Phylogeny of the deep-sea cirripede family Scalpellidae (Crustacea, Thoracica) based on shell capitular plate morphology

ANDREW SCOTT GALE*

School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

A cladistic analysis of 23 extant species of the deep-sea pedunculate cirripede family Scalpellidae was undertaken, based on 61 shell plate characters, and taking the Jurassic–Cretaceous scalpellomorph genus *Cretiscalpellum* as an out-group. The consensus tree shows progressive morphological change from basal to more derived taxa, but a derived group is marked by major morphological innovation, including 27 character state changes that permit subdivision of the family into two sharply demarcated clades – the more basal group is here placed within a redefined Scalpellinae (*Arcoscalpellum*, **Arcuatoscalpellum** gen. nov., **Diotascalpellum** gen. nov., *Graviscalpellum*, **Regioscalpellum** gen. nov., and *Scalpellum*), and a more derived group named **Amigdoscalpellinae subfam. nov.** that shows numerous progressive trends in morphology, permitting the recognition of three genera (*Amigdoscalpellum*, *Catherinum*, and *Weltnerium*). The phylogeny is independently supported by a recently published multiple DNA marker-based molecular phylogeny. The more basal Scalpellinae appeared in the Aptian (Early Cretaceous, 120 Mya), and derived Amigdoscalpellinae were already present by the Campanian (Late Cretaceous, 78 Mya), represented by **Catherinum anglicum sp. nov.** and *Amigdoscalpellum bellulum* from the UK Chalk. Specialized receptacles to accommodate dwarf males in the apical interior of the scutum evolved at least three times during the history of the scalpellids.

INTRODUCTION

The Scalpellidae is a family of predominantly deep-sea pedunculate cirripedes including approximately 250 valid species, which are currently placed in 29 genera and eight subfamilies (Young, 2007). It is considered to represent a monophyletic entity, on the basis of both morphological and molecular studies (e.g. Young, 2007; Pérez-Losada *et al.*, 2008). The family has an extensive fossil record extending back into the mid-Cretaceous (Aptian, 125 Mya; Withers, 1935; Buckeridge, 1983).

The genus *Scalpellum* Leach, 1817 was used in the 19th and early 20th centuries as a broad concept, and

as defined by Darwin (1851a) included pedunculate taxa possessing a relatively small number of lateral plate pairs (between four and six), encompassing all Scalpellidae and Calanticidae of current classifications. In his description of the *Challenger* cirripedes, Hoek (1883) included 43 species in *Scalpellum*, and suggested the possibility of further subdivision.

Tentative attempts to subdivide *Scalpellum* into groups and subgenera were begun by Pilsbry (1907) and Hoek (1907), who both used the form of the carina and the morphology of the dwarf males to characterize a number of subgenera and groups (for an exhaustive review, see Young, 1999). The genera were discussed by Withers (1953), who synonymized extensively, and the *Treatise on Invertebrate Paleontology* (Newman, Zullo

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*Corresponding author. E-mail: andy.gale@port.ac.uk

& Withers, 1969) included just three genera in the family, which would now be considered as scalpellids: *Scalpellum*, *Mesoscalpellum* Hoek, 1907, and *Arcoscalpellum* Hoek, 1907.

The next decade saw a great proliferation of scalpellid genera: in a taxonomic account of the Antarctic cirripedes, Newman & Ross (1971) created seven new genera, and Zevina (1978a,b) added a further 22 genera, classified into eight subfamilies. Subsequently, Newman (1996) elevated three of these subfamilies to family status (Calanticidae, Lithotryidae, and Pollicipedidae), leaving eight subfamilies and 29 genera for the scalpellids.

The proliferation of new genera was commented on by Foster (1980: 523), 'The Scalpellidae have recently been reclassified by Zevina (1978a,b), who built on an earlier proposal by Newman & Ross (1971), but the classification is still more convenient than natural'. Young (1999: 186) subsequently applied cladistic analysis to the genera in order to assess the monophyly of subfamilies. He commented that, 'The characters used for supra-specific taxonomy are homoplastic, therefore forming paraphyletic subfamilies'. He also noted that the basal group Arcoscalpellinae and its constituent genera were probably paraphyletic, citing *Trianguloscalpellum* as an example (Young, 1998, 1999); however, Young's 2007 review of extant scalpellids followed Zevina's generic classification in detail, although he commented on the significance of growth-dependent features in scalpellid classification, which had not been taken into account in previous studies. In his papers on scalpellids, Paulo Young seldom provided generic diagnoses, an exception being *Amigdoscalpellum* (Young, 2007: 59). A subsequent paper by Shalaeva & Boxshall (2014) refigured Hoek's *Challenger* scalpellids (Hoek, 1883), provided revised generic diagnoses based on the translation of Zevina's original descriptions, and summarized points of discussion made by Young (notably the 1998 and 2007 papers). A paper on the molecular phylogeny of Antarctic scalpellomorph cirripedes (Linse *et al.*, 2013) implied the paraphyly of species assigned to *Arcoscalpellum*.

The present study of scalpellid plate morphology was initially stimulated by Jens Høeg, whose detailed work on scalpellid reproductive systems (Buhl-Mortensen & Høeg, 2006, 2012; Yusa *et al.*, 2011) posed important questions concerning the phylogenetic relationships of species. Recently, Lin *et al.* (2015) have published a molecular phylogeny of pedunculate thoracicans using multiple DNA markers. Their scalpellid phylogeny (Lin *et al.*, 2015: fig. 3) compares well with the results obtained here from morphological analysis. In particular, this work suggested extensive poly- and paraphyly of the genera. In this paper, I undertake a systematic investigation of scalpellid plate morphology, using both articulated individuals and isolated plates, and

following the procedures adopted for verrucomorphs and basal balanomorphs by Gale (2014b) and Gale & Sørensen (2014), respectively. Polarity is identified from the use of the Cretaceous scalpellomorph genus *Cretiscalpellum* as an out-group (see discussion below).

MATERIAL AND METHODS

SPECIMENS

Twenty extant scalpellid species were selected in order to represent a significant part of the diversity of the group (Table 1); only fully grown specimens were used. Specimens were cleaned with hypochlorite, and both entire specimens and isolated, cleaned plates were photographed with either a USB camera (Veho 100) or an SEM, depending on the size of the material. Fossil material held in the Natural History Museum, London, UK, was also studied and figured. The images were used to develop a character list and matrix (Appendix S1; Table S1), which was analysed by PAUP to provide phylogenetic analysis.

Institutional abbreviations: BGS, British Geological Survey, Keyworth, Nottingham, UK; NHMUK, Natural History Museum, London, UK; SM, Sedgwick Museum, Cambridge, UK.

MORPHOLOGICAL ANALYSIS

The scalpellid body is sharply demarcated into an oval, laterally compressed capitulum, and a flexible peduncle, which bears alternating columns of plates (Fig. 1A, B). There is a marked and consistent difference in size between the large species assigned to (1) *Regioscalpellum* gen. nov. (Young, 2007: *Regioscalpellum regium* Thomson, *Regioscalpellum gigas* Hoek, and *Regioscalpellum darwini* (Hoek)), (2) *Arcoscalpellum* (*Arcoscalpellum sociabile* (Annandale) and *Arcoscalpellum michelottianum* Seguenza), and (3) *Graviscalpellum* (*Graviscalpellum pedunculatum* Hoek), which commonly attain capitular heights of several centimetres (Fig. 2), and other scalpellids (Fig. 3), which rarely exceed 1 cm (Young, 2007). Abbreviations are given in Table 2.

The capitulum in scalpellids comprises 14 plates (paired scuta, terga, upper latera, inframedian latera, rostrolatera, carinolatera, plus an unpaired rostrum and an unpaired carina). The rostrum is lost in some scalpellids (Young, 1998) and, exceptionally, the rostrolatus is also lost in the aberrant *Scalpellopsis* Broch, 1922 (Young, 2001). The out-group, *Cretiscalpellum*, additionally possesses paired subcarinolatera and a subcarina (Fig. 4) absent in all other taxa considered here.

The curved carinal (dorsal) margin of the capitulum is formed by the narrow, tall, triangular carina, the upper carinal margin of the tergum, and the carinolatera. The rostral margin is made up of the occludent margins of the terga and scuta, and the lateral

Table 1. Details of extant scalpellid species examined during this study

| Name	Identification	Locality	Name used here
Catherinum albatrossianum (Pilsbry, 1907)	H. Broch	64°24'N, 28°50'W 1484 m	*Catherinum albatrossianum*
Verum striolatum (G.O. Sars, 1877)	H. Broch	Ingolf Exped., 63°13'N, 6°32'W 1783 m	*Catherinum striolatum*
Arcoscalpellum sociabile (Annandale, 1905)	?	32°25'N, 28°33'W Japan, 200 m	*Arcoscalpellum sociabile*
Arcoscalpellum michelottianum (Seguenza, 1876)	H. Broch	20°10'N, 117°30'W China Sea 704 m	*Arcoscalpellum michelottianum*
Amigdaloscalpellum hispidum (G.O. Sars, 1890)	H. Broch	549 m, Lofoten Islands	*Catherinum hispidum*
Weltnerium nymphocola (Hoek, 1883)	H. Broch	Biofar Stn 274, 698 m	*Weltnerium nymphocola*
Trianguloscalpellum rubrum (Hoek, 1883)	?	West of Nagasaki, Japan	*Diotascalpellum rubrum*
Ornatoscalpellum stroemii (M. Sars, 1859)	?	Dana station no. 5840, 330 m	*Weltnerium stroemii*
Tarasovium cornutum (G.O. Sars, 1879)	?	Biofar Stn 770, 583 m	*Weltnerium cornutum*
Catherinum recurvitergum (Gruvel, 1900)	P. Young	Stn 190 off Durban, 29°42'S, 33°19'W, 2790 m	*Catherinum recurvitergum*
Catherinum tortilum (Zevina, 1973)	P. Young	Stn 190 off Durban, 29°42'S, 33°19'W, 2790 m	*Catherinum tortilum*
Verum novaezelandiae (Hoek, 1883)	P. Young	Stn 302, Ceylon, 19°42'N, 86°48'E, 1210 m	*Catherinum novaezelandiae*
Amigdaloscalpellum rigidum (Aurivillius, 1898)	P. Young	Stn 190 off Durban, 29°42'S, 33°19'W, 2790 m	*Amigdoscalpellum rigidum*
Arcoscalpellum mamillatum (Aurivillius, 1898)	P. Young	Stn 190 off Durban, 29°42'S, 33°19'W, 2790 m	*Amigdaloscalpellum mamillatum*
Arcoscalpellum sculptum (Hoek, 1907)	?	Stn 234, Mombassa–Madagascar, 4940 m	*Amigdaloscalpellum sculptum*
Arcoscalpellum truncatum (Hoek, 1883)	A.S. Gale	Indian Ocean, off Rodrigues Island	*Amigdaloscalpellum truncatum*
Scalpellum stearnsi Pilsbry, 1890	H. Broch	Japan, 32°25'N, 128°33'W, 366 m	*Scalpellum stearnsi*
Scalpellum scalpellum (Linnaeus, 1767)	H. Broch	Hillboek, Lutken, 1861 m	*Scalpellum scalpellum*
Trianguloscalpellum regium (Thomson, 1873)	P. Young	Stn 665, Kermadec Deep, 36°58'S, 178°21'E, 2530 m	*Regioscalpellum regium*
Trianguloscalpellum darwini (Hoek, 1883)	P. Young	Stn 235, Mombassa–Madagascar, 4940 m	*Regioscalpellum darwini*
Trianguloscalpellum gigas (Hoek, 1883)	P. Young	Stn 235, Mombassa–Madagascar, 4940 m	*Regioscalpellum gigas*
Tarasovium natalense (Barnard, 1924)	P. Young	Station 196, off Durban, 29°55'S, 30°20'E, 445–490 m	*Weltnerium natalense*
Tarasovium valvulifer (Annandale, 1910)	Annandale	No information	*Weltnerium valvulifer*
Anguloscalpellum pedunculatum (Hoek, 1883)	Yusi Yocha	Japan	*Graviscalpellum pedunculatum*
Ornatoscalpellum gibberum (Aurivillius, 1892)	Jens Hoeg	South America	*Weltnerium gibberum*
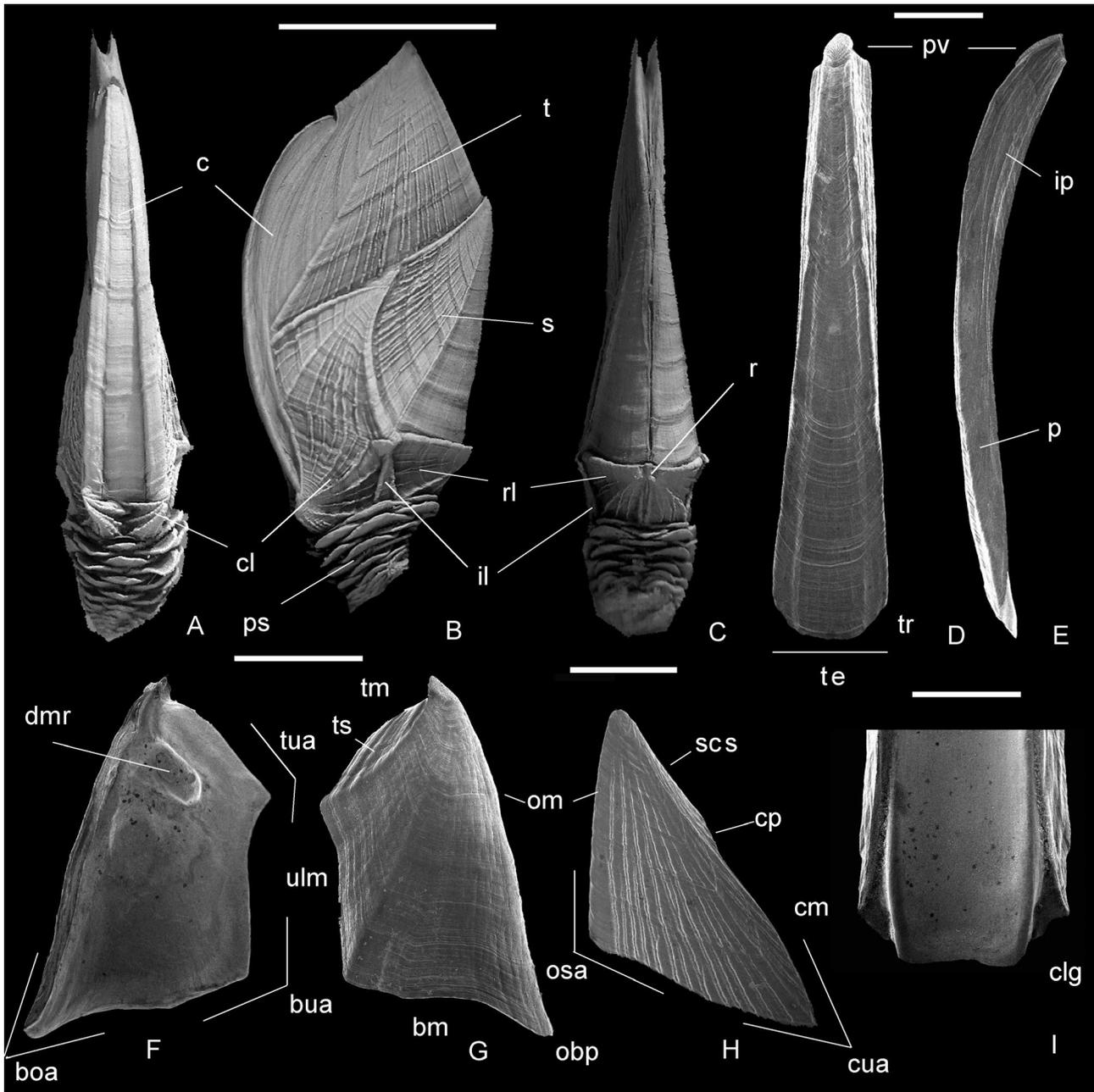
Figure 1. Morphology and nomenclature of the scalpellid capitulum, and constituent carina, tergum, and scutum. A–C, I, *Amigdoscalpellum truncatum* (Hoek, 1883): A, dorsal (carinal) view; B, lateral view; and C, ventral (rostral) view. D, E, carina of *Catherinum striolatum* (G.O. Sars, 1877) in dorsal and lateral aspect. F, G, scutum of *Weltnerium stroemii* (M. Sars, 1859) in internal and external views, respectively. H, *Amigdoscalpellum rigidum* (Aurivillius, 1898), tergum in external aspect. For abbreviations, see Table 2. For details of localities etc., see Table 1. Scale bars: A–C, 5 mm; D–I, 1 mm.

margin of the rostrolatera. The aperture, which permits extension of the cirri and penis, extends from above the scutal adductor to the apex of the terga.

There is a marked difference between large scalpellids that possess a thick, pilose cuticle (Young, 2007) and the smaller group, which have a thinner cuticle.

Additionally, the smaller group have proportionately thinner, more delicate plates.

There is some diversity of sculpture in scalpellids. The out-group, *Cretiscalpellum*, includes both forms, which have a very inconspicuous, weak radial sculpture (*Cretiscalpellum aptiensis* Withers; Fig. 4A, B), and
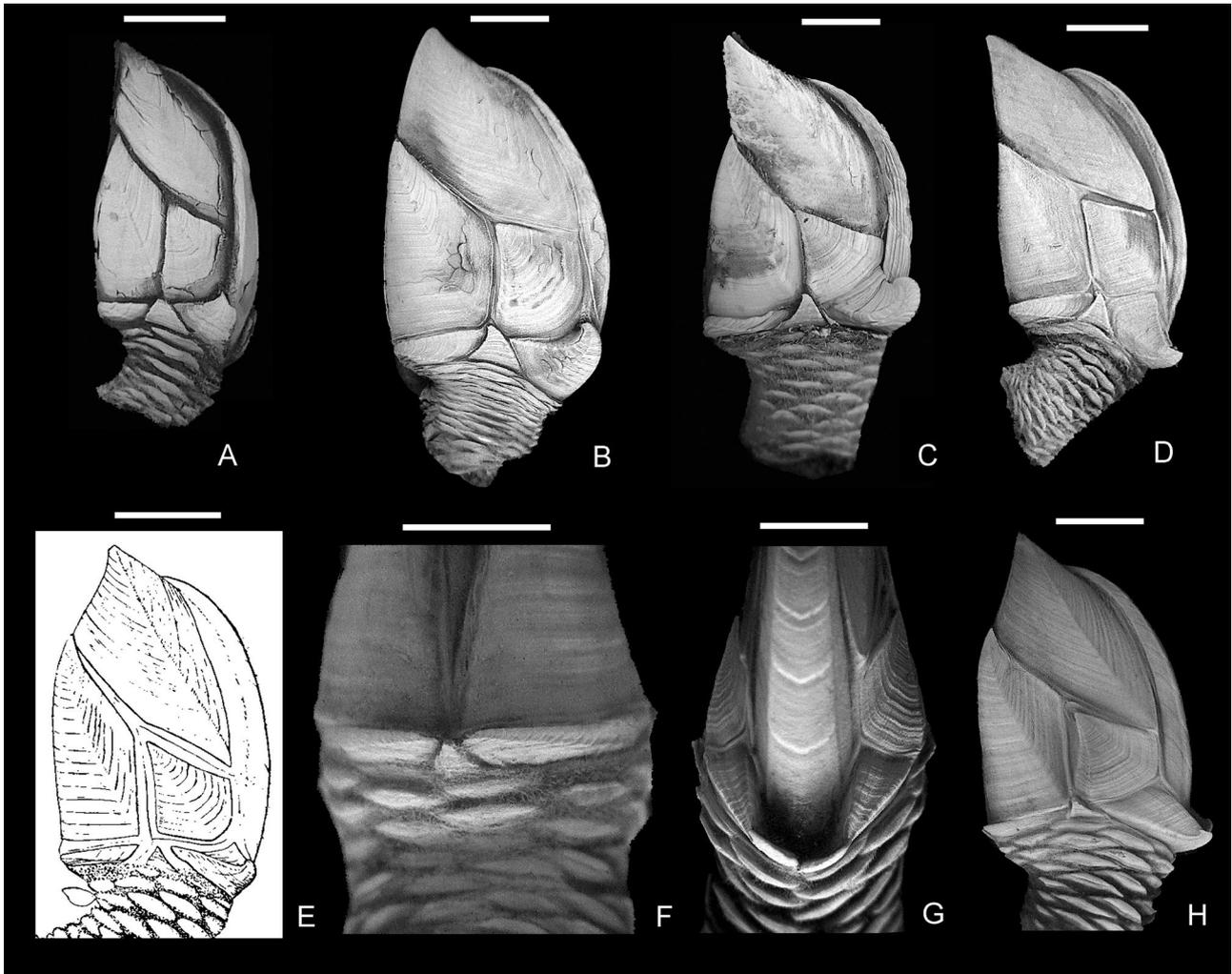
Figure 2. A–E, H, Scalpellinae in lateral aspect: A, *Diotascalpellum rubrum* (Hoek, 1883); B, *Regioscalpellum regium* (Thomson, 1873); C, *Arcoscalpellum michelottianum* (Seguenza, 1876); D, *Arcoscalpellum sociabile* (Annandale, 1905); E, *Arcoscalpellum regina* (Pilsbry, 1907); F–H, *Graviscalpellum pedunculatum* (Hoek, 1883); F, ventral (rostral) aspect; G, dorsal (carinal) view; H, lateral view. See Table 1 for details of localities etc. Scale bars: 5 mm.

those in which a strong, sriate radial sculpture is developed [*Cretiscalpellum striatum* (Darwin, 1851); Fig. 4C–M]. The group of large extant scalpellids (*R. regium*, *R. darwini*, *Arcoscalpellum michelottianum*, *Arcoscalpellum sociabile*, and *G. pedunculatum*) possess variably distinct commarginal growth lines (Fig. 2). In the genus *Amigdaloscalpellum* (Fig. 3E–G), and large individuals of some species of *Catherinum* (*Catherinum striolatum* G.O. Sars, Fig. 3A; *Catherinum recurvitergum* Gruvel, Fig. 3B), radial ribs are well developed, a feature that is characteristic of all members of *Amigdaloscalpellum* (Young, 2007). *Catherinum novaezelandiae* (Hoek) and *Weltnerium nymphocola* (Hoek) (Fig. 3C, D) are dominated by commarginal growth lines, but a weak, coarse radial sculpture is present on the carinolatus, upper latus, and

inframedian latus of *Weltnerium stroemii* (M. Sars) (Fig. 3H).

