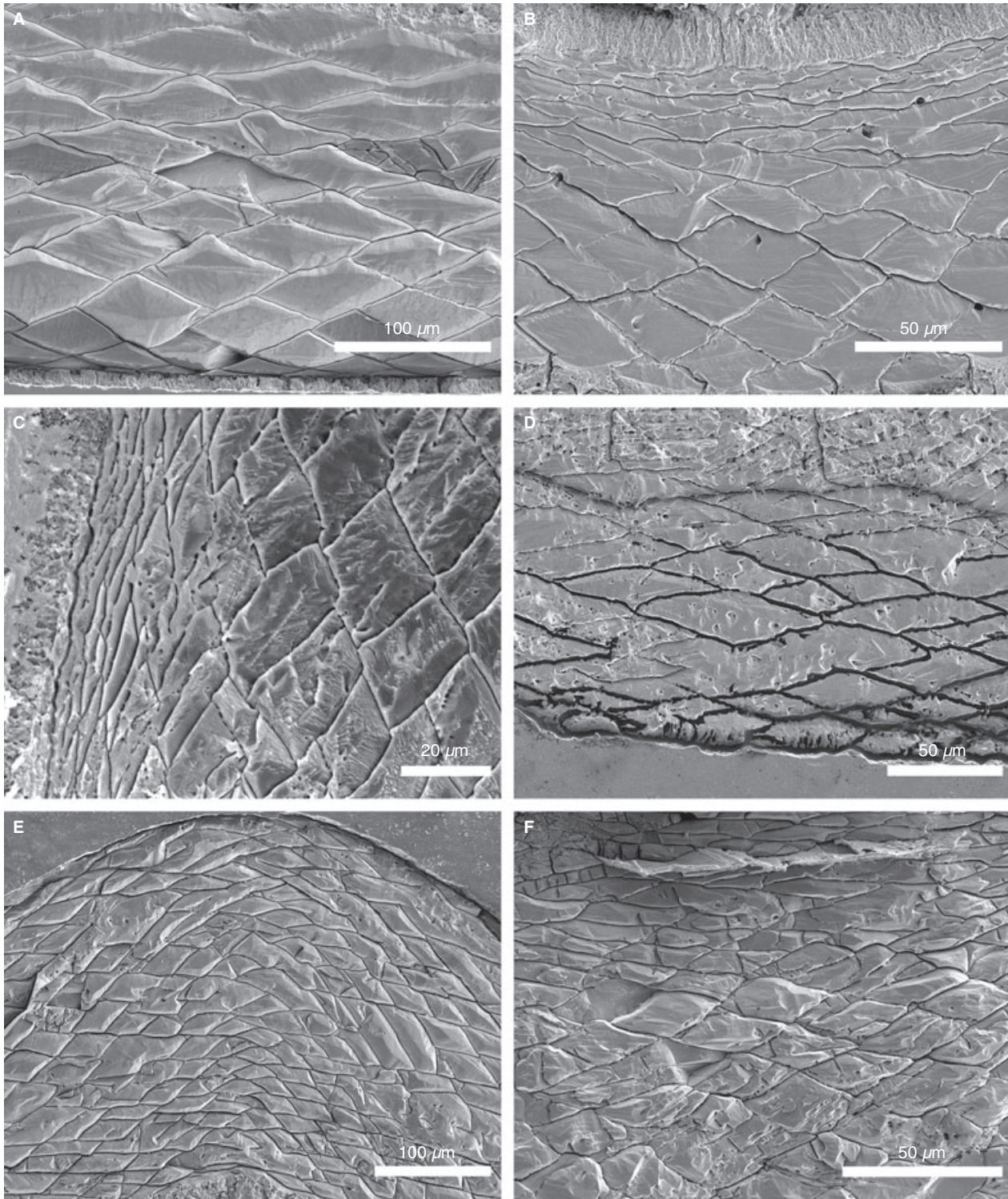
Pattern of secondary layer microstructure	Stylized section of the shell	Associated type of crura		Superfamilies
Leptinoid		Raducal	Raduliform Canaliform Calcariform	Rhynchonelloidea Hemithiridoidea Rhynchotrematoidea Dimerelloidea
		Ensimergal	Mergiform Ensiform	
Eurinoid		Septifal	Falciform Subfalciform Septiform Hamiform	Pugnacoidea Wellerelloidea Norelloidea
		Arcual	Arcuiform Spinuliform	

TEXT-FIG. 10. Correspondence between shell microstructural patterns and crural types. (Updated from Radulović *et al.* 2007, fig. 13).

ther checking for a number of groups not included in this study.

