

Two new British Cretaceous Epitoniidae (Gastropoda): evidence for evolution of shell morphology

R. J. Cleavely

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD.

Synopsis

Extensive preparation of the holotype of *Funis crebricostatus* Gardner 1876, from the Upper Campanian, reveals that it has a distinctive and elaborate ornament which justifies the erection of a new genus *Crossotrema*. A recently-discovered high-spined, solely spirally ornamented Albian epitoniid is named *Funis spirornatus*.

Ornament complexity and shell form within the Epitoniidae are discussed and used to suggest possible evolutionary trends within the family.

Introduction

The discovery of two new taxa, while examining material in preparation for a general revision of Cretaceous Epitoniidae, has prompted this short paper.

Apart from considerations of their stratigraphical and geographical distribution, the classification of fossil mollusca is solely dependent upon shell morphology and comparison with living forms. However, the classification of the Recent Epitoniacea is generally regarded as 'being in a complex nomenclatorial tangle' (Clench & Turner 1950 : 223). This confusion is partly the result of a paucity of good material, but has also arisen from the mistaken interpretation of the overlapping characters occurring within the family.

Dushane (1974 : 4) and Robertson (1971 : 62) believe that to classify epitoniids solely on the basis of shell characters is quite inadequate. They advocate a more biological approach utilizing non-morphological information on populations relating to their ecology, biochemistry and behaviour. However, in the restricted field of fossil epitoniids the use of shell ornament provides an acceptable classification.

Recent Epitoniidae are world-wide in distribution, rich in number of species and occur in a remarkable range of depths in all seas. Their fossil record suggests that the family has exhibited these characteristics since the Aptian. Throughout their history, the Epitoniidae appear to have formed a small proportion of the total marine molluscan fauna. However, during the Cretaceous this proportion appears to have comprised numerous individuals of a small number of species, whereas since the Eocene they are represented by a richer variety of species but with relatively fewer individuals. In general, Cretaceous species were much larger than later forms, particularly Recent ones. The majority of Cretaceous species have ornament composed of strong axial ribs and fine spiral cords above a marked basal keel. These features are characteristic of *Confusiscula* De Boury 1909, a genus to which many species have been assigned. Clench & Turner (1950 : 223) commented that the diversity shown by the Epitoniidae, both in the past and present, indicated that they were and are still 'an exceedingly vigorous family'.

The available descriptive literature on British Cretaceous Epitoniidae is virtually restricted to the original work of J. Starkie Gardner (1876). Particular species have been described by others in general works, e.g. J. de Carle Sowerby *in* Fitton (1836) and *in* Dixon (1850), and by Seeley (1861), but no other appraisal of the family has been attempted.

There has been little research on the fossil occurrence of this family outside Britain except for the notable reviews of De Boury (1890–1917) and Cossmann (1912); shorter contributions have been made by Wollemand (1908), Durham (1937) and Sohl (1964).

It is the great rarity of fossil epitoniids that has convinced me of the need to describe these unique, but incomplete, British Cretaceous specimens, in the belief that other examples are unlikely to be discovered. I am not aware of any similar material in the collections of the Institute of Geological Sciences, the Sedgwick Museum, Cambridge, or the University Museum, Oxford.

Systematic Descriptions

British Museum (Natural History) register numbers are given of all the specimens figured. Specimens with numbers prefixed by G or GG are fossils in the Department of Palaeontology; other numbers refer to the Recent Mollusca collections of the Department of Zoology.

Class **GASTROPODA** Cuvier, 1797

Superfamily **EPITONIACEA** Berry, 1910

Family **EPITONIIDAE** Berry, 1910 [Lamarck, 1812 (? 1811), vernac.]

Genus **CROSSOTREMA** nov.

TYPE SPECIES. *Funis crebricostatus* Gardner 1876, designated here.

DIAGNOSIS. Moderately large, elongate turreted shell with strongly convex, firmly joined whorls. Elaborate axial and spiral sculpture, of equal significance, consisting of crenulate frilled opisthocyrt collabral lamellae and primary and secondary spiral cords. Lamellae alternate on adjacent whorls, obscuring the impressed suture. Whorls lacking varices; imperforate.

NAME. Greek, κροσσωτός, flounced, frilled + τρήμα, a hole, aperture.