In most thoracicans capitular plate growth takes place incrementally from the apex (umbo) by the addition of successive sheets of calcite internally, which progressively expands the plate margin. In the case of the carina, terga, and rostra, this commences adjacent to the primordial valves [except in the aberrant species *Trianguloscalpellum balanoides* (Hoek, 1883); see Broch, 1922, refigured by Newman *et al.*, 1969, in which primordial valves are also developed on the upper latus and some peduncular plates]. Usually the umbo remains apical in position throughout growth, but it may become central or basal in position, characters that have been used extensively in taxonomy (e.g. Withers, 1953; Zevina, 1981).

Figure 3. Lateral aspects of Amigdoscalpellinae: A, *Catherinum striolatum* (G.O. Sars, 1877); B, *Catherinum recurvitergum* (Gruvel, 1900); C, *Catherinum novaezelandiae* (Hoek, 1883). D, *Weltnerium nymphocola* (Hoek, 1883); E, *Amigdaloscalpellum rigidum* (Aurivillius, 1898); F, *Amigdaloscalpellum truncatum* (Hoek, 1883); G, *Amigdaloscalpellum sculptum* (Hoek, 1907) H, *Weltnerium stroemii* (M. Sars, 1859). See Table 1 for localities. Scale bars: 5 mm.

Table 2. Abbreviations

bm	basal margin of scutum
boa	basal–occludent angle of scutum
bua	basal–upper latus angle of scutum
c	carina
cl	carinolatus
clg	carinolatus groove on carina
cm	carinal margin on tergum
cp	carinal point – on tergum
cu	carinal umbo
cua	carinal–upper latus angle
dmr	dwarf male receptacle on scutum
il	inframedian latus
ip	intraparietes on carina
ilm	inframedian latus margin
lm	lateral margin on carinolatus
ils	inframedian latus surface on carinolatus
ls	lateral surface on rostrum
mr	median ridge on rostrum
om	occludent margin on tergum and scutum
p	parietes on carina
pm	peduncular margin on carinolatus
pv	primordial valves on carina, scutum, tergum
r	rostrum
rl	rostrolatus
rs	rostral surface on rostrolatus
scs	supracarinal surface on tergum
scm	supracarinal margin on tergum
ss	subumbonal surface on rostrum
su	scutal umbo
t	tergum
te	tectum on carina
tm	tergal margin on scutum
tr	tectal ridge on carina
ts	tergal surface on scutum
tua	tergal–upper latus angle on scutum
u	umbo
uls	upper latus surface on carinolatus
ulm	upper latus margin on carinolatus

Growth in most thoracican plates extends outwards from the umbo in an arc determined by the angles of the sides of the plate; in the carina, this is usually a relatively low angle, but in the scuta of forms such as *Zeugmatolepas* (Zeugmatolepadidae) with central umbones it can approach 180°.

In many neobalanomorphs, wall plates grow both basally and apically, by the development of lateral extensions from the parietes called alae and radii (Darwin, 1854; Otway & Anderson, 1985; Anderson, 1994; Gale & Sørensen, 2014), which are sharply demarcated by an upward turn in the growth lines. This was called diametric growth by Anderson (1994), and it serves to permit expansion of the orifice with growth.

A similar plate-growth strategy is present in many scalpellomorphs (Calanticidae and Scalpellidae), in which outgrowths from the plate margins adjacent to the umbo develop, initially as a low shelf that may extend apically above the umbo, or laterally on one or both sides of the plate (Fig. 5). The growth strategy is well illustrated by the ontogeny of *Scalpellum stearnsi* Pilsbry, 1890 (Fig. 5A–G), in which apical extensions (green) appear initially on the inframedian latus and progressively enlarge (Fig. 5B–G); concomitantly, the intraparietes on the carina enlarge, and eventually displace the carinal umbo to a subapical position (Fig. 5F, G). Extensions on the upper latus form an inverted V-shaped structure (Fig. 5F, G); finally, a prong-like extension develops on the scutum in the fully grown form (Fig. 5G).

These structures were called 'subepidermal secondary flanges' by Foster (1978). The surface of this shelf is marked by stepped growth lines, different from those on the rest of the plate (e.g. green area in Fig. 5H), and the umbo becomes subapical in position as a result. This growth mode is here called polymetric growth, and it probably developed as an effective means of infilling spaces in the tessellation of plates that make up the flattened box-shaped capitulum of groups such as scalpellids. A change in shape of any one plate would necessitate concomitant change in other plates in order to infill the resulting spaces in the tessellation.

Polymetric growth also provides important phylogenetic information. The shelf-like outgrowths with well-demarcated growth lines were initially encased in epidermal tissue, but subsequently became part of the external surface of the plate, flush with the rest of the surface, and the two sets of growth lines became incorporated into a single pattern. This is exemplified by *R. regium* and related species, in which a short, well-demarcated polymetric shelf is developed on the upper latus margin of the carinal latus (Figs 6P, 10J). In *Arcoscalpellum michelottianum*, *Arcoscalpellum sociabile* (Figs 2C, D, 6F, K, P), and all more-derived scalpellids this has become a wing-like extension of the carinal latus, which contacts both the upper latus and carina. The degree of demarcation and sculpture of these polymetric structures thus provides some evidence of the level of derivation from an ancestral state, which can be illustrated with carinae of the Cretaceous genus *Virgiscalpellum* Withers, 1935. Less-derived taxa possess clearly demarcated intraparietes, on which closely spaced growth lines run parallel with the tergal margin (*Virgiscalpellum* sp. nov; Fig. 5J, K); in the derived *Virgiscalpellum beisseli* (Bosquet & Müller, 1857), a sculpture of radial ribs extends seamlessly across the entire carina (Fig. 5L, M). Similar progress can be seen on the upper latus of *W. stroemii* (Fig. 5I), in which the upper region represented by the shelf in Figure 5H has an identical growth-line pattern and sculpture to the remainder of the plate.
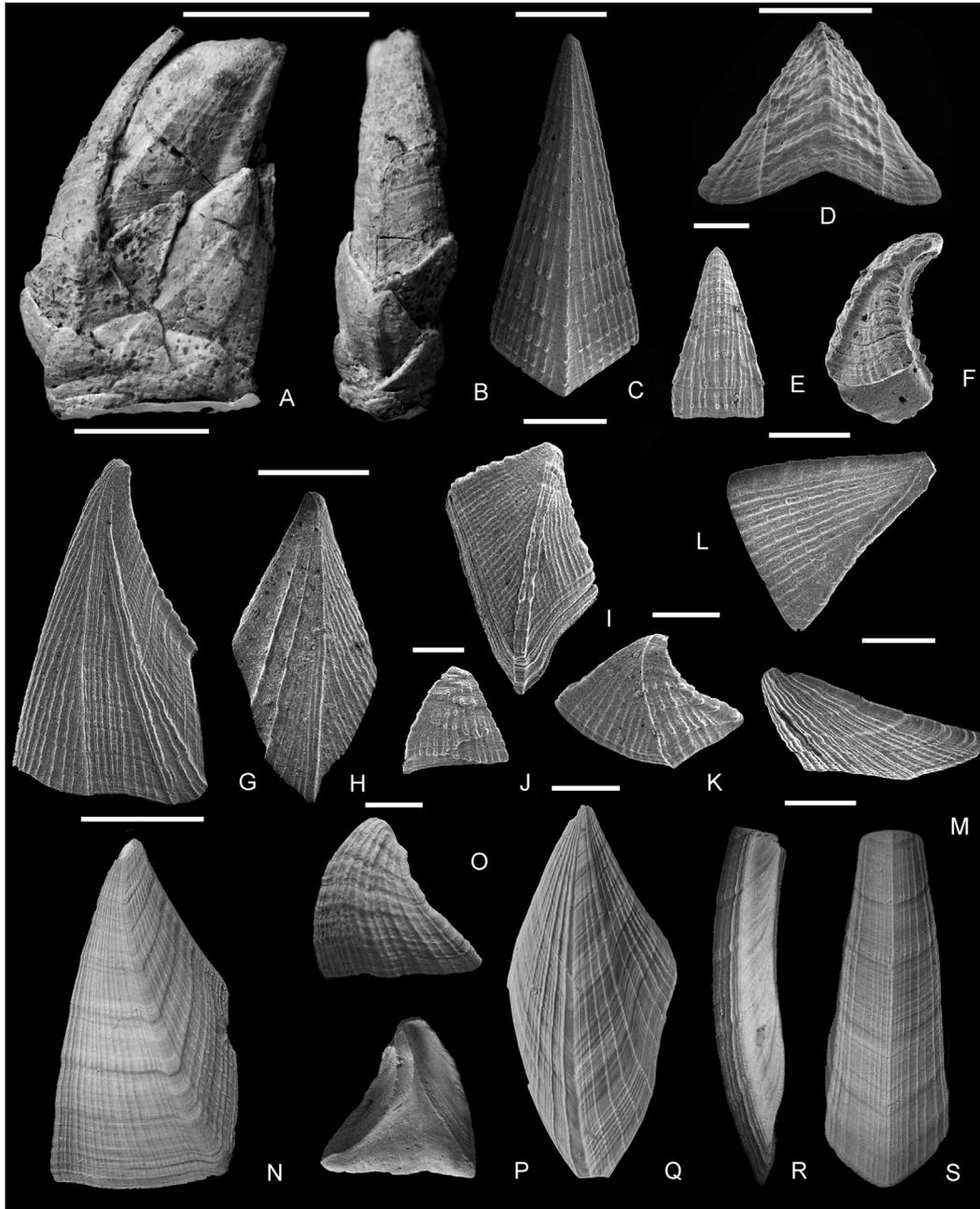
Figure 4. Comparative morphology of out-group and basal scalpellid. A, B, *Cretiscalpellum aptiensis* Withers, 1935, capitulum, in lateral and carinal aspects. Bargate Stone, upper Aptian, Shackleford, Surrey, UK. Holotype, BGS 49533 (original of Withers, 1935, pl. 13, fig. 1). C–L, *Cretiscalpellum striatum* (Darwin, 1851b): C, carina (NHMUK IC 1191); D, F, rostrum NHMUK IC 1192); E, subcarina (NHMUK IC 1193); G, scutum NHMUK IC 1194); H, tergum (NHMUK IC 1195); I, carinolatus (NHMUK IC 1196); J, subcarinolatus (NHMUK IC 1197); K, inframedian latus (NHMUK IC 1199); L, upper latus (NHMUK IC 1200). Upper Campanian, Upper Chalk, Keswick, Norwich, UK. M–S, *Arcuatoscalpellum arcuatum* (Darwin, 1851b). M, exterior of rostrolatus (NHMUK IC 1221). N, exterior of scutum (NHMUK IC 12222). O, P, carinolatus (original of Collins, 1974, pl. 11, fig. 10, NHMUK In. 61368). Q, tergum (original of Collins, 1965, pl. 90, fig. 12, NHMUK In. 64259). R, S, carina in carinal and lateral aspect (NHMUK In. 1754). M, N, Upper Albian, Gault Clay. M, *cristatum* subzone (Bed 8i), Folkestone, Kent. O–Q, *orbignyi* subzone, Paddlesworth, Kent. R, S, Dunton Green, Kent. Note similarities in sculpture and overall valve morphology; the taxa differ importantly in the presence of a subcarina and subcarinolatus in *Cretiscalpellum*; these are absent from **Arcuatoscalpellum gen. nov.** Scale bars: A–B, 10 mm; N, Q, 5 mm; R, S, 2 mm; C, G, H, O, P, 1 mm; D–F, I–M, 0.5 mm.
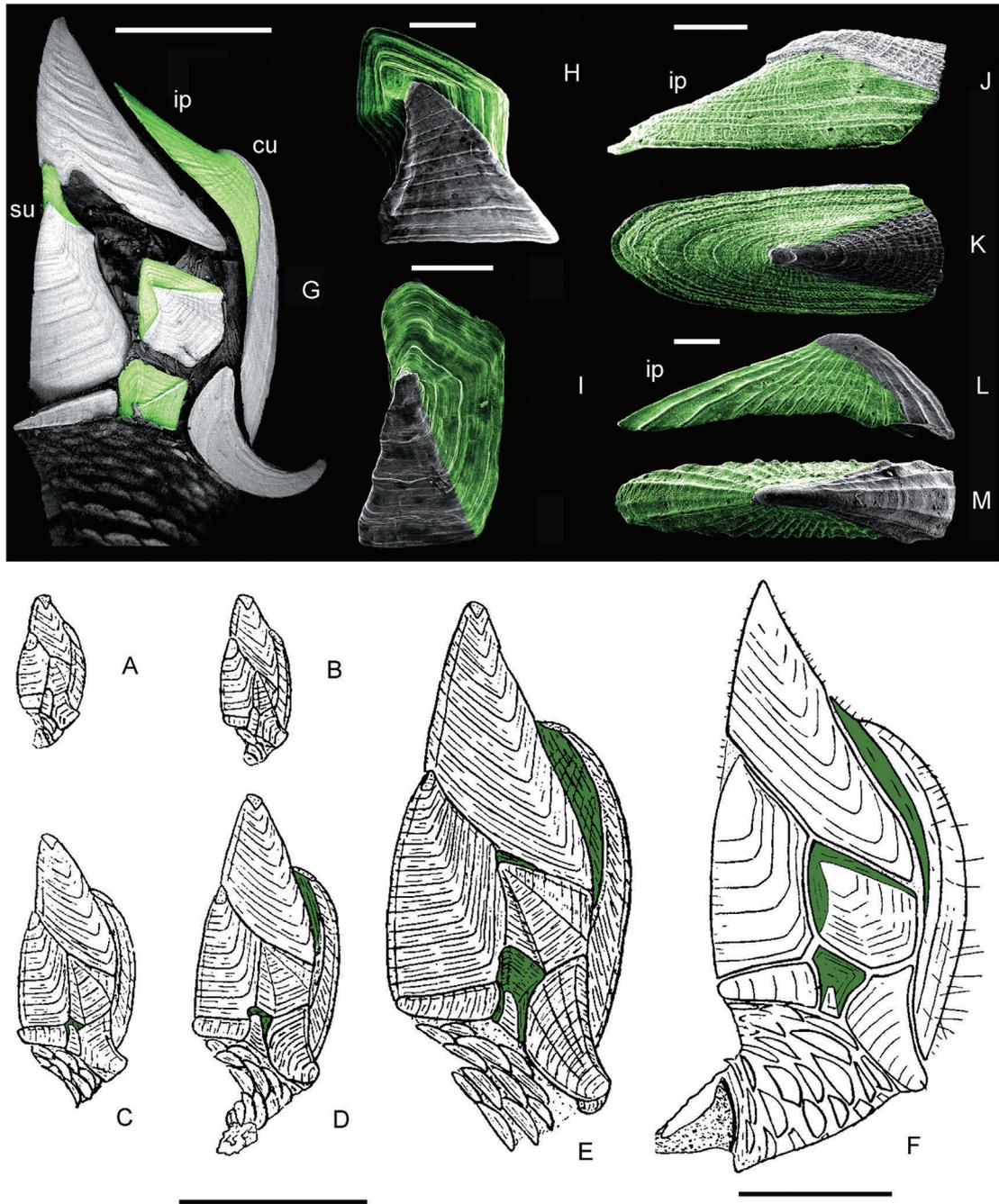
Figure 5. Scalpellidae to show polymetric development of valves. A–G, ontogenetic sequence of *Scalpellum stearnsi* Pilsbry, 1890, with progressive development of polymetric outgrowths on the carina (ip, intraparietes), upper latus, inframedian latus, and finally the scutum (G), shown in green. This growth pattern has the effect of moving the umbones to a subapical position (e.g. su, scutal umbo; cu, carinal umbo in G). A–F are modified after Withers (1953: figs 13–19). B, *Arcoscalpellum quadratum* (Dixon, 1850), inframedian latus, Eocene, Ypresian, London Clay, Sheppey, Kent, UK, showing subepidermal polymetric outgrowth, forming a contact with the scutum and upper latus (NHMUK In. 3440). Note the difference in surface sculpture between the external surface and the outgrowth. C, inframedian latus, *Weltnerium nymphocola* (Hoek, 1883), in which the polymetric portion of the plate (green) is flush with the rest of the plate, and has an identical sculpture. D, E, carina of ***Virgiscalpellum* sp. nov.**, upper Campanian, Keswick Pit, Norwich, Norfolk, UK (Wood, 1988), to show polymetric intraparietes (green), which differs in sculpture from the parietal and tectal surface. F, G, carina of *Virgiscalpellum beisseli* (Bosquet and Müller, in Bosquet, 1857), in which the tectum, parietes, and intraparietes all have an identical sculpture of coarse radial ribs. Same locality. Scale bars: A, 5 mm; B–G, 1 mm.
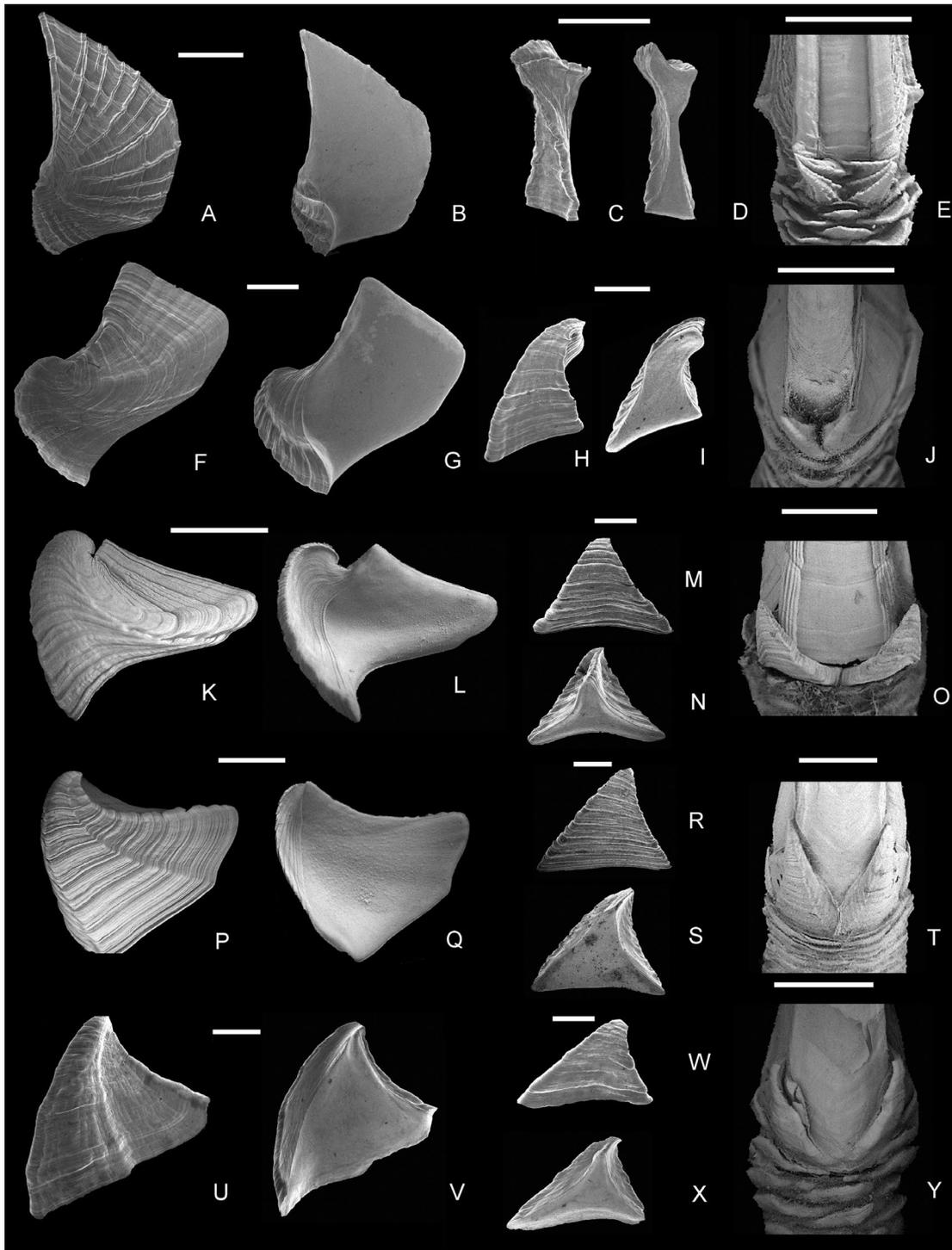
Figure 6. Evolution of lateral plate morphology, dorsal side: A–E, *Amigdoscalpellum truncatum* (Hoek, 1883); F–J, *Arcoscalpellum sociabile* (Annandale, 1905); K–O, *Arcoscalpellum michelottianum* (Seguenza, 1876); P–T, *Regioscalpellum regium* (Thomson, 1873); U–Y, *Diotascalpellum rubrum* (Hoek, 1883). External aspect of carinolatus (A, F, K, P, U); interior of carinolatus (B, G, L, Q, V); external view of inframedian latus (C, H, M, R, W), interior of inframedian latus (D, I, N, S, X); dorsal (carinal) view of capitulum (E, J, O, T, Y). See Table 1 for details of localities. Note the migration of the position of the carinolatus umbo from apical to nearly basal, the progressive incurvature of the umbo, and the development of an upper latus surface. The lower four species are assigned to the Scalpellinae, the uppermost one to the Amigdaloscalpellinae. Scale bars: A–E, J, K–T, Y, 1 mm; F–I, U–X, 0.5 mm.