It may be rather premature to speculate which pattern could be the more primitive. Nonetheless, if one does take into account that the leptinoid pattern is extremely similar to what is widely known in terebratulides (Williams 1968; MacKinnon and Williams 1974) as well as in most spiriferides (MacKinnon 1974) and athyrides (Alvarez 1990), this may be taken as a hint that it could represent a plesiomorphic state. Conversely, the eurinoid condition could be suggestive of an apomorphic state (derived more than once ?), because it closely resembles the pattern recorded in a highly specialized group of athyrides, the konickinoids (Dagis 1974; MacKinnon 1974).

A nice example of the usefulness of concurrent lines of evidence involves representatives of the genera *Homaletarhynchia* and *Harmignirhynchia*. These taxa were initially proposed as subgenera of *Cretirhynchia* Pettitt, 1950 in a preliminary revision by Simon and Owen (2001). After close examination of published serial sec-

tions and original peels, their allocation to cretirhynchiines (tetrarhynchiid hemithiridoids) was queried and they were tentatively raised to generic status (Manceñido *et al.* 2007, pp. 2736–2741), because of the great resemblance of their inwardly concave crura with the subfalciform–hamiform series and overall similarity to apheleslines (basiliolid pugnacoids). In an independent parallel study, resorting to SEM microscopy, excavated crura were demonstrated to be subfalciform (with serrated distal edges) and the shell microstructure identified as non-homogeneous 'coarse fibrous' (i.e. eurinoid), as opposed to raduliform and 'fine fibrous' (i.e. leptinoid), respectively in true *Cretirhynchia s.s.* Hence, on that basis, formal transfer of *Homaletarhynchia* to Basiliolidae was soundly accomplished, and its possible ancestral rôle to *Aphelesia* also suggested (Motchurova-Dekova and Simon 2007, p. 119; Motchurova-Dekova *et al.* 2008, p. 237).

Additional work (still in progress by NMD, Eric Simon and others) has recently revealed that perhaps a mixed type of shell microstructure may be distinguishable (as