REMARKS. The complicated sculpture of *Crossotrema* (described below), suggests some relationship with the living genus *Cirsotrema* Mörch, 1852 (Fig. 3), but the lack of varices readily distinguishes *Crossotrema* from all other cirsotremids. Its apparent lack of either a marked basal disk, cord, or carination supplied another distinctive character. The alternation of its axial lamellae on adjacent whorls differs from the virtually continuous ornament exhibited by many Tertiary and Recent cirsotremid species, as a result of the coalescence of the axial ribs on neighbouring whorls.

Crossotrema is separated from *Cirsotremopsis* Thiele, 1928 by the latter's turreted outline, deep sutural channel and relatively weaker development of spiral sculpture. Yet, the comparable nature of their complex ornament (explained below) indicates a close affinity.

Investigations of other epitoniids, e.g. in the Australian Tertiary (Tate 1890), possessing ornament of axial lamellae revealed that such sculpture was dissimilar to that of *Crossotrema*. The North American Cretaceous species placed in *Striaticostatum* by Sohl (1964 : 317) have axial ribs composed of multiple lamellae; they can be further distinguished by the presence of a basal disk, an outer lip varix and only weak development of spiral sculpture.

Inevitably, *Crossotrema* has ornamental components in common with the epitoniids *Amaea* H. & A. Adams 1853 (see Fig. 14), *Amaea* (*Scalina*) Conrad 1865 [= *Ferminoscala* Dall 1908] and *Epitonium* (*Asperiscalia*) Boury 1909, but the characteristic rectangular reticulate sculpture shown by the shells of all these Recent genera confirms their distinct identities.

Cossmann (1912 : 17), when he outlined the significance of the basal disk in the shell morphology of the Epitoniidae, began by stressing the great variability shown by this feature within the family. Although the basal disk, or its other manifestations such as basal cord and basal angulation, are used to distinguish taxa at several levels in Epitoniidae classification, this variability in strength and structure makes it an unreliable indicator of relationship (Clench & Turner 1951 : 250).

The key to the Epitoniidae provided by Burch (1956) utilized fine differences in the nature of the basal disk and ornamental varices to separate the various taxa mentioned above, but it is largely confined to considerations of Recent genera. If this key were followed, the absence of both varices and basal disk in *Crossotrema*, together with its equal development of both spiral

and axial ornament, would separate it as a genus. The intricate and delicate ornament enables *Crossotrema* to be distinguished from all other Cretaceous epitoniids that have simpler and coarser axial ribs and are placed in either *Claviscala* Boury 1909 or *Clathroscala* Boury 1890b.

Cossmann (1912 : 53) recorded *Cirsotrema* (*Coroniscala*) *tournoueri* (Briart & Cornet 1877) [= *C. briarti* (Boury 1890a)], from the Montian of Belgium, as the earliest cirsotremid. However, the recognition that '*Funis*' *crebricostatus* Gardner is a cirsotremid extends the range of the group firmly back into the Cretaceous. The relative equality of both its axial and spiral sculpture elements would conform with the expected ornament of an ancestral form, although the elaborate frilled lamellae must be considered to represent a specialized character. This last feature, particularly the occasional occurrence of composite lamellae in the ornament of *C. crebricostata*, leads to the conjecture that it might be precursory to the cellular varices and multilayered lamellae occurring in the Cretaceous (Maastrichtian) *Striaticostatum*, Tertiary *Cirsotremopsis* and Recent *Cirsotrema*. Particular examples of Recent species with such features would be *C. togatum* Hertlein & Strong 1951, and the extreme development occurring in *C. dalli* Rehder 1945. The ornament in all these taxa consists of different combinations and degrees of emphasis of the same basic components as are present in the earlier genus *Crossotrema*. Extending this argument it is also possible to speculate that Recent *Amaea* (*Scalina*) may have a common ancestry with the genus. The occurrence of intermediate forms in the East African Neogene (see p. 240) and the Upper Cretaceous of north Africa (Abbass 1963, Wanner 1902), support such a view. Cossmann (1912 : 53) had considered that the genus *Cirsotrema* had achieved a cosmopolitan distribution by the Eocene. Rehder (1945 : 127) later postulated a geographical basis for grouping the numerous species assigned to this genus and also recognized stratigraphical restrictions. He indicated that true *Cirsotrema*, type species *C. varicosa* (Lamarck 1822), Fig. 3, was restricted to the Indo-Pacific region.

The only apparent anomaly in this argument is the lack of the distinctive cirsotremid features such as varices and basal disk in the single specimen assigned to *Crossotrema*. Yet, remembering the remarks of Cossmann (mentioned above) on the extreme variability of these features this is not so remarkable, nor is the fact that other Albian epitoniids had evolved a distinctive basal disk.