Carina

The unpaired, dorsally positioned carina is rhomboidal or triangular in dorsal view, and between four (Fig. 4C) and eight (Fig. 1A, B) times taller than broad. A strong apicobasal ridge is present in *Cretiscalpellum*, but absent in Scalpellidae, which are characterized by the separation of the external surface of the carina into a dorsal, flat tectum (t), sometimes delimited laterally by tectal ridges (tr, Fig. 1D), wall-like parietes, and the variable presence of polymetric structures called intraparietes (ip), which develop along the tergal margin, effectively infilling the gap between the carina and tergum (Darwin, 1851a; Withers, 1928, 1935) (Fig. 1D, E). They are not developed in *Diotascalpellum rubrum* (Hoek), *R. regium*, and *Arcoscalpellum michelottianum*, but are present in all other taxa and are large in *W. stroemii* (Fig. 3H). Tectal ridges (tr, Fig. 1D, E) are developed in *Amigdoscalpellum truncatum* (Hoek) (Fig. 6E), *Amigdoscalpellum rigidum* (Aurivillius, 1888) (Figs 3E, 7X), and *Ca. striolatum* (Fig. 7S). The interior basal portion of the carina may be notched for articulation with the carinolatera (clg, Fig. 1I). The carinal umbo is commonly apical in scalpellids, but is subapical in *W. stroemii* (Fig. 3H). Carinae were extensively used by Withers (1935) to characterize Cretaceous species and groups.

Terga

The terga underwent significant change during the evolution of scalpellids. Plesiomorphically, the terga are rhomboidal in outline, and the surfaces on either side of the apicobasal line are subequal, often slightly smaller on the carinal side (*Arcoscalpellum michelottianum*, *Arcoscalpellum sociabile*, *Cretiscalpellum*, *D. rubrum*, *G. pedunculatum*, and *R. regium*, Figs 2, 4, 8I), and there are discrete upper and lower carinal margins. The scutal/occludent angle is obtuse, at about 140°. In all more derived taxa [*Amigdoscalpellum mamillatum* (Aurivillius, 1898), *Am. rigidum*, *Am. truncatum*, *Ca. novaezelandiae*, *Ca. striolatum*, *W. nymphocola*, *W. stroemii*; Fig. 1H, 8J–L] the terga are triangular, the single carinal margin is almost straight, and the angle between the scutal/occludent angle is about 110°. Additionally, there is a peak in the carinal margin where the surface accommodates the tip of the carina (cp, e.g. Fig. 1H), above which a low, triangular surface is present [supracarinal surface (scs), Figs 1H, 8J–L]. A further discrete triangular region is present adjacent to the occludent margin, called the occludent surface (os, Figs 1H, 8J–L).

Scuta

Plesiomorphically, the scuta are subtriangular, and the basal, occludent, and upper latus margins are set close to right angles; the apex is upright, the upper latus margin is straight, and the tergal margin simple (*Arcuatoscalpellum arcuatum* Darwin, Fig. 4N;

Arcoscalpellum michelottianum, Fig. 2C; *Arcoscalpellum sociabile*, Fig. 2D; *Cretiscalpellum*, Fig. 4G; *D. rubrum*, Figs 2A, 8A, E; *G. pedunculatum*, Fig. 2H; *R. regium*, Fig. 2B). In derived forms, the outline of the scutum is trapezoidal, because the angle between the basal and occludent margins (boa) is acute (Fig. 1F, G), and the angle between the basal and upper latus margins is obtuse (bua, Fig. 1F, G; *Am. mamillatum*, Fig. 3G; *Am. rigidum*, Fig. 3E; *Am. truncatum*, Fig. 3F; *Ca. recurvitergum*, Fig. 3B; *Ca. striolatum*, Fig. 3A). The trapezoidal form is exaggerated in *Ca. novaezelandiae*, *W. nymphocola*, and *W. stroemii* (Fig. 3C, G, H), and the rostral angle forms a process in *W. nymphocola* and *W. stroemii* (obp, Figs 1F, G, 3D, H, 8D, H). In the derived group, the apex of the scutum is sharply acuminate and incurved (Fig. 8C–E, H–J); there is a small flange on the tergal margin on which the growth lines deflect towards the apex, called the tergal surface (ts, Figs 1G, 8B–D); the umbo of the upper latus rests in a groove on the scutum, marked by an inflection of the upper latus margin (Figs 3, 8C–D). The apical interior of the scutum is unmodified in *Diotascalpellum* gen. nov. (Fig. 8E), *Regioscalpellum* gen. nov., *Arcoscalpellum michelottianum*, and *Arcoscalpellum sociabile* (Fig. 9B), but a short triangular embayment for dwarf males is present in *Am. rigidum* (Figs 8F, 9C) and *Am. truncatum*. This is elongated and deepened in *Catherinum hispidum* (G.O. Sars) (Fig. 8G), *Ca. novaezelandiae* (Fig. 9D), *W. nymphocola*, and *W. stroemii* (Fig. 8H). This derived condition was illustrated by Darwin (1851a: pl. 6, 1b′, 1c′, 2a′) in the scalpellid species *Weltnerium ornatum* (Gray, 1848) and *W. stroemii*.

Rostrum

An unpaired, symmetrical rostrum is present in all thoracicans crownward of the Carboniferous *Praelepas* (Newman *et al.*, 1969), with the exception of the Lepadidae. Although it is absent in a few scalpellids (e.g. Young, 1998), all of the taxa in the present study possess a rostrum, albeit sometimes a tiny one. In the out-group *Cretiscalpellum* (Figs 4D, F, 10A) the rostrum is triangular, slightly broader than tall, possesses a triangular raised central ridge, and lateral triangular wing-like processes (ls), which are overlapped by the rostrolatera. In scalpellids rostra fall into three categories: (1) broad, trapezoidal–triangular forms, with a subumbonal surface, broadly similar to those in the out-group, and a large triangular external surface (*Arcoscalpellum michelottianum*, Fig. 11I; *Arcoscalpellum sociabile*, Fig. 11E; *D. rubrum*, Fig. 11Q; *R. regium*, Fig. 11M); (2) tiny, oval–rhomboidal rostra, in which the external surface is limited to a small apical region (*Am. rigidum*, Fig. 12Q; *Am. truncatum*, Fig. 11A; *Ca. novaezelandiae*, Fig. 12I; *Ca. striolatum*, Fig. 12M); (3) rectangular–trapezoidal forms with a flat external surface that extends over the height of the plate

Figure 7. Evolution of lateral plate morphology, dorsal side: A–E, *Weltnerium stroemii* (M. Sars, 1859); F–J, *Weltnerium nymphocola* (Hoek, 1883); K–O, *Catherinum novazelandiae* (Hoek, 1883); P–T, *Catherinum striolatum* (G.O. Sars, 1877); U–Y, *Amigdoscalpellum rigidum* (Aurivillius, 1898). External aspect of carinolatus (A, F, K, P, U); interior of carinolatus (B, G, L, Q, V); external view of inframedian latus (C, H, M, R, W); dorsal (carinal) view of basal capitulum (D, I, N, S, X); enlarged lateral view of basal capitulum (E, J, O, T, Y). Note the changes in the nature of the articulation between the carinolatera of a pair (interpenetrant, X; opposed double articulation, D, I, N, S) and those in the shape of the inframedian latus (triangular, W; waisted hourglass, M, R; pentagonal, C, H). See Table 1 for details of localities. Scale bars: A–C, F–H, M, P-R, U–V, 0.5 mm; D, E, I, J, N, O, S, T, X, Y, 1 mm.
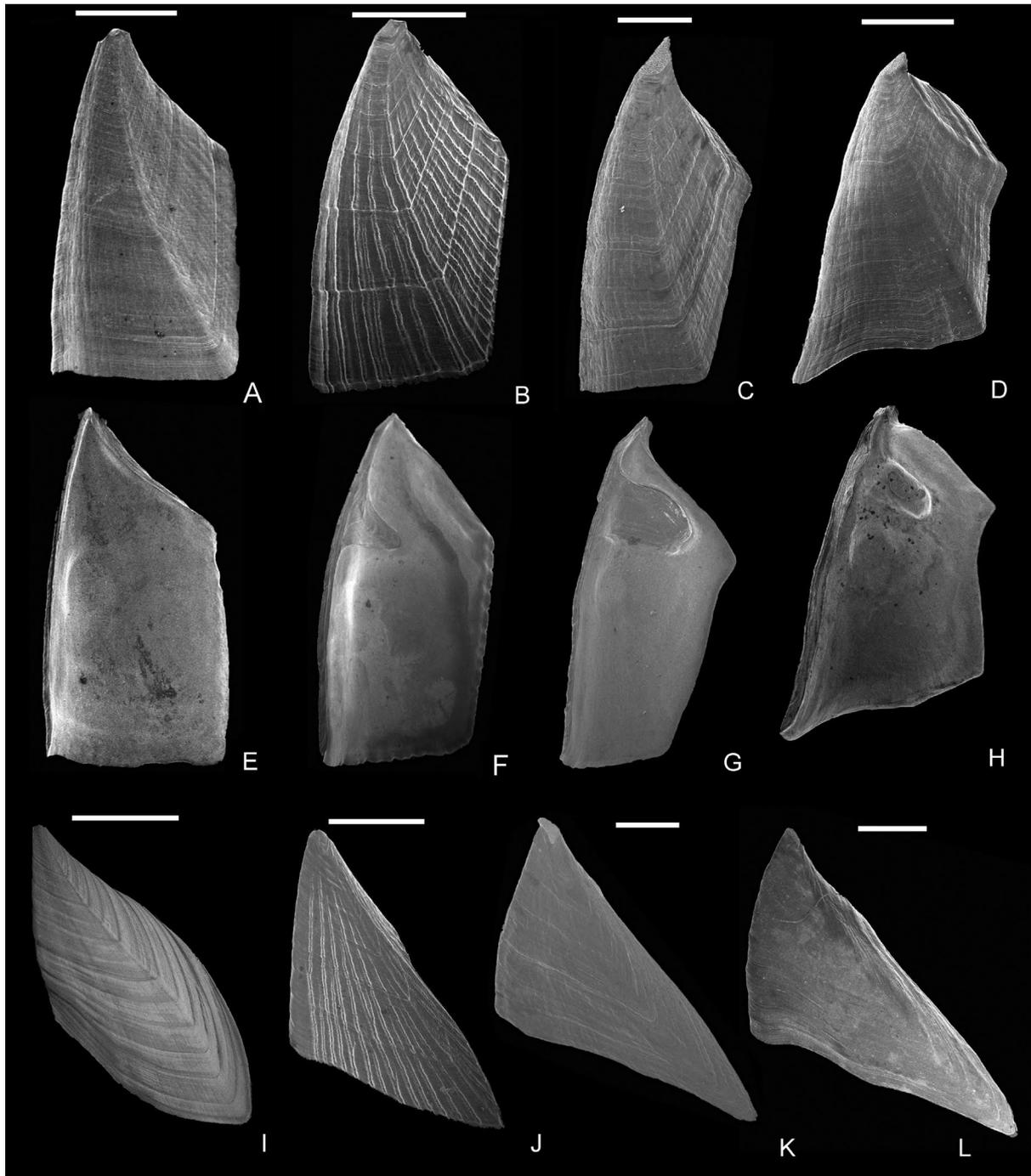
Figure 8. Scalpellid scuta and terga. Scuta: A, E, *Arcoscalpellum sociabile* (Annandale, 1905); B, F, *Amigdoscalpellum rigidum* (Aurivillius, 1898); C, G, *Catherinum hispidum* (G.O. Sars, 1890); D, H, *Weltnerium stroemii* M. Sars, 1859). Terga: I, *Arcoscalpellum michelottianum* (Seguenza, 1876); J, *Amigdoscalpellum rigidum*; K, *Catherinum hispidum*; L, *Weltnerium stroemii*. See Table 1 for details of localities. Note the overall progression of morphological change from left to right in the shape of the scutum, with the basal–occludent angle becoming more acute, and the basal–upper latus angle more obtuse, leading to a more trapezoidal outline. Additionally, a small tergal surface develops, and the umbo becomes incurved, and the dwarf male receptacles become larger and better defined. The terga change from an oval–rhombic outline (I) to a right triangular one (J–L), the ventral margin has developed a narrow supracarinal surface (scs), with an inflexion where the tip of the carina rests against the carinal margin. See Table 1 for details of localities. Scale bars: K, 2 mm; A, E, F, J, M, N, 1 mm; B–I, L, 0.5 mm.
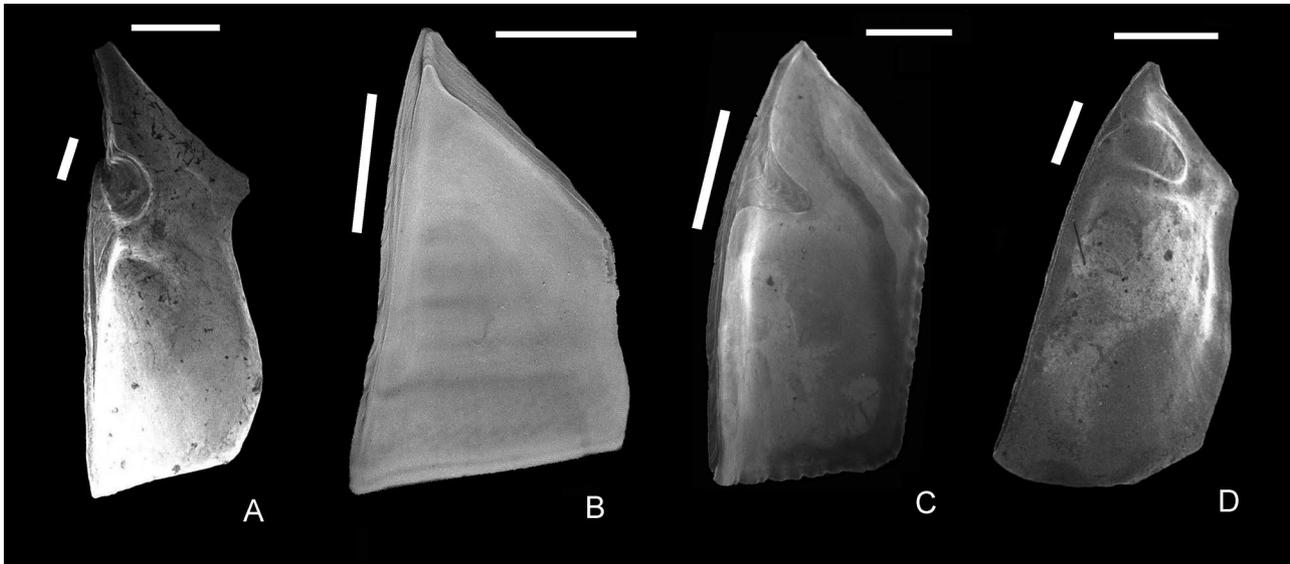
Figure 9. Receptacles for dwarf males on the interior of scuta. A, *Scalpellum scalpellum* (Linnaeus, 1767), note deep oval depression adjacent to umbo. B, *Arcoscalpellum michelottianum* (Seguenza, 1876), in which receptacle is long and shallow; compare with Buhl-Mortensen & Høeg 2006). C, *Amigdaloscalpellum rigidum* (Aurivillius, 1898), with a shallow V-shaped depression. *Catherinum novaezelandiae* (Hoek, 1883) has a deep, sharply defined receptacle in an apical position. Position of dwarf male receptacles/attachment sites indicated. See Table 1 for localities for extant taxa. Scale bars: B, 5 mm; A, 1 mm; and C, D, 0.5 mm.

(*W. nymphocola*, Fig. 12E; *W. stroemii*, Fig. 12A). The form of the rostrum, and its relationships with the rostrolatera, are among the most distinctive variable features within the Scalpellidae (see Figs 11, 12); compare the illustrations of basal scalpellids (*Arcoscalpellum michelottianum*, *Arcoscalpellum sociabile*, *Diotascalpellum* gen. nov., *Regioscalpellum* gen. nov.; Fig. 11E–T) with those of derived forms (Figs 11A–D, 12).