TEXT-FIG. 9. Examples of taxa with homogeneous eurinoid microstructure. A, *Probolarina faxensis* (Posselt), NHMM GM 2005.52, Fakse Quarry, Denmark, Danian. Dorsal valve, whole shell thickness, note thin primary layer below. B, *Pseudogibbirhynchia erycina* (Di Stefano), GI BAS M686-3, Dobravitsa – 1, Sofia district, Bulgaria, Upper Toarcian, Layer 7 (upper part), Bukorovtsi Member of the Ozirovo Fm. Ventral valve, sulcus, whole shell thickness, primary layer above. C, *Costerymnaria italica* Motchurova-Dekova and Taddei Ruggiero, PMNUF 71/M 16999, San Polomatese, Molise, S. Italy, Upper Cretaceous, Cenomanian. Portion of the shell, external surface and primary layer on the left. D, *Septocrurella sanctaeclarae* (Roemer), NMNHS F-30929, Beli Mel, Montana district, Bulgaria, Lower Callovian. Dorsal valve, whole shell thickness, primary layer decorticated. E, *Cirpa* cf. *langi* Ager, NMNHS F-31700 (KA-23), Tranak, Kazaldzha kaya, Burgas district, Bulgaria, upper part of Carixian and base of Domerian. Rib in the ventral valve, whole shell thickness, primary layer decorticated. F, *Scalpellirhynchia scalpellum* (Quenstedt), NMNHS F-31701 (K-53), Kotel, Sliven district, Bulgaria, base of Domerian. Portion of the dorsal valve.
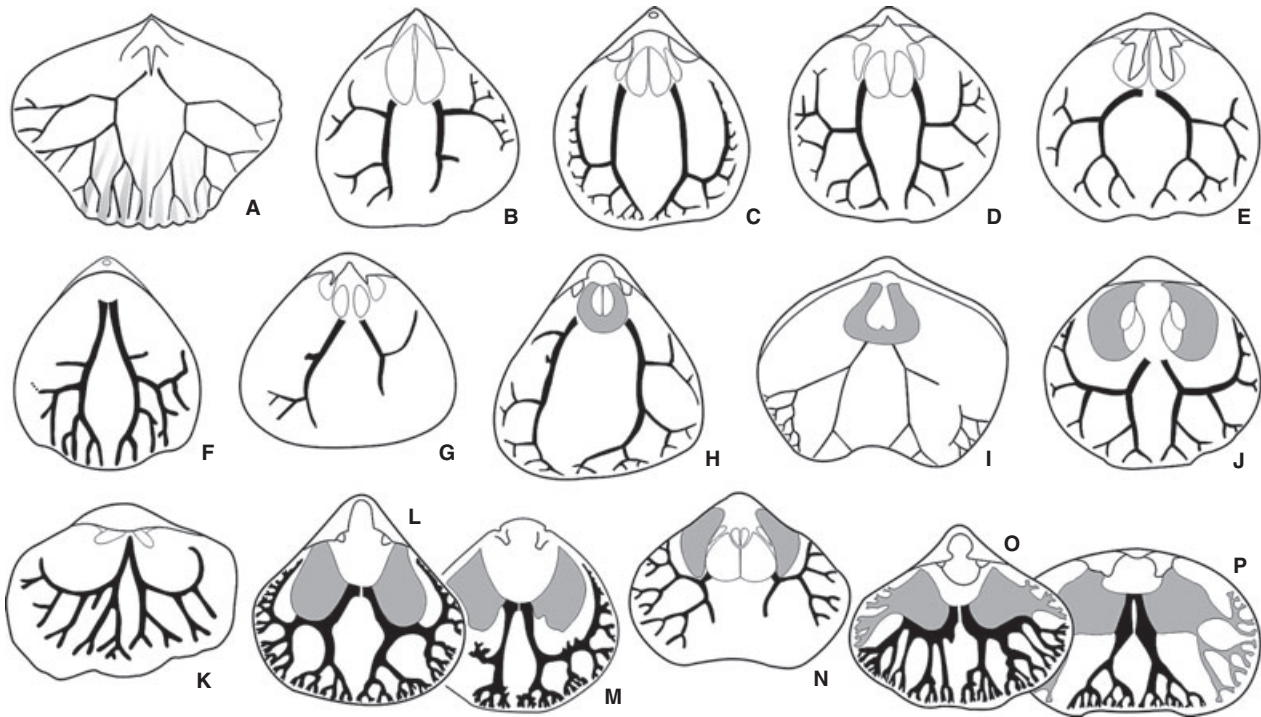
TEXT-FIG. 11. Examples of mantle canal patterns, both fossil (A–B, F, I–K, N) and extant (C–E, G–H, L–M, O–P); A–E, pugnacoids; F–H, norelloids; I–J, rhynchonelloids; K–P, hemithiridoids; A, dorsal internal mould of late Jurassic *Lacunosella*. B, latex mould of ventral valve of late Oligocene *Aetheia*. C, ventral interior of Recent *Basiliola*. D–E, ventral, dorsal interiors of Recent *Rhytirhynchia*. F, dorsal internal mould of mid Triassic *Norella*. G–H, dorsal, ventral interiors of Recent *Hispanirhynchia*. I, dorsal internal mould of late Triassic *Superbirhyncha*. J, dorsal internal mould of early Jurassic *Cuneirhynchia*. K, dorsal interior of Eocene *Tegulorhynchia*. L–M, ventral, dorsal interiors of Recent *Hemithiris*; N, ventral internal mould of late Cretaceous *Bohemirhynchia*. O–P, ventral, dorsal interiors of Recent *Notosaria*. Sketches adapted from: Quenstedt 1871 (A, J), Bittner 1890 (F), Cooper 1959 (B, C–E, G–H), Williams and Rowell 1965 (L–M, O–P), Nekvasilová, 1973 (N), Bitner 1996 (K), Siblík 2002 (I) (courtesy of the GSA and The University of Kansas, the Smithsonian Institution, Palaeontologia Polonica, O. Nekvasilová, M. Siblík).