Rostrolatus
The rostrolatus imbricates the rostrum on its ventral margin, and its upper margin shallowly overlaps the base of the scutum (Fig. 1B, C); its median margin articulates with the inframedian latus, and the basal margin contacts peduncular scales. A transverse ridge runs from the umbo to the angle of the basal margin and inframedian latus margin (Fig. 10G, H). The rostrolatera in scalpellids fall into two well-demarcated morphological groups: (1) a basal group in which these are broad, low, and gently concavo-convex, and in which the concave facet for rostral articulation extends over the height of the plate (Fig. 11E–T); (2) a more derived group in which the plates are subrectangular to subtriangular, only slightly broader than tall, in which the rostral articular surface forms a short triangular

Figure 10. Homologies of scalpellid plates: A, *Cretiscalpellum striatum* (Darwin, 1851b), rostrum; B, E–G, J, K, *Regioscalpellum regium* (Thomson, 1873); C, H, I, *Amigdaloscalpellum rigidum* (Aurivillius, 1898); N, O, R, *Amigdaloscalpellum truncatum* (Hoek, 1883); C, *Weltnerium stroemii* (M. Sars, 1859); P, *Diotascalpellum rubrum* (Hoek, 1883). *Arcoscalpellum sociabile* (Annandale, 1905), L, M. A–D, ventral view of rostrum, lateral process that articulates with interior of rostrolatus is coloured brown. Note shape changes, from triangular–trapezoidal (A, B), to oval–rhombic (C), to triangular with large flat exterior face (D). E–I, rostrolatera. E–G, plesiomorphic broad, low morphology, with tall concave articular facet for rostrum (brown). H, I, derived condition, in which the pair of triangular plates have a long ventral articulation, the small rostrum is largely internal, and the rostral articular surface extends over only half the height of the plate (brown in I, rs, see also Figs 1C, 11). J–P, carinolatera. P, plesiomorphic condition, in which a low flange (olive green) overlaps the upper latus. J, L, development of the upper latus surface (blue), from a polymetric flange in (J), which extends in all more-derived taxa to become a tall surface (e.g. K; see also Figs 6, 7). K, M–O, interior of carinolatus, with carinal surface coloured pink, and lateral surface coloured lime green. In the plesiomorphic condition, the lateral surface is external (J), but this becomes internal (M) and the paired carinolateral articulate at the base. In the derived condition (N, O), the lateral surface has developed three ribs with intervening grooves that interlock with those on the opposing plate (e.g. Fig. 6E). A flat articulation surface (mauve) has also developed. Q, R, interior of carinae, to show articular surfaces for carinolatus.
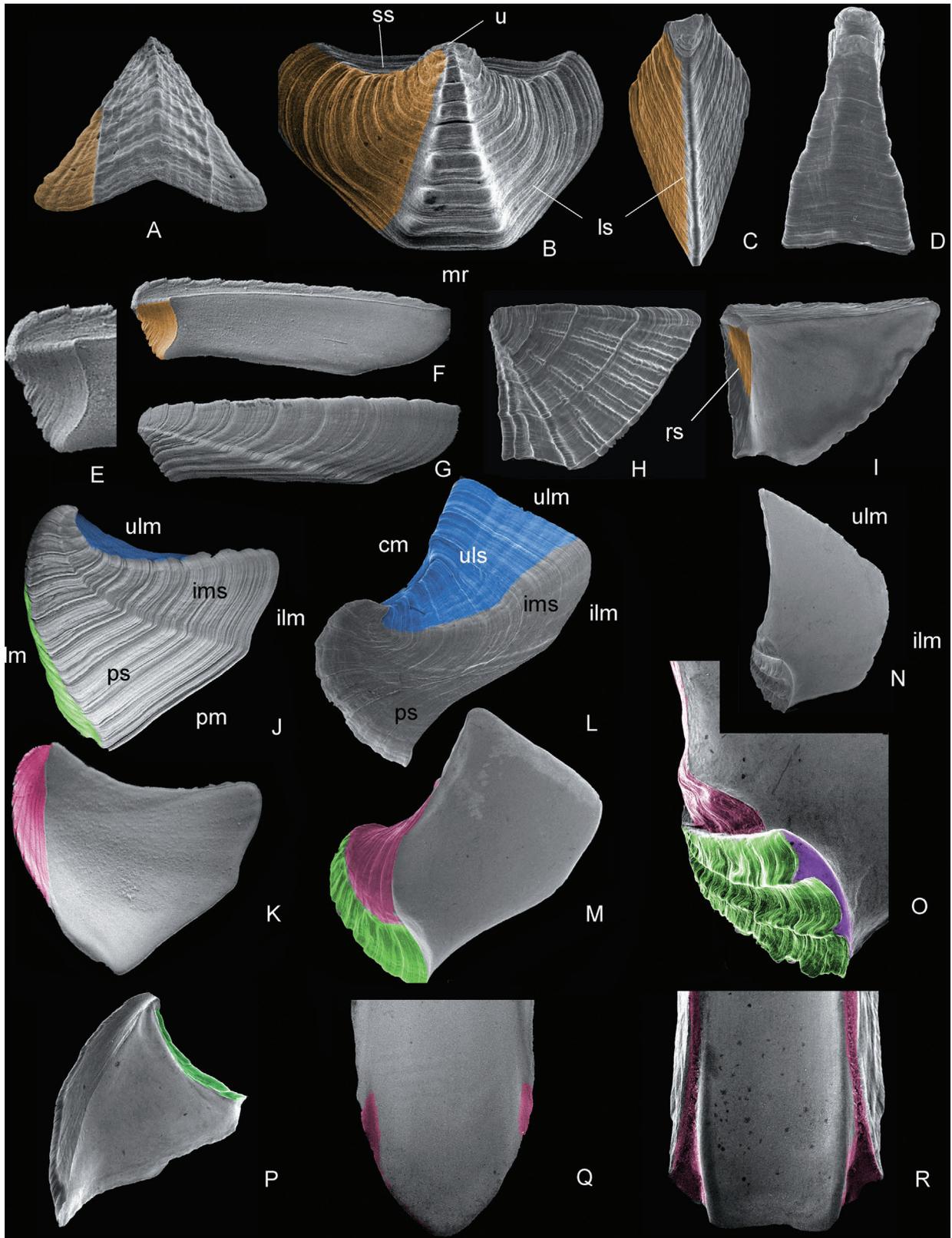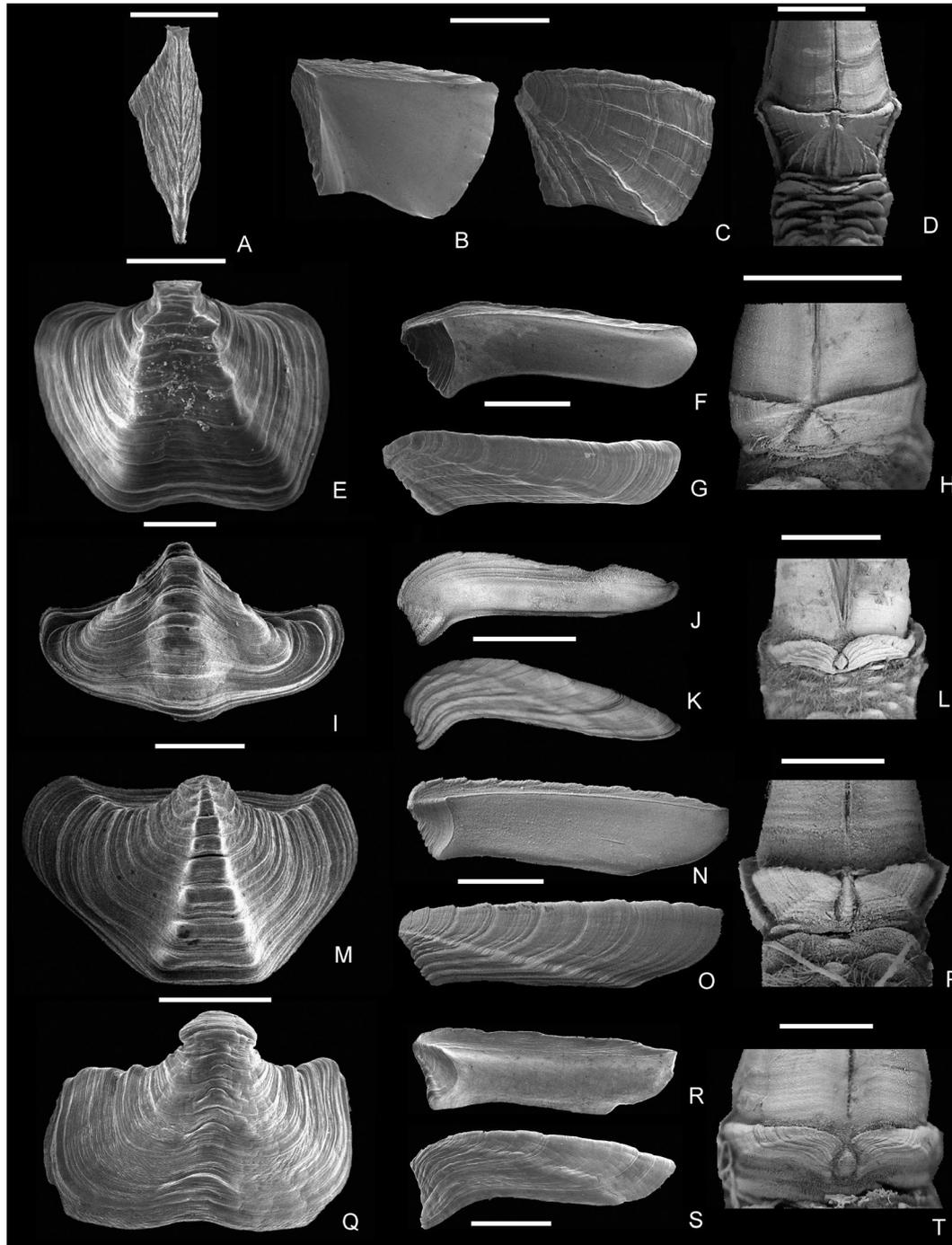
Figure 11. Evolution of rostra and rostrolateral plate morphology, ventral side: A–D, *Amigdoscalpellum truncatum* (Hoek, 1883); H, *Arcoscalpellum sociabile* (Annandale, 1905); I–L, *Arcoscalpellum michelottianum* (Seguenza, 1876); M–P, *Regioscalpellum regium* (Thomson, 1873); Q–T, *Diotascalpellum rubrum* (Hoek, 1883). Rostrum in ventral (rostral) aspect (A, E, I, M, Q); rostrolatus in external (C, G, K, O, S) and internal (B, F, J, N, R) views. Basal capitulum in ventral (rostral) aspect (D, H, L, P, T). Note similarity of plesiomorphic taxa (E–T), in which the rostrolatus is broad and low, and the rostrum is trapezoidal to triangular and chunky. The rostrolatera do not contact over the midline in these taxa. Note striking morphological differences in the more derived *Amigdoscalpellum truncatum* (A–D), in which the rostrolatus is narrower and taller, the plates meet over the midline, and the rostrum is tiny, tall, rhomboidal, and almost completely covered by the rostrolatera. The rostral articulation only extends over half of the rostrolatus (see also Fig. 10C, H, I). Scale bars: L, P, 2 mm; B–D, F–H, J, K, N, O, T, 1 mm; A, I, M, R, S, 0.5 mm; and E, Q, 0.2 mm.

Figure 12. Evolution of rostra and rostrolatera plate morphology, ventral side: A–D, *Weltnerium stroemii* (G.O. Sars, 1859); E–H, *Weltnerium nymphocola* (Hoek, 1883); I–L, *Catherinum novazelandiae* (Hoek, 1883); M–P, *Catherinum striolatum* (G.O. Sars, 1877); Q–T, *Amigdoscalpellum rigidum* (Aurivillius, 1898), rostrum in ventral rostral aspect (A, E, I, M, Q); rostrolatus in external (B, F, J, N, R) and internal (C, G, K, O, S) views. Basal capitulum in ventral (rostral) aspect (D, H, L, P, T). The rostrum is tiny, with only a small external face (I, M, Q) in more basal taxa. In the most derived taxa, the central ridge has an external surface over the height of the plate (A, B). Scale bars: A–D, F–H, J–L, N–P, R–T, 0.5 mm; E, I, M, Q, 0.2 mm.

facet on the upper part of the inner surface of the plate (Figs 11A–D, 12A–T).

Upper latus

The upper latus infills the space between the scutum and tergum in basal scalpellomorphs, and slightly overlaps both plates (e.g. zeugmatolepadids, see Gale, 2014a: fig. 9). In *Cretiscalpellum* (Fig. 4A) and basal scalpellids (Fig. 2), the plate is overlapped by the carinolatus, and in all scalpellids the upper latus has developed a margin in contact with the carina, which is of variable height. In *Arcoscalpellum michelottianum* (Fig. 2C) and *Ca. striolatum* (Fig. 3A) this is low, and the upper latus is consequently subtriangular in outline; in other taxa the carinal margin is proportionately long and the upper latus is trapezoidal to subrectangular. The upper latus displays several significant morphological changes in the scalpellids, including the development of a discrete, short, straight margin in contact with the inframedian latus in *Catherinum* spp. (Fig. 3A–C), *W. nymphocola* (Fig. 3D), and *W. stroemii* (Fig. 3H). Additionally, the umbo of the upper latus overlaps the scutum, resting in a shallow groove, in several taxa (*Am. mamillatum*, *Am. rigidum*, *Am. truncatum*, Fig. 3F, G; *Catherinum* spp., Fig. 3A–C). In *Ca. novaezelandiae* (Fig. 3C), *W. nymphocola* (Fig. 3D), and *W. stroemii* (Fig. 3H) the umbo of the upper latus is subapical.

Inframedian latus

The inframedian latus rests between the subcarinolatus and the rostrolatus in *Cretiscalpellum* (Fig. 4A), and is overlapped by the subcarinolatus but overlaps the rostrolatus. In scalpellids, the inframedian latus slightly overlaps both the rostrolatus and the carinolatus plesiomorphically (Fig. 2), and has no specialized contact with the upper latus, although it abuts this plate in *Arcoscalpellum michelottianum* (Fig. 2C). The basal scalpellid inframedian latus is low, triangular, and the umbo is slightly inclined towards the rostrolatus (Figs 2, 6H, I, M, N, R, S, W, X). In a more derived group, including *Am. mamillatum* (Fig. 3G), *Am. rigidum* (Figs 3E, 7W), and *Am. truncatum* (Figs 1B, 6C, D), the plate is tall and triangular, and does not always contact the upper latus. The umbo is in an apical position in the species of *Amigdoscalpellum*, *Arcoscalpellum*, *Diotascalpellum* gen. nov., *Graviscalpellum*, and *Regioscalpellum* gen. nov. investigated herein. In all other scalpellids studied, the inframedian latus has a subapical umbo (central to basal), and has developed short, discrete articulation surfaces with both the scutum and the upper latus (*Ca. novaezelandiae*, Fig. 7M, O; *Ca. striolatum*, Fig. 7R, T; *W. nymphocola*, Fig. 7H, J; *W. stroemii*, Fig. 7C, E). The inframedian latus has an hourglass shape, with an expanded base and minimum width at the level of the umbo in *Ca. novaezelandiae* and *Ca. striolatum* (Fig. 7R, M). The growth of a

polymetric shelf adjacent to the umbo and contacting the rostrolatus (Fig. 6G, H) is seen in *Arcoscalpellum sociabile*, and is developed further in fossil *Arcoscalpellum* (Fig. 5B). The shape and umbonal position of the inframedian latus have been used extensively in the taxonomy of scalpellids by Zevina (1978a,b, 1981), as discussed below in the systematic section.

Carinolatus

The carinolatera of scalpellids are highly diverse in shape, umbonal position, and in the presence and nature of articulation between the paired plates, the carina, upper latus, and inframedian latus. These features have not been discussed in any detail in previous studies, but because they evidently afford important phylogenetic information they are described more comprehensively here. The out-group *Cretiscalpellum* possesses two pairs of plates in the position of the carinolatus: an upper pair, usually rhomboidal in outline (Fig. 4I), and a lower pair (subcarinolatus of Withers, 1935: fig. 29), which are nearly equilaterally triangular (Fig. 4J), and overlap the subcarina. It has been presumed that the subcarinolatera were subsequently lost in evolution, together with the subcarina (Withers, 1935), because lower latera, including the subrostrum, are widely developed in more basal scalpellomorphs and are not present in scalpellids; however, the close similarity in shape between the subcarinolatus of *Cr. striatum* (Fig. 13Q, R) and the carinolatus of the Cretaceous scalpellid species *Arcuatoscalpellum arcuatum* (Fig. 13O, P) raises the possibility that these are actually homologous plates. Because of this uncertainty, the carinolatus of the late Early Cretaceous *Arcuatoscalpellum arcuatum* is taken as representing the plesiomorphic condition for scalpellids. This provides an essential indication of polarity, and the succession of taxa illustrated in Figures 6, 7, and 13 (bottom to top) are interpreted as representing a phylogenetic trend towards a more derived carinolatus morphology.

Group 1

In *Arcuatoscalpellum arcuatum*, the carinolatus (Fig. 13O, P) is nearly equilaterally triangular, the umbo is apical, the dorsal margin is convex, and an inframedian latus surface is not differentiated. On the interior of the plate, two concave facets are present: the ventral facet strongly overlaps the basal margin of the upper latus; the dorsal facet imbricates the basal margin of the carina. In *D. rubrum* (Fig. 13K, L) and the closely related Late Cretaceous species *Diotascalpellum fossula* (Darwin) (Fig. 18A–C) a slightly inset inframedian latus surface is sharply differentiated, and on the interior, the facet that overlapped the upper latus is reduced to a narrow rim.
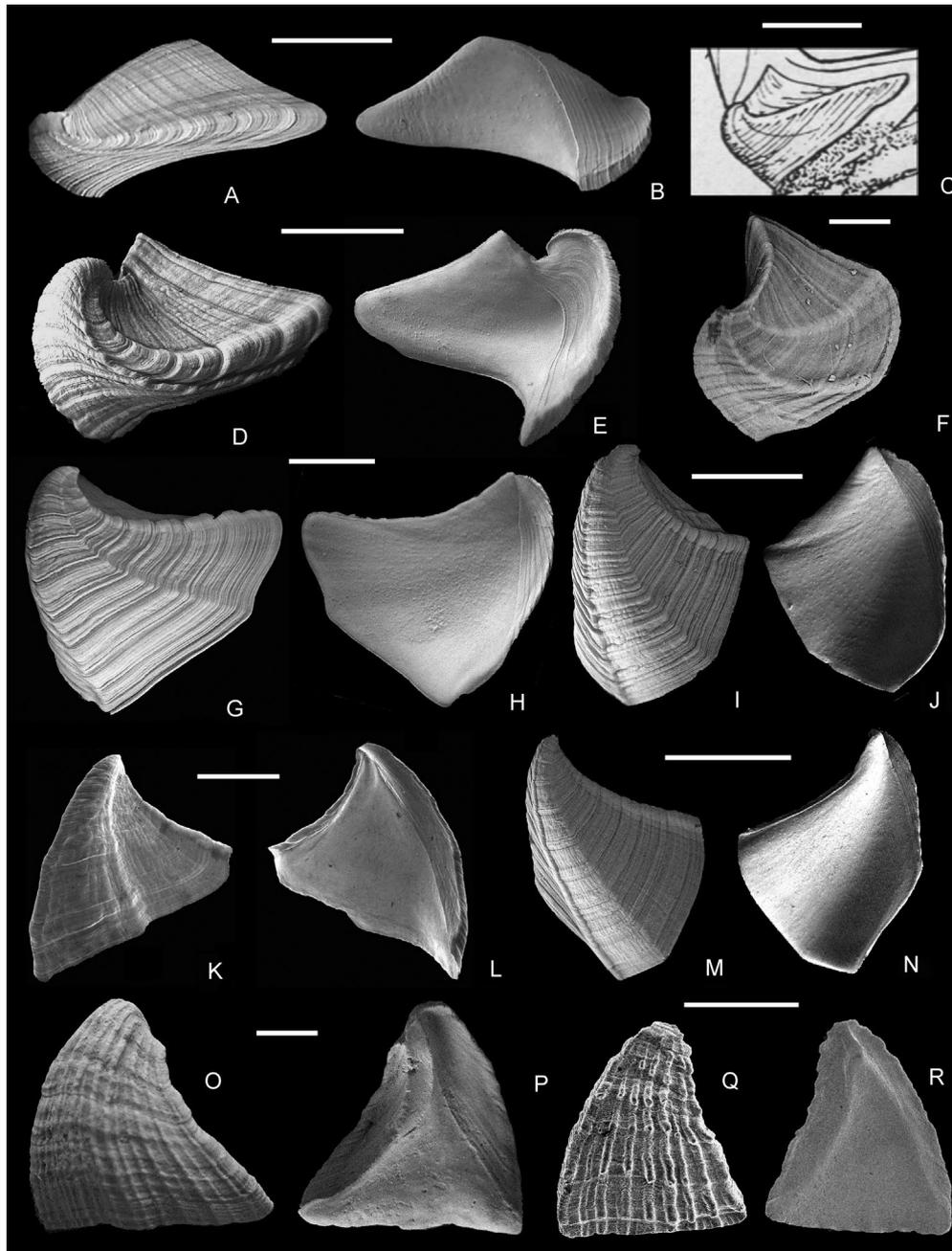
Figure 13. Carinolatera: A, B, *Arcoscalpellum pedunculatum* (Hoek, 1883); C, *Arcoscalpellum regina* (Pilsbry, 1907); D, E, *Arcoscalpellum michelottianum* (Seguenza, 1876); F, *Arcoscalpellum quadratum* (Dixon, 1850), London Clay, Eocene, Minster, Sheppey, Kent, UK (original of Withers, 1953, pl. 26, fig. 13), NHMUK In. 34504; G, H, *Regioscalpellum regium* (Thomson, 1873); I, J, *Regioscalpellum darwini* (Hoek, 1883); K, L, *Diotascalpellum rubrum* (Hoek, 1883); M, N, *Diotascalpellum gigas* (Hoek, 1883); O, P, *Arcuatoscalpellum arcuatum* (Darwin, 1851b), Albian, Gault Clay, Paddlesworth, Kent, NHMUK In. 61368; Q, R, *Cretiscalpellum striatum* (Darwin, 1851b), Campanian chalk, Norwich, UK. NHMUK IC 1198. Comparative morphology of carinolatus in out-group *Cretiscalpellum* and Scalpellinae to illustrate morphological variation and phylogenetic trends. Note the overall progression in morphology from the out-group (Q, R), through *Arcuatoscalpellum arcuatum* (P, Q), to *Diotascalpellum* (*D. rubrum*, K, L), involving differentiation of the inframedian latus surface. In the more derived *R. regium* (G, H), *R. darwini* (I, J), and *R. gigas* (M, N) the umbo is incurved, has migrated to a more dorsal position, and a low internal shelf has developed adjacent to the upper latus. In *Arcoscalpellum* (*Arcoscalpellum michelottianum*, D, E; *Arcoscalpellum quadratum*, F), the umbo is more incurved, the apex subapical, and a upper latus surface has developed (see Fig. 10 for nomenclature). Scale bars: A–I, M, N, 1 mm; K, L, O–R, 0.5 mm.

Group 2

In *R. regium* (Figs 6P, Q, 13G, H; see also Pilsbry, 1907, pl. 2, figs 3, 10), *R. darwini* (Fig. 13I, J), and the Late Cretaceous species *Regioscalpellum maximum* (J. de C. Sowerby) (Fig. 18N, O, P, S) a low, concave polymeric flange has grown inwards from the umbo of the carinolatus, and then is inflected sharply to extend for about two-thirds along the length of the upper latus margin (ulm, Fig. 10J, blue coloured); in life, this is covered with thick tissue. The ridge of this structure adjacent to the umbo contacts the base of the carina. Additionally, the umbo has become more incurved, and the dorsal margin more convex. There is no specialized contact between the paired carinolatera. Discrete lateral (green, adjacent to lm), peduncular (ps), and inframedian (ims) surfaces have developed (Fig. 10J).

Group 3

In *Arcoscalpellum michelottianum* (Figs 2C, 6K, L, 13D, E), *Arcoscalpellum quadratum* (Dixon, 1850) (Fig. 13F), and *Arcoscalpellum sociabile* (Figs 2D, 6F, G) the internal flange has become an external upper latus surface (uls, blue coloured in Fig. 10L), the upper margin of which contacts the upper latus. The internally directed part of the flange has become a carinal margin (cm), which contacts the sides of the carina. At the same time, the umbo has become more strongly enrolled (Fig. 6F) and the dorsal margin more convex. The lateral surface of the carinolatus (green in Fig. 10M) has become inturned onto the interior of the plate, and the base of this contacts the base of the opposing carinolatus of the pair.

The shape and relationships of the carinolatus present in group-3 species such as *Arcoscalpellum sociabile* are essentially similar to those of all more-derived scalpellids (Figs 6A–E, 7), all of which possess a carinal margin, a tall upper latus surface, an enrolled umbo, and articulation between the pair of carinolatera. The most important modifications involve the nature of this articulation. In *Am. truncatum* (Figs 6B, E, 10O) and *Am. rigidum* (Fig. 7V, X) there is a flat articular contact between the pair (purple in Fig. 10O), and the lateral surface is modified into three ridges and grooves that run from the umbo, and interdigitate (Figs 6E, 7X) over the plane of contact. In *Ca. striolatum* the ridges oppose (Fig. 7S), whereas in *Ca. novaezelandiae* (Fig. 7N), *W. nymphocola* (Fig. 7F, I), and *W. stroemii* (Fig. 7B, D) the articular facet has rotated to a vertical position, forming an inner, taller articulation (Fig. 7D, I, N), and the umbones form a separate, shorter articulation. In some taxa, a separate carinal surface forms on the carinolatus adjacent to the carinal margin (e.g. *Ca. novaezelandiae*, Fig. 7K).

Peduncle

The peduncle of extant scalpellomorph cirripedes is made up of columns of plates that form at the boundary between the peduncle and the capitulum, usually after the full compliment of capitular plates have been added (Newman & Ross, 1998; Young, 2001). This is true in all taxa that have been studied, with the exception of the scalpellid *Scalpellopsis* (Young, 2001), in which peduncular plates are added before the final laterals. Thus, the youngest plates are usually found at the contact with the capitulum. The plates in scalpellids are added alternately in two series, sc–l–sr and rl–cl, which correspond with the eponymous capitular plates. Plesiomorphically, eight columns of plates are present (Newman & Ross, 1998; Young, 2001), but some scalpellids have a reduced number, and calanticids and pollicipedids have generated a very large number of small plate rows (Young, 2001). In the taxa studied here, eight columns are present in all but *Am. truncatum* and *Am. rigidum*, in which seven columns are present.

RESULTS

CLADISTIC ANALYSIS

Extant calanticids are unsuitable as an out-group for the Scalpelllidae, because their capitular plate development is highly variable, with 15–60+ laterals developed in various taxa (Jones & Hosie, 2009). Additionally, although they have long been classified as falling within (Zevina, 1981) or close to the scalpellids, molecular analysis places the calanticids as sister group to all extant thoracicans except *Ibla*, thus rather far removed from the Scalpellidae (Pérez-Losada *et al.*, 2008). The genus *Cretiscalpellum* Withers, 1922 is abundant in the later Cretaceous (Albian–Maastrichtian), and first appears in the Late Jurassic (Tithonian; Gale, 2014a). Although sometimes classified as a calanticid, the valve morphology is very similar to that of basal scalpellids in overall form and sculpture (Fig. 4; Buckeridge, 1983). *Cretiscalpellum* differs from scalpellids in its possession of paired subcarinolatera and a subcarina (Withers, 1935), and probably gave rise to scalpellids by the loss of these plates. It is therefore used as an out-group to the Scalpellidae. The highly derived and autapomorphic genus *Scalpellum* was not included in the analysis (see below).

Heuristic analysis of 23 extant species using 61 characters in PAUP (Appendix S1; Table S1) yielded a consensus tree (Fig. 14) that provides a clear and well-supported picture of scalpellid phylogeny, forming a ladder of nested groups leading crownwards from the out-group to the most derived forms (nodes numbered 1–15). Although the changes superficially appear to represent a continuous morphocline, the introduction of synapomorphies is actually concentrated at three nodes, which represent major evolutionary steps in plate morphology. The most basal of these, node 6, involves 27 character changes, and with 100%
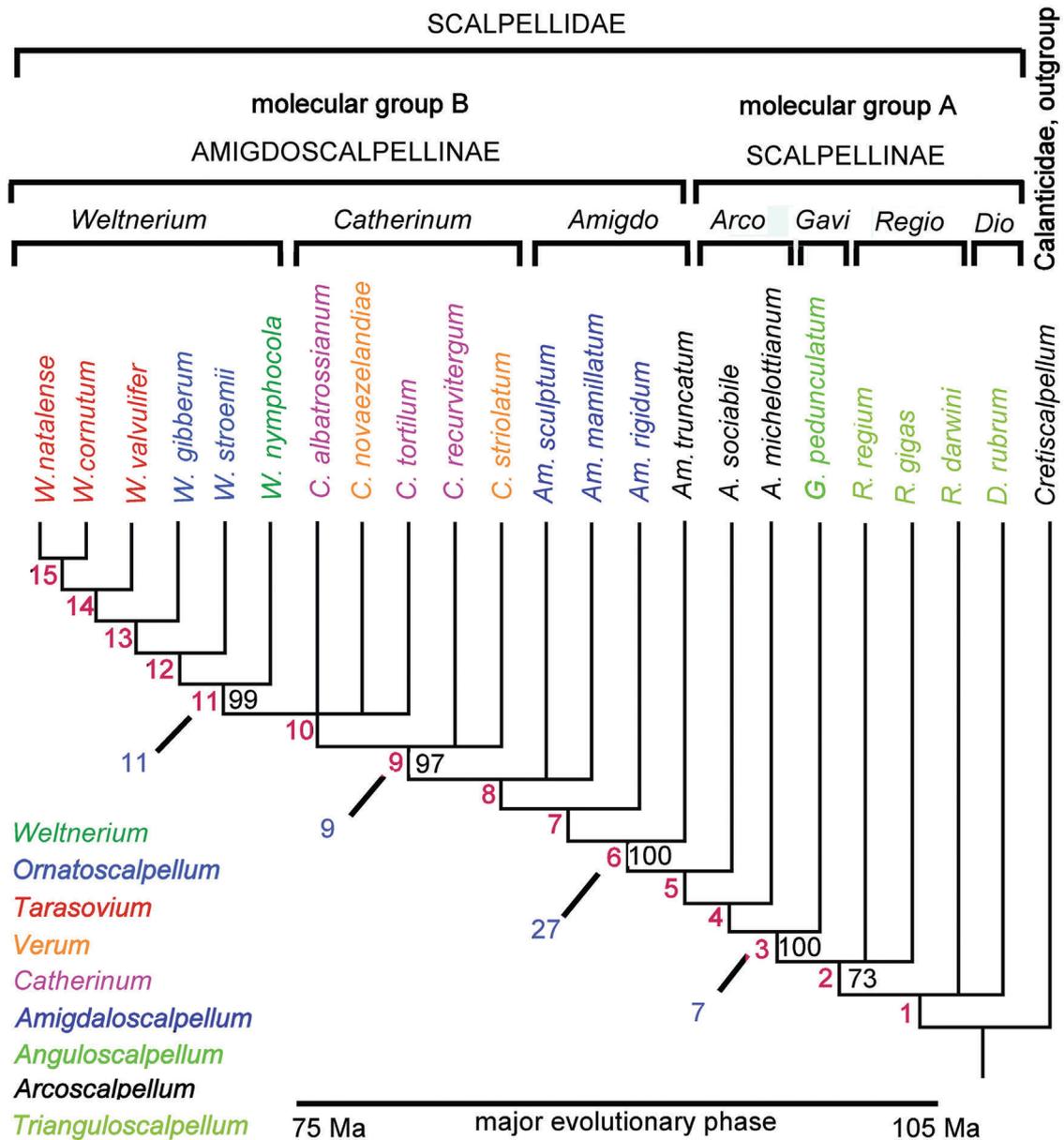
Figure 14. Cladogram of 23 extant species of Scalpellidae, a consensus tree based on heuristic, unconstrained analysis (PAUP) of 61 shell-plate characters. Nodes numbered, bootstrap support values shown. Numbers of character changes at nodes 3, 6, 9, and 11 are shown; note the major change crownwards of *Arcoscalpellum sociabile*, at which 27 changes (node 6) occur. Taxa close to *Diotascalpellum rubrum* [*Diotascalpellum angustatum* (Geinitz, 1843)] appeared at about 105 Mya, and *Catherinum* at 75 Mya. This suggests that much of the evolutionary diversification of the family had occurred before the end of the Cretaceous. Molecular groups A and B of Lin *et al*. (2015: fig. 3) correspond exactly with the Scalpellinae and Amigdoscalpellinae. Abbreviations, *Amigdo*, *Amigdoscalpellum*; *Arco*, *Arcoscalpellum*; *Gavi*, *Gaviscalpellum*; *Regio*, *Regioscalpellum*; *Dio*, *Diotascalpellum*.

bootstrap support is positioned at the base of a derived group that includes *Amigdaloscalpellum*, *Catherinum*, and *Weltnerium*, included in Amigdoscalpellinae subfam. nov. (see below). Within this group, significant changes occur at the base of a clade including *Catherinum* and more derived taxa (node 9,

nine changes, 97% bootstrap support), and at the base of *Weltnerium* (node 11, 11 changes, 99% bootstrap support). *Weltnerium* includes the morphologically most derived scalpellids, which also show highly specialized reproductive strategies (Buhl-Mortensen & Høeg, 2006, 2012).

The morphological tree derived here (Fig. 14) shows numerous similarities with the molecular phylogeny of Lin *et al*. (2015: fig. 3), although many taxa are different to those used in the present study. Group A corresponds exactly with the Scalpellinae as defined here, and group B corresponds with the Amigdaloscalpellinae (see Systematic Account, below). Secondly, within group B species referred to *Weltnerium* are the most derived, and species referred to *Amigdaloscalpellum* are the most basal, exactly paralleling the morphological analysis (Fig. 14). Group C (subgroup of group A) of Lin *et al*. (2015: fig. 3) is divided into two groups, one including *Arcoscalpellum hirsutum* (Hoek, 1883) and *Arcoscalpellum michelottianum*, the other including *R. regium*, corresponding precisely with the generic classification proposed here. In the molecular tree, *Scalpellum* is positioned within the other (unlettered) subgroup of group A, together with species here assigned to *Diotascalpellum* gen. nov. and *Graviscalpellum*. In the present study, *G. pedunculatum* occupies a more derived position within the Scalpellinae (Fig. 14).

The major difference between the trees derived from morphological and molecular analysis lies in the topology of the trees; the morphological data generate a tree that is a 'ladder' in which taxa have a sequential nested arrangement, leading progressively from the most plesiomorphic to the most apomorphic species (Fig. 14). In contrast, molecular analysis provides a branching 'tree', in which subgroups are rather sharply defined (Lin *et al*., 2015: fig. 3). The potential significance of these differences must await further study.

EVIDENCE FROM THE FOSSIL RECORD

The foregoing account provides evidence to support a scalpellid phylogenetic tree that represents a morphocline leading from least-derived taxa (closest to the out-group) through to the most-derived forms, such as *W. nymphocola*, which is both morphologically and reproductively very highly modified. It is now also possible to place fossil scalpellid taxa in this tree, in order to provide a minimum date for individual nodes on the cladogram (Smith, 1994). The Scalpellidae have an abundant fossil record in the Cretaceous and Cenozoic (e.g. Withers, 1935, 1953; Collins, 1973; Zullo, 1990; Harzhauser & Schlögl, 2012), but all taxa described have been referred to three genera: *Scalpellum* (Eocene–present day), *Arcoscalpellum* (Cretaceous–present day), and *Virgiscalpellum* (Late Cretaceous). It is therefore important to reassess the affinities of fossil scalpellids in the light of both the classification of Zevina (1978a,b, 1981) and the modifications proposed in this paper.

Fossil taxa assigned to Arcoscalpellum Hoek, 1907
In his monographic treatment of Cretaceous Cirripedia, Withers (1935) referred most fossil species that would now be considered as scalpellids to either the genus *Arcoscalpellum* or the very distinctive Cretaceous genus *Virgiscalpellum* Withers, 1935 (Aptian–Maastrichtian). He referred a single species, *Scalpellum glauerti* Withers, with a bifid tergum, to *Scalpellum* (*Neoscalpellum*), which was subsequently assigned to a new genus, *Pachyscalpellum* Buckeridge, 1991. Withers (1935) split Cretaceous *Arcoscalpellum* into three groups (A. arcuatum Gp, A. fossula Gp, and A. maximum Gp), based on numerous plate characters, most notably of the carina. Zullo (1990) supported this division, and identified *Arcoscalpellum conradi* (Gabb, 1876) from the eastern seaboard of the USA as a Palaeocene descendant of the *Arcuatoscalpellum fossula* group, thus extending Withers' classification into the Cenozoic.

It is now possible to integrate Withers' (1935) fossil '*Arcoscalpellum*' groups into the classification proposed here for extant basal members of the Scalpellidae (see below), based largely on the detailed comparative morphology of the carinolatus and its articulation with the carina and upper latus.

1. *Arcuatoscalpellum* gen. nov., for the *Arcoscalpellum arcuatum* group of Withers (1935). Cretaceous, Albian–late Maastrichtian (Fig. 4N–S). This represents the plesiomorphic condition for scalpellids, and displays significant similarities with the outgroup, including the divergently striated sculpture, the overlap between the carinolatus and upper latus, and the median ridge on the carina (Fig. 4C).
2. *Diotascalpellum* gen. nov., based on the living *Scalpellum diota* Hoek, 1907 (for an extended redescription, see Chan, Prabowo & Kwen-Shen, 2009), and including the *Arcuatoscalpellum fossula* group of Withers (1935). These forms are distinguished by the presence of a well-defined inframedian latus surface on the carinolatus, and minor overlap of the carinolatus over the upper latus (Figs 13K–O, 18A–G).
3. *Regioscalpellum* gen. nov., based on the living cosmopolitan *Scalpellum regium* Thomson, 1873, and including the *Arcuatoscalpellum maximum* group of Withers (1935). These forms are characterized by the presence of a crescentic polymetric shelf on the carinolatus adjacent to the upper latus. The overall morphology is remarkably similar in Cretaceous and living forms (e.g. Fig. 13G, H, *R. regium*; Fig. 18N, O, P, S, *R. maximum*).
4. *Arcoscalpellum*, based on the type species *Pollicipes michelottianus* Seguenza, 1876. Forms with a tall upper latus surface and carinal margin. Including

the extant *Arcoscalpellum hirsutum* (Hoek, 1883) and *Arcoscalpellum quadratum* (Dixon, 1850) from the Eocene.

It is interesting to note that Withers (1928) identified the presence of an apical, internal pit for complemental (dwarf) males in a Cretaceous scutum, which he subsequently described as *Arcoscalpellum bellulum* Withers, 1935 from the upper Campanian chalk of Norwich, UK. The morphology of the pits and the shape of the two known scuta, and the distinctive, even striation of their exterior, justify referral to the living genus *Amigdoscalpellum*. *Arcoscalpellum turinensis* Withers, 1953, from the Miocene close to Turin, Italy (Withers, 1953), is also referred to *Amigdaloscalpellum*.

Processing large quantities of upper Campanian chalk from various localities close to Norwich, Norfolk, UK, has yielded a suite of small and fragile scalpellid valves (scuta, terga, carinae, and carinolatera; Fig. 19C–K, N–Q, T, V), which are closely comparable with those of extant species of *Catherinum*, and are described below as *Catherinum anglicum* sp. nov. Distinctive characters include the incurved, acuminate apex of the scutum, and the large dwarf male receptacle. Additionally, *Arcoscalpellum singletoni* Withers, 1953 from the Miocene of Australia can be referred to *Catherinum*.

Morphology and origin of Scalpellum
Morphologically, the genus *Scalpellum* Leach, 1817 is a very distinctive form, in which the capitulum is broad, the umbones of the carina and scutum are subapical, the umbo of the carinolatus is basal, and the carinolatus typically has the form of a laterally projecting horn, recurved in some species (Fig. 15). Additionally, the inframedian latus is broad with a basal umbo, and the upper latus has a subapical umbo. Material of the genus was not included in the cladistic analysis because the species are so strongly autapomorphic. Four extant species were placed in the genus by Zevina (1981), namely *Scalpellum scalpellum* (type species), *Scalpellum typicum* Broch, 1947, *Scalpellum stearnsi* Pilsbry, 1890, and *Scalpellum gibbum* Pilsbry, 1907. Two of these are considered here: the widespread Indo-Pacific *S. stearnsi* (Chan *et al.*, 2009; Fig. 15A, E, H, L–P, herein) and the north-west European *S. scalpellum* (Southward, 2006; Fig. 15B–D, F–K, herein). It is noteworthy that Withers (1953) described numerous fossil *Scalpellum* from the Eocene to the present day (see also Harzhauser & Schlögl, 2012).

Scalpellum has been placed in the Scalpellinae Pilsbry, 1907 by Zevina (1981), together with *Pteroscalpellum*, *Barbascalpellum*, *Compressoscalpellum*, and *Ornatoscalpellum*. This group was defined principally by the presence of a strongly bowed carina with a subapical umbo and the low umbo on the inframedian latera. It is evident that the subfamily is paraphyletic, because *W. stroemii* is shown here to represent a parallel development (Fig. 14).