already noticed in Motchurova-Dekova and Simon (2007) for *Homaletarhynchia limbata*). The secondary fibrous layer (not homogeneous) is differentiated into alternating sublayers of two types of fibres: anisometric anvil-like and more isometric rhomboidal fibres. A similar pattern is also observed in some representatives formerly attributed to *Cretirhynchia*. The formal revision of some taxa, which seem to combine mixed types of microstructure and a variant of subfalciform? crura, is forthcoming (by Eric Simon and NMD).

MANTLE CANAL PATTERNS

Although they had been occasionally recorded by some keen, observant, nineteenth-century palaeontologists (like Davidson, Quenstedt, Bittner, etc.) modern studies on brachiopod mantle canal systems were pioneered by Öpik (1934) for fossil forms, and Williams (1956) for extant ones, see also Williams *et al.* (1997, pp. 410–422). The

likelihood that their analysis could also help revealing broad kinships among rhynchonellides was recently reaffirmed (cf. Manceñido and Owen 2001, p. 197; Manceñido *et al.* 2007, pp. 2727–2730). Selected representative examples are illustrated herein in Text-figure 11. They show that a simplified, widely dichotomous, sparsely distributed pattern seems prevalent among Mesozoic and recent pugnacoids (basilioline, acanthobasilioline, lacunoselline, and aetheine basiliolids; Text-fig. 11A–E) which is similar to what is known in a few fossil and extant norelloids (norellid and frieleiid; Text-fig. 11F–H). On the other hand, among recent and fossil hemithiridoids, peripherally more densely branched patterns are known, sometimes inequidistributed saccate (e.g., hemithiridids and tetrarhynchiids) and sometimes apocopate lemniscate (notosariids and cyclothyridids; Text-fig. 11K–P). The pattern in fossil rhynchonelloids (Text-fig. 11I–J) looks similar to that shown in hemithiridids and perhaps is somewhat intermediate between it and the pattern in basiliolids.

CONCLUDING REMARKS

1. The value of crural types and their groupings for a better understanding of the systematic and evolutionary framework currently applied to post-Palaeozoic Rhynchonellida is corroborated; in addition, detailed studies of crural types draw attention to the significance of heterochronic processes in the development of evolutionary novelties or in the nature of recoveries from severe biotic crises.

2. From an evolutionary/developmental ('evo-devo') perspective, further studies of ontogenetic development of crura should be encouraged.

3. It is confirmed that basic patterns of shell structure are an important feature in establishing evolutionary kinship and for optimizing the 'Treatise' classification. Among post-Palaeozoic Rhynchonellida, the close correspondence between superfamilies having crura of the radical and ensimergal groups with leptinoid shell microstructure is noteworthy, whereas superfamilies possessing crura of the septifal and arcual groups correlate remarkably well with eurinoid shell microstructure.

4. A crucial test for our assertion may come from Palaeozoic genera presently assigned to the Pugnacoidea when they are investigated by SEM. It is predicted that only those stocks with septifal crura will yield eurinoid microstructure, whereas those with raducal crura (such as petasmariids, ladogiids, yunnanellids) will more likely reveal a leptinoid pattern.

5. A preliminary but promising proposal for a broad twofold subdivision of rhynchonellide mantle canal patterns is outlined. In this context, the advantage of analysing multiple morphological characters and, at the same time, of applying a variety of techniques is ratified.

6. The consistency of the morpho-structural features discussed invites us to reconsider the suitability of dividing the order Rhynchonellida at subordinal level. By further refining the current scheme, there is the possibility of generating a stable and robust classification that may help clarify taxonomic relationships.

Editor. Fernando Alvarez

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