The ancestry of *Scalpellum* was traced by Withers (1953) to the genus *Arcoscalpellum*, in the Eocene, based partly on study of the ontogeny of *S. stearnsii*, and also on the distribution and morphology of fossils. Withers (1953: figs 13–18) illustrated the ontogeny of *S. stearnsi*: young *S. stearnsi* strongly resemble *Arcoscalpellum*, and up to a capitular height of 6.4 mm, the only plate with a subapical umbo is the inframedian latus. The bowed, subapical carinal umbo is present at a capitular height of 8.5 mm, but the subapical scutal umbo and the distinctive apical extension of the scutum developed last. Withers (1953: 15) remarked that, 'it is evident that species included in *Scalpellum* s. str. were derived late from the *Arcoscalpellum* stock . . .'

The morphology of the rostrum and rostrolatus in *Scalpellum* certainly support a more basal position for the genus within the Scalpellidae. The rostrum is trapezoidal in outline, with a large subumbonal surface (Fig. 15E, F), and is similar in form to that in *Arcoscalpellum michelottianum* (Fig. 11E). The rostrolatera are broad, low, and gently concavo–convex in both *Scalpellum* and basal scalpellids (compare Figs 11F, G and 15L, M).

There is now additional morphological and fossil evidence to support Withers' claim, in the form of a stratigraphical succession of species leading from the early Eocene *Arcoscalpellum quadratum* (Dixon, 1850), through *Arcoscalpellum venablesi* Withers, 1953 [both from the Lower Eocene (Ypresian) London Clay of Bognor Regis, UK], on to *Scalpellum fischeri* Bertrand, 1891 from the Middle Eocene (Lutetian) Calcaire Grossier of the Paris Basin (Figs 16, 17). As Withers (1953) remarked, the latter species is close to the extant *S. stearnsi*.

There is progressive change in morphology between these three species. The scutum (Fig. 16A, B, G, H, M, N) becomes progressively more elongated and narrow apically, and gradually develops the pointed process apical to the umbo that is characteristic of *Scalpellum*. The tergum (Fig. 16C, I, O) changes from a rhombic to triangular form, and the carinal margin becomes more concave. The apical part of the carina develops a shelf beneath the umbo in *Arcoscalpellum venablesi* (Fig. 16J–L), which becomes more apically extended in *S. fischeri*, as the umbo adopts a subapical position (Fig. 16D–F). The lateral plates also display significant changes (Fig. 17): the rostrolatera in *Arcoscalpellum quadratum* (Fig. 17M, N) are similar to those found in many basal scalpellids (see Fig. 11F, G, J, K, N, O, R, S), with a broad, low outline and a concave facet for articulation with the rostrum on the interior. In *Arcoscalpellum venablesi* (Fig. 17H, I), the plate has broadened, and the rostral surface has become elongated and flat, as in *Scalpellum* (Fig. 17B, C). The
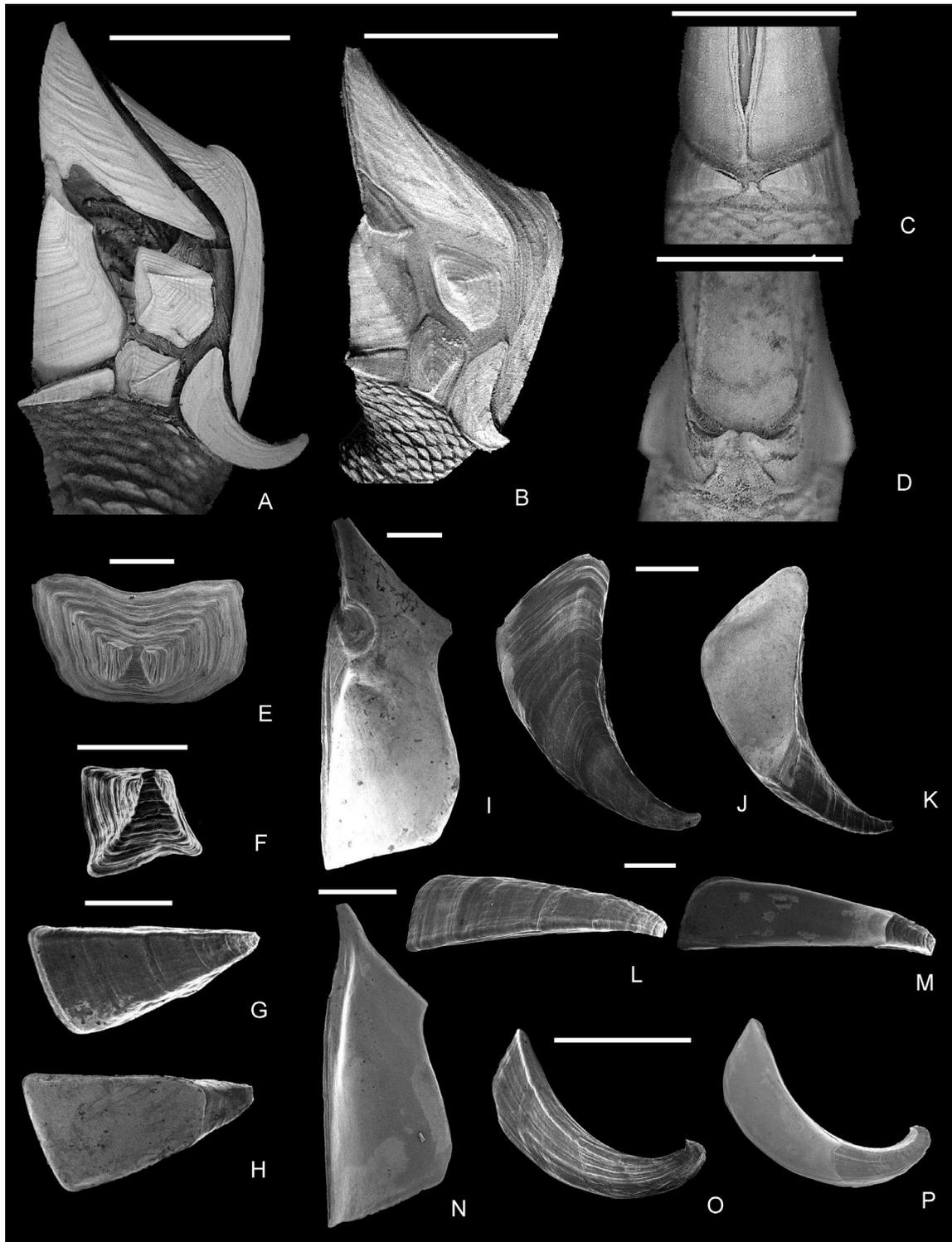
Figure 15. A, E, L–P, *Scalpellum stearnsi* (Pilsbry, 1890): A, capitulum, in lateral aspect; E, rostrum, in ventral aspect; J, K, exterior and interior of carinolatus; L, M, exterior and interior of rostrolatus; N, interior of scutum. B–D, F–K, *Scalpellum scalpellum* (Linnaeus, 1776): B, capitulum, in lateral aspect; C, ventral (rostral) view of base of capitulum; D, dorsal (carinal) view of base of capitulum; F, rostrum in ventral aspect; G, H, rostrolatus, exterior and interior views; I, interior of scutum; O, P, carinolatus, external and internal views. See Table 1 for localities and details. Scale bars: A, 10 mm; B, N, 5 mm; C, D, 2 mm; G–M, O, P, 1 mm; E, 0.5 mm; F, 0.2 mm.
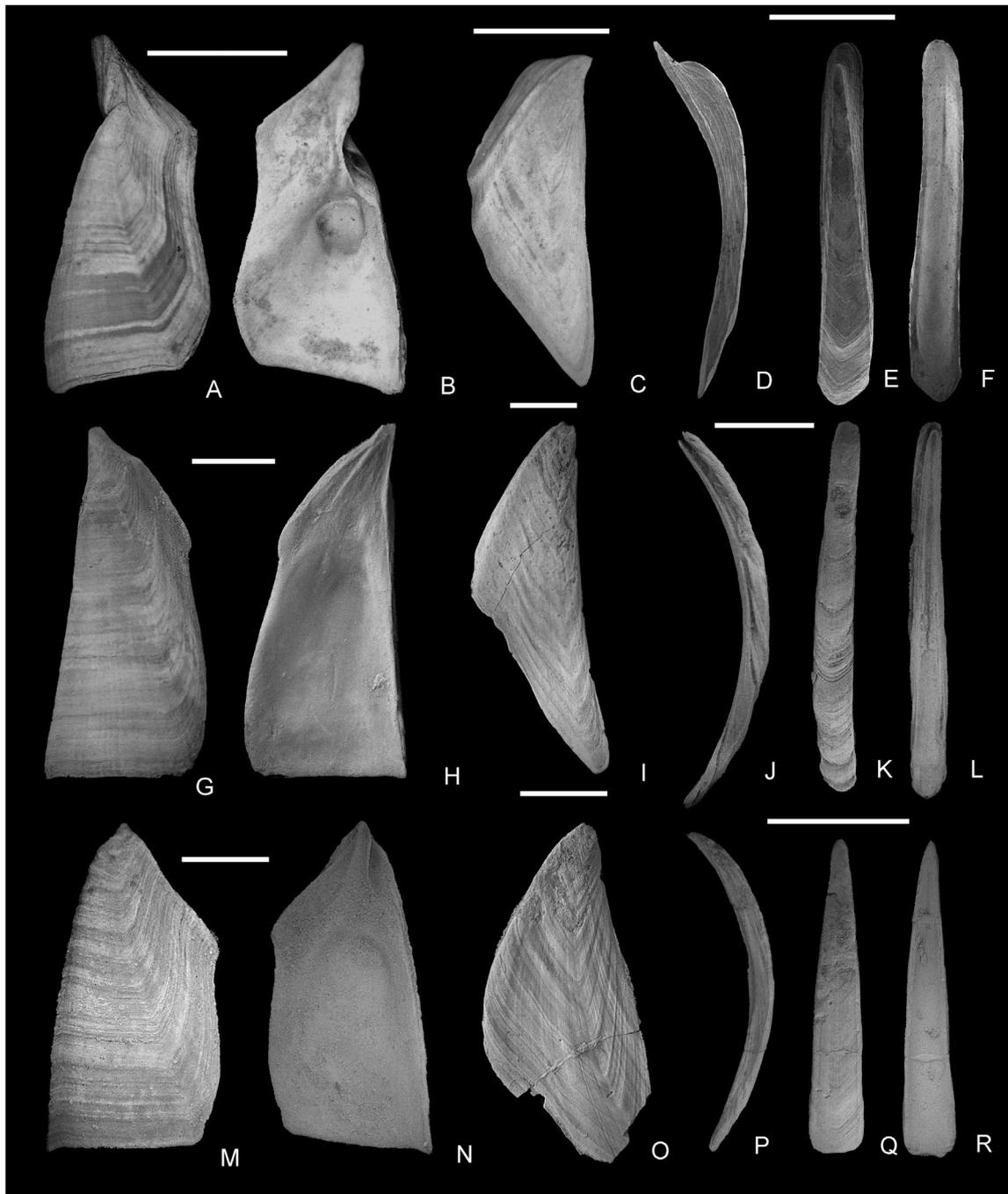
Figure 16. Eocene Scalpellinae, to illustrate the evolutionary origin of the genus *Scalpellum*. Scuta, terga, and carinae. A–F, *Scalpellum fischeri* Bertrand, 1891, Lutetian, Calcaire Grossier, Chaussy, near Mantes (Seine-et-Oise), Paris Basin, France. A, B, scutum, external and internal views (original of Withers, 1953, pl. 38, figs 3, 4), NHMUK In. 39466. C, tergum, external view (original of Withers, 1953, pl. 38, figs 5, 6), NHMUK In. 39468. D–F, carina (original of Withers, 1953, pl. 38, fig. 1), NHMUK In. 39465. L, *Arcoscalpellum venablesi* Withers, 1953, lower Ypresian, Division B1 of London Clay ('Fish Tooth Bed'), Bognor Regis, Sussex, UK. G, H, scutum, in external and internal views (original of Withers, 1953, pl. 63, fig. 1), NHMUK In. 39072. I, tergum (original of Withers, 1953, pl. 63, fig. 4), NHMUK In. 39072. J–L, carina (original of Withers, 1953, pl. 63, fig. 1), NHMUK In. 39033. M–R, *Arcoscalpellum quadratum* (Dixon, 1850), lower Ypresian, Division A3 of London Clay ('Bognor Rock'), Bognor Regis, Sussex, UK. M, N, scutum. O, tergum. P–R, carina. NHMUK In. 32543–32550. Note the progressive elongation of the apical part of the scutum, the change in shape of the tergum, and the subapical migration of the carinal umbo. Compare with extant *Scalpellum* in Figure 15. Scale bars: 5 mm.
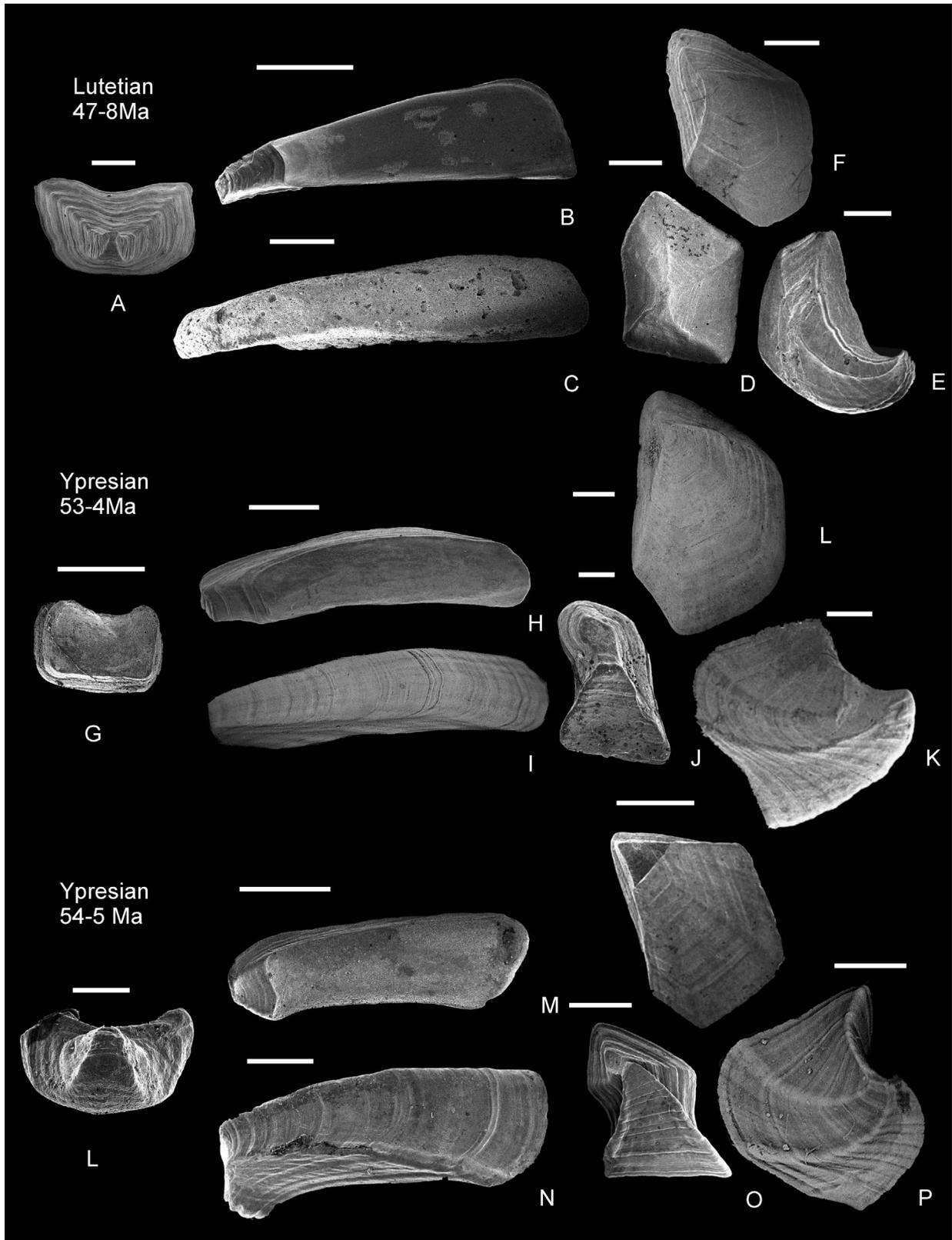
Figure 17. Eocene and recent Scalpellinae, to illustrate the evolutionary origin of the genus *Scalpellum* (see also Fig. 16). A, B, *Scalpellum stearnsi* Pilsbry, 1890: A, rostrum; B, rostrolatus, internal view. C–F, *Scalpellum fischeri* Bertrand, 1891, Middle Eocene, Lutetian, Calcaire Grossier, Chaussy, near Mantes (Seine-et-Oise), Paris Basin, France: C, rostrolatus, exterior view, NHMUK In. 39541. D, inframedian latus, NHMUK In. 39540; E, carinolatus, NHMUK In. 39549; F, upper latus, NHMUK In. 39440. G–K, *Arcoscalpellum venablesi* Withers, 1953, Lower Eocene, Ypresian, Division B1 of London Clay, Bognor Regis, Sussex, UK: G, rostrum, NHMUK In. 44796; H, I, carinolatus (original of Withers, 1953, pl. 63, fig. 16). NHMUK In. 39086; J, inframedian latus, NHMUK In. 44994; K, upper latus (original of Withers, 1953, pl. 63, fig. 13), NHMUK In. 39083. K, carinolatus (original of Withers, 1953, pl. 63, fig. 20), NHMUK In. 3939091. L–Q, *Arcoscalpellum quadratum* (Dixon, 1850), lower Eocene, Ypresian, London Clay, Minster, Isle of Sheppey, Kent, UK: L, rostrum, NHMUK In. 44795; M, N, rostrolatera, NHMUK In. 34506, In. 34439; O, inframedian latus, NHMUK In. 34440; P, carinolatus (original of Withers, 1953, pl. 26, fig. 13), NHMUK In. 34504; Q, upper latus, NHMUK In. 34504. Note that the rostrum changes from a trapezoidal ventral outline in *Arcoscalpellum quadratum* (L) to a rectangular one in *Arcoscalpellum venablesi* and *S. fischeri* (G, A); the rostrolatus in *Arcoscalpellum quadratum* (M, N) is typical of basal scalpellines (e.g. Fig. 11F, G, J, K, N, O, R, S), which possess a rectangular plate with a rounded concave socket for articulation with the rostrum. In *Arcoscalpellum venablesi* (H, I) and *Scalpellum* (B, C) the rostrolatus tapers ventrally, and the socket becomes an elongated trapezoidal surface. Scale bars: A, 0.5 mm; B–P, 1 mm.

umbo of the carinolatus progressively develops a recurved, horn-like process (Fig. 17E, K, P), and the inframedian latus becomes progressively more flattened, and the umbo positioned more basally (Fig. 17D, J, O).

The stratigraphical age of *Arcoscalpellum venablesi*, of approximately 50 Mya, pre-dates the oldest reliable record of *Scalpellum*, *S. fischeri*, from the Middle Eocene (Lutetian) Calcaire Grossier, of the Paris Basin, at 47 Mya (Fig. 16A–F; Withers, 1953). There is therefore both morphological and stratigraphical support for the hypothesis that *Arcoscalpellum venablesi* represents the evolutionary origin of *Scalpellum*, and that the genus was derived from *Arcoscalpellum*; thus, it is a basal scalpellid. The subfamily Scalpellinae (sensu Zevina, 1981) is subsequently polyphyletic.

DISCUSSION

Cladistic analysis of shell plate morphology (61 characters used; Fig. 14) for 23 extant species of scalpellids, belonging to eight genera, used the Cretaceous genus *Cretiscalpellum* as an out-group. This has provided the first phylogeny of the family, which broadly supports the suggestion of Young (1998) that large species assigned by Zevina (1981) to *Trianguloscalpellum*, in which all plates possess apical umbones, are likely to occupy a basal position. The tree (Fig. 14) demonstrates a clear morphological progression from basal forms, here assigned to the new genera *Diotascalpellum* gen. nov. and *Regioscalpellum* gen. nov., through *Arcoscalpellum*, to species of *Amigdaloscalpellum*, and on to *Catherinum*. The most derived clade includes forms assigned by Zevina to *Weltnerium*, *Tarasovium*, and *Ornatoscalpellum*. The morphological progression is shown pictorially in Figures 7–9 (carinal side) and 11–12 (rostral side), from the bottom to the top of the page. Although these illustrations should not be taken as a real phylogenetic succession, they serve to illustrate the progressive morphological modifications that took place during the evolution of the family. The most important of these are described below.

1. Migration of the umbo of the carinolatus from an apical to a nearly basal position (Figs 6, 7), associated with incurvature of the umbo and shortening of the lateral margin. This all occurred in the basal (pre-*Amigdoscalpellum*) part of the family.
2. Formation and progressive enlargement of an upper latus surface and elongated carinal margin on the carinolatus (Figs 6, 7), also during early evolution.
3. Development of an articulation between opposing carinolatera, which evolved interpenetrant ridges (e.g. Figs 6E, 7X), then later developed a double symmetrical articulation (Fig. 7D, I, N).
4. Change in shape of the inferior median latus from a triangular, through rectangular, to pentagonal outline (Figs 6, 7), accompanied by basal migration of the umbo and development of an articulation with the scutum.
5. Dramatic changes in the size and shape of the rostrum, from a basal subtrapezoidal–triangular form of equal height to the rostrolatera, to a small, oval elongate form half the height of the rostrolatera (Figs 11A, 12I, M, Q). In the most derived condition, the rostrum developed a triangular, smooth external face (Fig. 12A, E).
6. Accompanying (correlative changes) in the rostrolatera, which plesiomorphically are broad and low (Fig. 11F, G, N, O, R, S), but became proportionately taller and subtriangular to subrectangular (Figs 11B, C, 12B, C, F, G, J, K, N, O, R, S).

These changes are not evenly distributed through the branches of the cladogram, but display a very specific pattern of distribution. In the basal group (*D. rubrum–Arcoscalpellum sociabile*) the features of the rostrum–rostrolatera are highly conservative, whereas the carinolatus, and its relationships with the upper latus and carina underwent considerable evolution (Fig. 11). The most dramatic modifications within the family took place immediately preceding the evolution of *Am. truncatum*, in which there were 27 changes in character state, involving fundamental shifts in rostral, rostrolateral, carinolateral, and inframedian latus morphology, accompanied by a reduction in size, cuticular thickness, and pilosity. The importance of this node is reflected in nomenclatorial changes, with both the admittedly paraphyletic basal group and the derived group recognized as subfamilies (below).

Further significant morphological changes occurred at the base of the group including species assigned to *Catherinum* (nine changes in character state), and again at the base of *Weltnerium* (11 changes). These major sets of character changes and synapomorphies are used to define genera (see below).

The extensive fossil record of the Scalpellidae (e.g. Withers, 1935, 1953) permits some calibration of the tree (Fig. 14). The oldest scalpellid, *Arcuatoscalpellum* gen. nov. appears in the early Aptian, at approximately 125 Ma (dates from Gradstein *et al.*, 2012). *Diotascalpellum* gen. nov. (*Diotascalpellum angustatum* Darwin) first appears in the late Albian, at 106 Mya, and *Regioscalpellum* gen. nov. (*R. maximum*) in the Coniacian at 89 Mya. By the late Campanian, at 75 Mya, both *Catherinum* and *Amigdoscalpellum* are present (see below). These dates are significant because the appearances of successive taxa are congruent with the order of nodes on the cladogram; the only exception is the late first occurrence of *Arcoscalpellum* at 55 Mya. Secondly, they suggest that the bulk of evolution in the Scalpellidae took place over the 40-Myr interval between the Aptian and late Campanian. This indicates that many of the extant genera have a Cretaceous origin, and that the modern representatives of the family record a large part of its phylogenetic history. The only group for which there is no fossil record is the most derived clade (*Weltnerium*).

Fossil evidence indicates that *Scalpellum* evolved from *Arcoscalpellum* in the Early Eocene (Withers, 1953; see also above). A remarkable feature of scalpellid genera as used here (see below) is their striking morphological conservatism. Cretaceous species of *Diotascalpellum* gen. nov. and *Regioscalpellum* gen. nov. can only be separated from living species using minor criteria of shell plate morphology (e.g. Figs 18, 19).

Much recent interest in scalpellids has focused on their reproductive strategies (Buhl-Mortensen & Høeg, 2006, 2012; Yusa *et al.*, 2011). Plesiomorphically, scalpellids are thought to be hermaphroditic (Foster, 1980), and the most basal living scalpellids identified here are hermaphrodites (*Diotascalpellum diota* (Hoek) and *D. rubrum*). More derived scalpellids (many Amigdaloscalpellinae) are androdioecious, the hermaphrodites housing dwarf males inside the scuta above the adductor muscle (Darwin, 1851a; Yusa *et al.*, 2011), and others are dioecious, with large females and dwarf males (Buhl-Mortensen & Høeg, 2006, 2012; Yusa *et al.*, 2011). The interior of the scutum (Figs 8, 9) thus provides evidence of the level of reproductive specialization that can be applied to the fossil record (Høeg *et al.*, unpubl. data).

At present, scalpellids are predominantly deep water in distribution. In the seas around north-west Europe, *S. scalpellum* occurs from the low water mark to depths of 400 m, but other diverse taxa (*Catherinum*, *Amigdoscalpellum*, and others) only occur below 200 m, in the bathyal zone and below (Southward, 2006). The greatest diversity is found in bathyal and abyssal

Figure 18. Fossil and recent Scalpellinae, to illustrate characteristics and affinities of fossil and extant taxa. A–C, *Diotascalpellum fossula* (Darwin, 1851b): A, capitulum in lateral aspect (original of Withers, 1935, pl. 26, fig. 3), Upper Cretaceous, Campanian, East Harnham, Wilts, UK, NHMUK In. 21559; B, C, carinolatus, external (B) and internal (C) views, Upper Campanian, Keswick, Norfolk, UK, NHMUK IC 1201. D, E, *Diotascalpellum scaniensis* (Gale, in Gale & Sørensen, 2015), carinolatus in external (D) and internal (E) views. Campanian, Ivö Klack, southern Sweden (original of Gale & Sørensen, 2015, fig. 10O, Q), NHMUK IC 964, 966). F, G, *Diotascalpellum rubrum* (Hoek, 1883), carinolatus. See Table 1 for details. H–K, *Arcoscalpellum quadratum* (Dixon, 1850); H, I, capitula in lateral aspect. Bognor Rock, Division A3 London Clay, Bognor Regis Sussex, UK. H, original of Withers (1953, pl. 26, fig. 1), NHMUK In. 3498. I, original of Withers (1953, pl. 26, fig. 2), NHMUK In. 34981. J, K, carinolatus in external and internal views, London Clay, Minster, Sheppey, Kent (original of Withers, 1953, pl. 26, fig. 13), NHMUK In. 34504 (image reversed). L, M, *Arcoscalpellum sociabile* (Annandale, 1905), carinolatus. See Table 1 for details of locality. N–P, S, *Regioscalpellum maximum* (J. de C Sowerby, 1829). N, capitulum in lateral aspect (original of William Smith, 1816; Withers, 1935, pl. 30, fig. 1). Upper Campanian, Norwich, Norfolk, UK, NHMUK I. 750. O, P, carinolatus, Coniacian chalk, Little Weighton, Yorks, UK, NHMUK In. 63523. S, oblique view of carinolatus to show polymetric shelf. Upper Campanian, *Belemnitella mucronata* zone, Cringleford, Norwich, UK. NHMUK IC 1202. Q, R, *Regioscalpellum sanchezae* (Withers, 1953), Upper Eocene, Cevro, Havana, Cuba. NHMUK In. 25998. Scale bars: H, I, 10 mm; A, O–R, 5 mm; J, K, S, 1 mm; B–G, L, M, 0.5 mm.
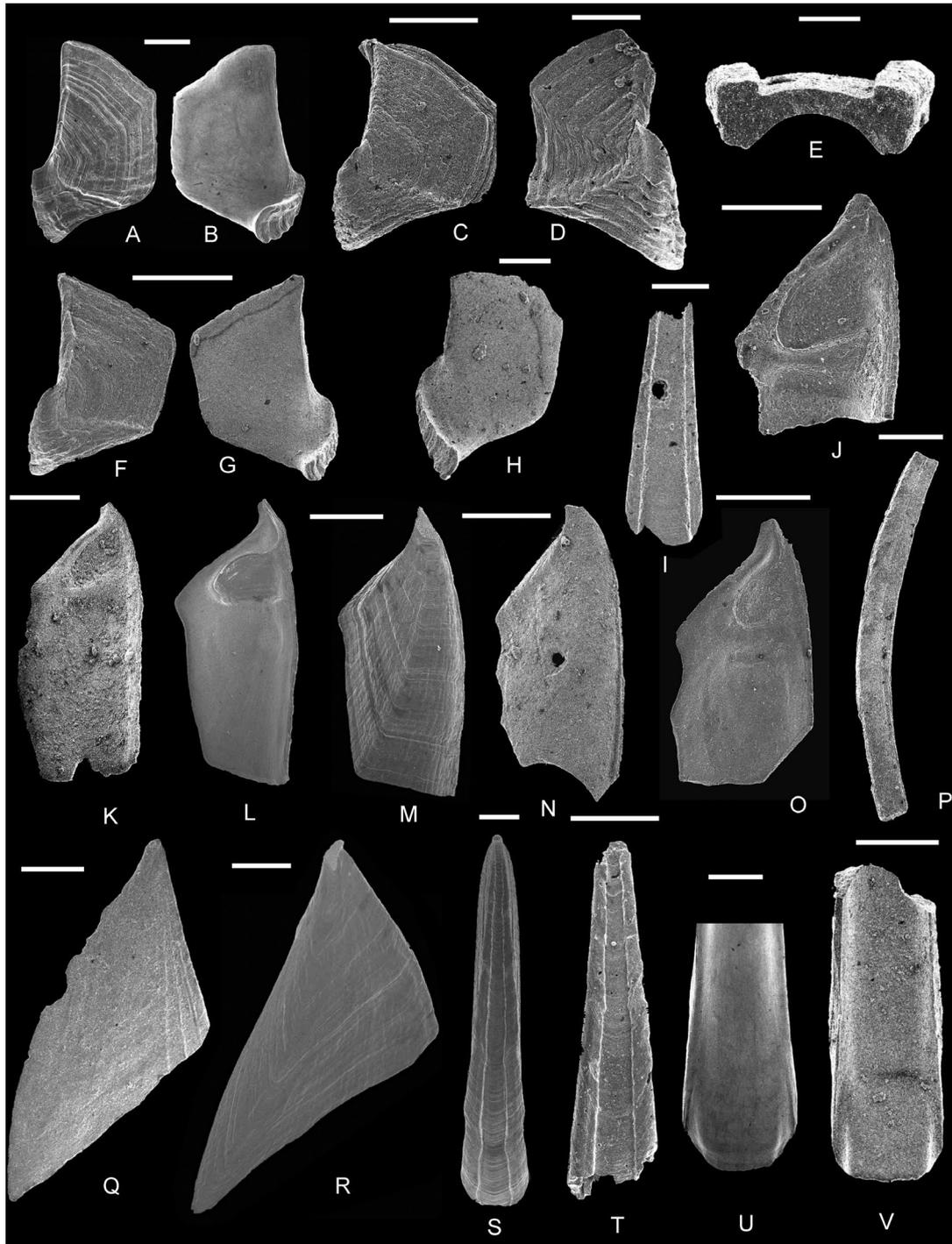
Figure 19. Fossil and recent *Catherinum*. C–K, N–Q, T, V, **Catherinum anglicum sp. nov.**, Upper Campanian, *Belemnitella mucronata* zone, Keswick, Norwich, UK; (O) is the holotype, the other specimens are paratypes. C, D, F, G, carinolatera in external (C, D, F) and internal (G, H) aspects (C, NHMUK IC 1203; D, 1204; F–G, 1206; H, 1208). E, transverse section of carina (NHMUK IC 1205); I, T, dorsal view of carinae (NHMUK IC 1209, 1216); P, lateral view of carina (NHMUK IC 1214); V, internal view of base of carina (NHMUK IC 1217); J, K, O, internal views of scuta, to show large pit for dwarf males (NHMUK IC 1210, 1211, 1213); N, external view of scutum (NHMUK IC 1212); Q, external view of tergum (NHMUK IC 1215). A, B, L, M, R, S, U, *Catherinum hispidum* (G.O. Sars, 1890). Recent, Norwegian Sea. A, B, carinolatus in external and internal views. L, M, external and internal views of scutum. R, external view of tergum. S, U, dorsal and internal views of carina. Scale bars: S, U, V, 1 mm; A–D, F, G, K–O, Q, R, T, 0.5 mm; E, H, P, 0.2 mm.

environments (Young, 2007); however, in the Cretaceous and Palaeogene they occurred commonly, sometimes abundantly, in shallow marine shelfal environments. For example, *Diotascalpellum scaniensis* (Gale in Gale & Sørensen, 2015) is common in coarse shell gravels deposited subtidally adjacent to a Campanian rocky shoreline at Ivö Klack in southern Sweden (Gale & Sørensen, 2015), probably in 20–30 m of water or even less. *Arcoscalpellum quadratum* occurs abundantly in the shallow marine sands of the Bognor Rock (London Clay, Ypresian) at Bognor Regis, Sussex, UK (Venables, 1963), which yields a high-energy assemblage of thick-shelled bivalves and was probably deposited in 10–20 m of water. Oligocene and later records of the family appear to be from deeper-water facies (e.g. Löffler & Nebelsick, 2001; Harzhauser & Schlögl, 2012), so their virtual exclusion from shelf seas (except *Scalpellum*) appears to date approximately to the end of the Eocene. There is no obvious reason for this change, as there do not appear to be dramatic differences between Eocene and later shelfal faunas or habitats.

A further interesting question is whether the scalpellids: (1) were an originally shallow-water family that subsequently colonized the deep sea; (2) were always a deeper-water family that periodically spread onto the shelves; or (3) originally extended from deep to shallow habitats, but were virtually excluded from the shelves in the Cenozoic. The problem here is the apparent absence of cirripedes in deep-water fossiliferous facies, particularly of Late Mesozoic age, which may be a result simply of their being overlooked. The presence of the deep-water *Catherinum* and *Amigdoscalpellum* in upper Campanian chalks of the UK, at the height of the Cretaceous sea level high (200 m above present; Hancock, 1990), however, could be taken as evidence that they had a long history in the deep sea about which we know very little.

SYSTEMATIC ACCOUNT

This section sets out to place the extant scalpellid taxa studied here, for which a phylogeny is presented (Fig. 14), into a taxonomic framework that reflects the morphological evolution of the group, and additionally incorporates some important fossil material, in order to put minimum dates on the nodes of the cladogram. This is controversial because it cuts directly across the classifications proposed by Newman & Ross (1971) and Zevina (1978a,b, 1981), which were used in a slightly modified form in the most recent taxonomic revision of extant forms by Young (2007). The classification is clearly provisional, because extensive molecular and reproductive studies on scalpellids are currently underway (e.g. Lin *et al.*, 2015), and it will be necessary to extend the study to incorporate many more taxa,

particularly those in which there is a significant reduction of capitular plates. A future, holistic classification of the Scalpellidae will require the integration of further morphological (arthropodal), reproductive and molecular information; however, the present study stands alone as a morphological and phylogenetic exercise.

FAMILY SCALPELLIDAE PILSBRY, 1907

Modified diagnosis
Scalpellomorphs that possess a maximum of 14 plates (carina, rostrum, paired scuta, terga, upper latera, carinolatera, rostrolatera, and inferior median latera), rarely 13, by secondary loss of the rostrum.

Remarks
This definition works effectively for all known living and fossil forms, with the exception of the highly derived *Scalpellopsis striatociliata* Broch, 1922. The record of a subcarina in the Cretaceous species *Diotascalpellum fossula* (Darwin, 1851b) by Hébert (1855) and Withers (1935) is not substantiated by a re-examination of the material. The family appears in the Aptian (Early Cretaceous, about 120 Mya), and is represented by abundant fossil and living forms. In the Cretaceous and the Palaeogene, species were common in shallow and deep marine environments, with palaeodepths of as little as 20–30 m. Neogene and present-day records are almost exclusively from the deep sea. The present study identifies two groups, which are taken as subfamilies.

SUBFAMILY SCALPELLINAE PILSBRY, 1907
MOLECULAR GROUP A OF LIN *ET AL.* (2015: FIG. 3)

Amended diagnosis
Scalpellids in which the rostrolatus is broad, low, strap-like, and gently incurved. The rostrum is broader than high, rectangular, trapezoidal or triangular, and large triangular lateral surfaces contact the interior of the rostrolatus. The articulation surface between the rostrum and rostrolatus extends over the entire height of both plates.

Included genera
Arcoscalpellum Hoek, 1907, *Arcuatoscalpellum* gen. nov., *Diotascalpellum* gen. nov., *Graviscalpellum* Foster, 1980, *Regioscalpellum* gen. nov., and *Scalpellum* Leach, 1817.

Remarks
This definition of Scalpellinae differs in major respects from that of Zevina (1978a), for whom the family was characterized by the subapical carinal umbo, the inflexed carina, and the subapical umbones of the upper and inframedian latus; however, the group as thus defined is polyphyletic (see above), and these

features evolved independently a number of times within the Scalpellidae. The subfamily is therefore rediagnosed to include the basal group of scalpellids shown in Figure 14, which are technically paraphyletic, but can be readily identified.

GENUS *SCALPELLUM* LEACH, 1817

Type species
Lepas scalpellum Linnaeus, 1767, by subsequent designation, Leach 1824.

Diagnosis
Derived scalpellines in which the carinal and scutal umbones are subapical, the carinolatus has a horn-like projection, often recurved, extending beyond the carinal margin, the inframedian latus is rectangular to slightly trapezoidal, with a low umbo, and the upper latus is rhomboidal with a subapical umbo; rostrum rectangular, pyramidal, with large subumbonal surface.

Included species
Lepas scalpellum Linnaeus, 1767, *Scalpellum stearnsi* Pilsbry, 1890, *Scalpellum gibbum* Pilsbry, 1907, and *Tarasovium orientale* Ren, 1983.

Remarks
Scalpellum evolved in the Eocene from *Arcoscalpellum*, and a transition series is presented here (Figs 16, 17; see above).

CLASSIFICATION OF THE NON-*SCALPELLUM* SCALPELLINAE

This group was identified originally by Pilsbry (1907) as the '*S. velutinum* (= *S. michelottianum* Seguenza, 1876) group', and was revived by Young (1998), who noted that one group of species assigned by Zevina (1981) to the genus *Trianguloscalpellum* was characterized by large size and the presence of a thick, pilose cuticle. He identified two morphological trends within the group: a tendency to plate reduction, and displacement of the umbo of the carinolatus to a subapical position. For material from the Cretaceous, Withers (1935) identified three groups of *Arcoscalpellum* (then used to cover most fossil scalpellids), the A. arcuatum Gp, the A. maximum Gp, and the A. fossula Gp, distinguished by numerous plate characters. Zullo (1990) was able to trace the persistence of the two last-named groups from the Cretaceous into the Palaeogene. The new classification presented here builds on the observations of Withers, Zullo, and Young, and identifies five genera, four of which are extant, which reflect the progressive evolution of scalpellines during and since the Cretaceous (see above). These are based largely on detailed characters of the carinolatus, and its articula-

tion with the carina and upper latus. The reclassification permits fossil taxa all traditionally assigned to *Arcoscalpellum* (Withers, 1935, 1953) to be placed in natural groupings with extant taxa. Two of the groups described here were referred to *Trianguloscalpellum* Zevina (1978a), by Zevina (1981) and Young (1998, 2007); however, the type species of this genus, *S. balanoides* Hoek, 1883, is a highly derived form that has additional primordial valves on the inframedian latus and some peduncular plates (see Broch, 1922), and is a hermaphrodite (Yusa *et al.*, 2011). It is possibly related to *R. gigas*, with which it shares a tall articulation between the paired carinolatera.

GENUS *ARCUATOSCALPELLUM* GEN. NOV.
FIGURE 4N–S

Type species
Scalpellum arcuatum Darwin, 1851b. Cretaceous, Albian–Cenomanian, UK.

Diagnosis
Basal scalpellines in which the carinolatus is slightly taller than broad, umbo apical, carinal margin convex, carina with median ridge; upper latus margin gently concave; inframedian latus surface not differentiated; on the interior, the surfaces overlapping the carina and upper latus are similar; external sculpture with strong radial ridges, weak reticulation.

Derivation of name
In eponymous reference to the type species.

Referred species
Scalpellum (*Arcoscalpellum*) *comptum* Withers, 1910 and *Scalpellum trilineatum* Darwin, 1851b. Cretaceous.

Remarks
Material of the type species is illustrated here (Fig. 4M–S). *Arcuatoscalpellum* gen. nov. is the most basal scalpellid known, and ranges from Aptian to latest Maastrichtian in age. It shares many characters with *Cretiscalpellum*, including the sculpture and simple triangular morphology of the carinolatus.

GENUS *DIOTASCALPELLUM* GEN. NOV.
FIGURES 2A, 6U–Y, 11Q–T, 13K–M, 18A–G

Type species
Scalpellum diota Hoek, 1907.

Diagnosis
Scalpellines in which there is no specialized contact between the carina and carinolatus, merely a cresentic concavity on the interior of the plate that forms a rim

slightly overlapping the upper latus; umbo of carinolatus upright, only slightly incurved, dorsal margin gently convex; inframedian surface of carinolatus well demarcated and slightly inset.

Derivation of name
In eponymous reference to the type species.

Included species
Scalpellum rubrum Hoek, 1883, *Scalpellum indicum* Hoek, 1883, *Pollicipes angustatus* Geinitz, 1843, *Scalpellum gracile* Bosquet, 1854, and *Scalpellum fossula* Darwin, 1851.

Remarks
Cretaceous and extant species of *Diotascalpellum* gen. nov. have a very similar carinolatus morphology (e.g. Fig. 18A–G). The prevalence and diversity of species of *Diotascalpellum* in the Cretaceous supports its basal phylogenetic position. The earliest records are from the upper Albian (*D. angustatum*; Withers, 1935).

GENUS *REGIOSCALPELLUM* GEN. NOV.
FIGURES 2B, 6P–T, 10J, K, 11M–P, 18N–S

Diagnosis
Scalpellines in which a concave, internal upper latus surface and short carinal margin is present on the carinolatus, covered by epidermis; umbones of carinolatus incurved, lateral margin of carinolatus strongly convex.

Type species
Scalpellum regium Thomson, 1873.

Derivation of name
In eponymous reference to the type species.

Referred species
Scalpellum darwini Hoek, 1883, *Scalpellum gigas* Hoek, 1883, *Scalpellum moluccanum* Hoek, 1883, *Pollicipes maximus* J. de C Sowerby, 1829, and *Arcoscalpellum sanchezae* Withers, 1953.

Remarks
The distinctive *R. maximum* (Fig. 18N, O, P, S) is common in Cretaceous chalks and marginal marine deposits from the Coniacian to the Maastrichtian (Withers,

1935), and *Regioscalpellum* gen. nov. is represented in the Eocene of Cuba by *Arcoscalpellum sanchezae* Withers, 1953.

GENUS *GRAVISCALPELLUM* FOSTER, 1980
FIGURES 2E–H, 13A–C

Type species
Scalpellum pedunculatum Hoek, 1883, by original designation.

Diagnosis
Scalpellinae in which the rostrolatera and inferomedian latera are very low in proportion to the height of the capitulum; carinolatera have an elongated rhomboidal outline, with a prominent ridge on the long axis; the umbonal region of the carinolatus is weakly involuted.

Included species
Scalpellum regina Pilsbry, 1907; *Arcoscalpellum ungulatum* Withers, 1953; *Graviscalpellum grantmackiei* Buckeridge, 1983.

Remarks
Foster (1980: 526) established *Graviscalpellum* to include 'Arcoscalpellids that are hermaphroditic, attain relatively large size and have lower latera about one tenth the height of the capitulum'. Subsequently, the genus was treated as a junior synonym of *Anguloscalpellum* Zevina, 1978b, because Zevina (1981) had included *S. pedunculatum* in that genus (e.g. Young, 2007); however, the type species of *Anguloscalpellum*, *Scalpellum angulare* Nilsson-Cantell, 1930, falls within the genus *Weltnerium* as redefined in this paper (trapezoidal scutum; deep, transversely elongated receptacle for dwarf male; rostrum with broad triangular external surface), and is evidently not related closely to *S. pedunculatum*. Therefore, *Graviscalpellum* is resurrected from synonymy to include both the extant *G. regina* (Pilsbry, 1907) and a number of fossil species from the Oligocene–Miocene of New Zealand (Buckeridge, 1983). The molecular phylogeny of Lin *et al.* (2015: fig. 3) shows *G. regina* and *G. pedunculatum* as closly related taxa.

GENUS *ARCOSCALPELLUM* HOEK, 1907
FIGURES 2C–H, 6F–O, 10L, M, Q, 11E–L, 13A–F, 18H–M

Type species
Scalpellum velutinum Hoek, 1883 (= *Scalpellum michelottianum* Seguenza, 1876).

Diagnosis
Scalpellines in which a large upper latus surface is present on the carinolatus; umbo strongly incurved,

carinal margin present; lateral surface of carinolatus inturned onto interior of plate, peduncular margin concave.

Included species
Scalpellum hirsutum Hoek, 1883, *Scalpellum sociabile* Annandale, 1905, and *Scalpellum quadratum* (Dixon, 1850; Eocene).

Remarks
The name *Arcoscalpellum* was formerly applied to most living and many fossil scalpellids (Withers, 1935, 1953; Newman *et al*., 1969). After the revisions of Zevina (1978a,b, 1981), the genus was used in a restricted sense and identified by the 'inframedian latus triangular, reaching upper latus, umbo apical' (Shalaeva & Boxshall, 2014: 21). This condition is shown here to be plesiomorphic for scalpellids, and the genus is therefore redefined with reference to the morphology of the type species, *Arcoscalpellum michelottianum*. It encompasses a small group of more derived Scalpellinae (e.g. Fig. 2C, D) in which the carinolatus is in possession of a carinal margin and an upper latus surface (Fig. 10L, M). It ranges from the Eocene to the present day.

AMIGDOSCALPELLINAE SUBFAM. NOV.
MOLECULAR GROUP B OF LIN *ET AL*. (2015: FIG. 3)

Diagnosis
Small, rather delicately constructed scalpellids in which the tergum is triangular, with a notched upper carinal margin to accommodate the tip of the carina, apical to which is a short supracarinal surface; scutum with discrete low tergal surface; carinolatus tall, umbo subapical, with well-developed carinal and upper latus margins; carinolatera of pair articulate firmly beneath carinal base; rostrolatus as tall as broad, subrectangular to subtriangular.

Discussion
This group is essentially identical with group B of Lin *et al*.'s (2015: fig. 3) molecular analysis, which includes a number of species studied here. The subdivision of this derived clade of scalpellids is provisional. The group is sharply and precisely defined by morphological characters, and the cladistic analysis indicates the direction of evolution; however, characters within the group are partly gradational.

1. The shape and relationships of the inferior median latus, used extensively in taxonomy by Zevina (1978a,b, 1981; see also Young, 2007; Shalaeva & Boxshall, 2014). Plesiomorphically, by comparison with the out-group, this is (1) triangular, (2) its apical margin does not extend to the scutum and upper latus, and (3) its umbo is apical (Figs 3, 6, 7). Note that there is considerable change in the shape and position of the umbo during ontogeny (Young, 2007). The development of two discrete surfaces, contacting the scutum and upper latus, respectively, appears to be a good synapomorphy of a more derived group of amigdoscalpellines, which is closely, and concomitantly, paralleled by the basal migration of the umbo. There also appears to be a division between a group with an hourglass-shaped ('waisted') inferior median latus (more basal) and a derived group in which the pentagonal plate is relatively broad, the lateral surfaces are parallel, and the umbo has migrated to the rostral margin.

2. Contact between the carinolatera, beneath the carina. The polarity can be determined by the fact that all taxa with a triangular inferior median latus (evidently plesiomorphic) also possess a highly modified contact that is marked by interdigitating, alternate ridges radiating down from the umbo of the plate (Figs 6E, 7X). The more derived character state is a symmetrical contact, in which either a few ridges oppose precisely (e.g. *Ca. recurvitergum*; Fig. 7S), or in which the articulation is divided into a more basal, flat, slightly protruding contact surface and and upper, depressed, and more horizontal contact, a lower extension of the carinal surface (e.g. *Catherinum novaezelandiae*; Fig. 7N).

3. The nature of the contact between the scutum and upper latus. Plesiomorphically (e.g. Fig. 2), this is a simple, straight contact with no overlap, but in more derived taxa the slightly recurved apex of the upper latus rests in a groove on the scutum (e.g. Fig. 3A, B, E–G). A notch is present in the upper latus margin of the scutum at the same level (Fig. 8C–D).

4. A sharp, acuminate, incurved umbonal tip on the scutum, incorporating the primordial valve, is present in more derived forms (Fig. 8C–D).

5. The shape of the scutum changes during the evolutionary history of the scalpellids, from a subtriangular plesiomorphic form, in which the basal-occludent and basal-upper latus margins are at nearly right angles (Fig. 8A, E), to become progressively more trapezoidal (Fig. 8C, D, G, H). This is brought about by the increasingly acute basal-occludent angle and the increasingly obtuse basal-upper latus angle (Fig. 1F).

6. The shape of the rostrum, and the extent and geometry of its external and internal surfaces. In *Amigdoscalpellum* and *Catherinum*, the rostra are oval, elongate, and very small, less than half the height of the rostrolatera. In the derived *Weltnerium*, the rostrum has a trapezoidal external surface, and the rostrum has the same height as the rostrolatera.

7. The shape and proportional size of the internal depression, between the umbo and the scutal adductor,

which serves to accommodate dwarf males. In basal amigdoscalpellines, this is a U-shaped notch, extending variably inwards from the occludent surface.

8. Surface sculpture. The basal amigdaloscalpelline *Amigdoscalpellum* possesses a ubiquitous radial sculpture of raised, rounded ridges on all plates except the carina (e.g. *Am. truncatum* and *Am. rigidum*). Species of *Catherinum* have variable sculpture, from entirely smooth to possessing variably developed radiating ridges, which increase during ontogeny (Young, 2007). Species of *Weltnerium* are smooth, except for a variable coarse sculpture in *W. stroemii*.

The cladistic analysis demonstrates that there is a clear morphological progression from plesiomorphic to derived states in these characters; however, subdivision into clearly defined groups, effectively diagnosing genera, is problematic, because although the trends are directional, there is significant overlap in the distribution of the character states. For example, there are taxa in which the inframedian latus is hourglass shaped and there is significant overlap between the upper latus and the scutum, but which retain an interdigitating contact between the carinolatera (e.g. Young, 2007). Thus, there appears to be a limit to the use of morphological characters for defining clades, and the ultimate resolution may only be achieved by molecular analysis. However, the present study, and the examination of available material and literature, supports subdivision into three genera, using characters of the inframedian latus (Zevina, 1978a,b, 1981).

GENUS *AMIGDOSCALPELLUM* ZEVINA, 1978B
FIGURES 1A–C, 3E–G, 6A–E, 7U–Y, 8B, F, J,
11A–D, 12Q–T

Type species
Arcoscalpellum manum Zevina, 1973, by subsequent designation Zevina, 1978b.

Diagnosis
Sculpture of strong, radially arranged, rounded raised ridges on all plates except carina; carinolatera articulate across midline by means of zig-zagging, alternating ridges that diverge from umbones. Umbones of carinolatera central to subcentral, close to base of carina, not prominent. Inframedian latus narrow, triangular, more rarely elongate, rectangular, umbo apical, often not extending to top of carinolatus and rostrolatus. Rostrum small, less than half the height of the rostrolatus, narrow, rounded oval rhombic outline.

Included species
Scalpellum vitreum Hoek, 1883, *Scalpellum rigidum* Aurivillius, 1898, *Scalpellum mamillatum* Aurivillius,

1898, *Arcoscalpellum truncatum* Hoek, 1883, *Scalpellum elegans* Hoek, 1907, *Scalpellum formosum* Hoek, 1907, *Scalpellum trapezoideum* Hoek, 1907, *Scalpellum semisculptum* Pilsbry, 1907, *Scalpellum aurivilli* Pilsbry, 1907, *Scalpellum galapaganum* Pilsbry, 1907, *Scalpellum rigidum* Aurivillius, 1898, *Scalpellum sculptum* Hoek, 1907, *Scalpellum (Arcoscalpellum) constellatum* Withers, 1935, *Arcoscalpellum pertosum* Foster, 1978, *Scalpellum (Arcoscalpellum) bellulum* Withers, 1935 (Cretaceous, Campanian, UK), and *Arcoscalpellum turinensis* Withers, 1953 (Miocene, Helvetian, Turin, Italy). Young (2007: 59–60) provided a useful discussion of extant species of *Amigdoscalpellum*, and suggested that extensive synonymy of taxa was a likely possibility.

Remarks
Thus defined, *Amigdaloscalpellum* appears to be a monophyletic entity. The distinctive radial sculpture is also present, albeit in a weaker and more restricted form, on some fully grown individuals of a few species of *Catherinum* (e.g. *Ca. australicum*, *Ca. recurvitergum*, and *Ca. striolatum*; see Young, 1998). These can, however, always be distinguished on the basis of the morphology of the inframedian latus and the overlap of the scutum by the upper latus. Note that the genus as here defined also includes some taxa traditionally referred to *Arcoscalpellum* (such as *Arcoscalpellum truncatum*), which fall naturally in *Amigdoscalpellum*.

GENUS *CATHERINUM* ZEVINA, 1978B
FIGURES 3A–C, 7K–T, 8C, G, K, 12I–P, 19A–V

Type species
Scalpellum recurvitergum Gruvel, 1900 (see redescription in Young, 1998).

Diagnosis
Inframedian latus waisted, hourglass-shaped, umbo central to nearly basal. Well-defined margins contact the scutum and upper latus. Contact between carinolatera usually flat, symmetrical. Rostrum tiny, oval, or rarely absent. Apex of scutum, acuminate, incurved. Upper latus overlaps scutum, fitting into notch in scutum. Scutum trapezoidal, basal–occludent angle about 80°, tergal–upper latus angle 100–115°.

Synonym
Verum Zevina, 1978b.

Included species
Scalpellum australicum Hoek, 1883, *Scalpellum novaezelandiae* Hoek, 1883, *Scalpellum recurvitergum* Gruvel, 1900, *Scalpellum striolatum* G.O. Sars, 1877, *Scalpellum hispidum* G.O. Sars, 1890, *Catherinum*

anglicum sp. nov. (Campanian, Cretaceous, UK), and *Arcoscalpellum singletoni* Withers, 1953 (Miocene, Balcombe Bay, Australia).

Remarks
As redefined here, *Catherinum* includes many of the species included in *Verum* by Zevina (1981). As noted by Young (2007), *Catherinum* fall into several distinct morphological groups. Although not dealt with here, many of the taxa assigned to *Annandaleum* (e.g. with strikingly reduced plates, such as *Annandaleum japonicum* Hoek, 1883), have an hourglass-shaped inferior median latus, at least in the juvenile stages, and are likely to be derived from species of *Catherinum* by plate reduction. *Planoscalpellum* Zevina, 1978b is a *Catherinum*-like form in which the upper latus umbo is unusually low on the scutum.

CATHERINUM ANGLICUM SP. NOV.
FIGURE 19C–K, N–Q, T, V

Diagnosis
Catherinum in which the occludent margin of the tergum is straight, and the external surface adjacent to this carries three ribs that diverge from the umbo. The upper part of the upper latus margin of the scutum is embayed. The carinolatus has a very broad upper latus margin.

Derivation of name
After East Anglia, in which the type material was collected.

Material
Fifty valves, including carinae, scuta, terga, and carinolatera, from the upper Campanian, *Belemnitella mucronata* zone chalk of Keswick and Cringleford Newfound Farm pits, Norwich, Norfolk, UK. The scutum illustrated is the holotype (Figure 19O), and the other illustrated valves are paratypes.

Description
The carina (Fig. 19E, I, P, T, V) is gently incurved towards the tergum, and the parietes are of even width; intraparietes are not developed. The tectal ridges are robust and broad (Fig. 19E, T), and the tectal surface between these is slightly convex. The tergum (Fig. 19Q) is elongated and triangular, and the carinal margin is slightly convex. Three radial ridges run from the umbo, subparallel with the occludent margin. The scuta (Fig. 19J, K, N, O) are concavo–convex, trapezoidal, and the umbo is pointed and incurved; the upper latus margin has a distinctive concavity just beneath the tergal–upper latus angle. A narrow groove runs parallel with the occludent margin. On the interior of the valve, a deep, oval dwarf male receptacle lies between

the apex and the scutal adductor scar. The carinolatus (Fig. 19C, D, F–H) has a low, incurved umbo, and a tall carinal margin. The long, straight upper latus and inframedian latus margins are set at right angles. The plate is very typical of *Catherinum* of the *Ca. hispidum* (Fig. 19A, B) and *Ca. striolatum* (Fig. 7P, Q) type.

Remarks
Catherinum anglicum sp. nov. is perhaps closest to the extant *Ca. hispidum* from the Norwegian Sea. The carinae are very similar indeed, both carrying very broad, robust tectal ridges (Fig. 19I, S, T), and with shallow short grooves for articulation with the carinolatus in the interior (Fig. 19U, V). The terga are similar in shape, but the scutal margin is convex in *Ca. hispidum* and straight in *Ca. anglicum* sp. nov. Three divergent ribs run from the umbo, adjacent to the occludent margin in *Ca. anglicum* sp. nov., but these are absent in the living species (Fig. 19Q, R). The scuta both possess an incurved umbo, and a large, deep pit for dwarf males (Fig. 19J–O), which is directed slightly more transversely in *Ca. hispidum*. The carinolatera are similar in shape (Fig. 19A–D, F–H), but the tergal margin is longer in *Ca. anglicum* sp. nov. It can be distinguished from small carinae of *Diotascalpellum fossula* by the absence of intraparietes. A further undescribed species of *Catherinum* is present in the Norwich chalk assemblage; this will be named subsequently.

This is a very small species: the scuta have a maximum height of 2 mm, and the total height of the individuals was probably not more than 5 mm. It was possibly attached to living crustaceans or pycnogonids, by analogy with the small extant species *Weltnerium nymphocola* (Hoek, 1883) and *Verum brachiumcancri* Weltner (see Buhl-Mortensen & Høeg, 2012).

GENUS *WELTNERIUM* ZEVINA, 1978B
FIGURES 1F, G, 3D, H, 7A–J, 8D, H, L, 12A–H

Type species
Scalpellum nymphocola Hoek, 1883, original designation of Zevina 1978b.

Diagnosis
Inframedian latus pentagonal, with subparallel lateral margins, somewhat taller than broad; umbo central, usually close to rostrolatus margin. Rostrum well developed, large trapezoidal to rectangular external surface, extending over full height of rostrolatera. Scutum markedly trapezoidal, scutal and tergal margins short, basal–occludent angle acute (60°), tergal–upper latus angle 120°. Pit for dwarf males deep, oval, transverse.

Synonyms
Ornatoscalpellum Zevina, 1978a, *Tarasovium* Zevina, 1978a (partim), and *Anguloscalpellum* Zevina, 1978b (partim).

Referred species
Scalpellum stroemii M. Sars, 1859, *Scalpellum gibberum* Aurivillius,1892, *Scalpellum ornatum* Gray, 1848, *Scalpellum nymphocola* Hoek, 1883, *Scalpellum convexum* Nilsson-Cantell, 1921, *Scalpellum cornutum* G.O. Sars, 1879, *Scalpellum natalense* Barnard, 1924, *Scalpellum valvulifer* Annandale, 1910, *Scalpellum recurvirostrum* Hoek, 1883, and *Scalpellum angulare* Nilsson-Cantell, 1930.

Remarks
Weltnerium, as diagnosed here, is a monophyletic derived group characterized by a pentagonal inferior median latus with a low umbo, a tall, narrow rostrum with a large external surface, a markedly trapezoidal scutum, and a large transverse receptacle for dwarf males. Forms with subapical carinal umbones ('*Ornatoscalpellum*') and projecting carinolatera (some '*Tarasovium*') fall into this category. It is not known from the fossil record.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Character list used in phylogenetic analysis.
Table S2. Matrix of character distribution used for phylogenetic analysis.