Crossotrema crebricostata (Gardner 1876)

Figs 5, 9

1876 *Funis crebricostatus* J. S. Gardner: 111; pl. 3, fig. 18.

MATERIAL. Holotype (and only specimen), BM(NH) Dept. of Palaeontology no. G 19065. J. S. Gardner coll.

LOCALITY AND HORIZON. Norwich, Norfolk; Chalk, Upper Campanian, Mucronata Zone.

DIMENSIONS. Actual height of incomplete specimen	= 27.6 mm
Estimated height of complete spire	= 59 mm
Diameter of whorl: 1st	= 14 mm
2nd	= 17.3 mm
3rd	= 21.9 mm (part cast, part shell)
External spire angle of preserved whorls	= 21° ¹

ORIGINAL DESCRIPTION. 'Shell elongated, angle 25°; whorls inflated and rounded; ribs numerous, probably twenty to twenty-five, very thin and salient; striae exceedingly strong and prominent, about one-third closer together than the ribs, which they cross, forming nodes at the intersections; suture indistinct. The height and prominence of the striae which is nearly as great as that of the ribs, give the shell a reticulated appearance, whilst the nodes at the frequent intersections give it a rugose aspect. There are very faint traces of ornamentation preserved on the cast' (Gardner 1876 : 111).

¹This is an approximation owing to the fragmentary nature of the specimen.

DESCRIPTION. The only specimen is lacking its early whorls and aperture. It consists of slightly more than two whorls of which only the shell of one side is preserved, the remainder being merely an internal mould with vestiges of the sculpture. The whorls are strongly inflated and joined, although separated by a deep, impressed suture that is obscured by the adapical curvature of the lamellae. There is some indication that the most abapical cord forms a slight basal ridge.

The shell ornament consists of elaborate and delicate axial lamellae (numbering 10, 11 and 12 on successive half-whorls) and spiral cords (Fig. 9). Shell growth from within the aperture culminates in thin frilled collabral lamellae. At the apertural margin, shell growth is reflected outwards and backwards to form a narrow flange, which appears to be normal to the whorl side and composes the lamella. Many become broken, producing a ragged and irregular appearance. These lamellae are opisthocyrt and their curvature is grossly accentuated at the adapical suture. The size of their crenulations is influenced by the spiral cords and is strongest towards the centre of the whorl, but weakens considerably adapically. The lamellae are seldom aligned, but generally alternate with those on adjacent whorls; occasionally coalescence occurs between those of successive whorls. Sometimes several lamellae emanate from virtually the same aperture, producing a composite reticulate network. Incomplete preservation of the shell prevents an accurate assessment of the frequency of this feature, but only a single instance is visible on each whorl and these are not aligned.

Spiral sculpture consists of strong double cords corresponding to the crest of each lamellar crenulation. The two cords, the abapical being slightly the weaker, are separated by a narrow groove. Nineteen composite cords are visible on the second preserved whorl, with the strongest eleven on the whorl side. The other eight weaken progressively towards the adapical suture. Interspaces are slightly broader than the two primary cords and secondary cords occur at their centre. All the spiral cords are crossed by fine collabral threads, which produce a slight beading on the primary cords and a lattice across the separating groove.

The base of the shell is not adequately preserved, but the lamellae extend part-way onto it and weaken. An umbilicus is not present.

REMARKS. *Preparation.* Preliminary examination of the holotype suggested that more of the specimen might be embedded within the chalk matrix. The use of an S. S. White Airabrasive tool confirmed that part of the shell ornament was perfectly preserved². In preparing the specimen, F. M. P. Howie of the Palaeontology Laboratory, BM(NH), used sodium bicarbonate (abrasive powder no. 4), and to minimize damage to the fragile frills of the shell kept the pressure of the carbon dioxide carrier gas between 10 and 20 psi. After cleaning, the exposed shell was hardened by using a three percent weight per volume solution of 'Butvar B98' in isopropanol.

Discussion. Although Gardner (1876) emphasized that only traces of ornament were preserved, the subsequent preparation of the holotype has revealed that this interpretation was inaccurate. The delicate, frilled sculpture immediately distinguishes *Crossotrema crebricostata* from the

²Hitherto rare examples of calcite preservation have only been known from the hard Irish Chalk of Co. Down.

Fig. 1 *Confusiscula dupiniana* (d'Orbigny 1842). Upper Greensand, Sidmouth, Devon. G 44. $\times 2$. (Shell composed of inflated convex whorls).

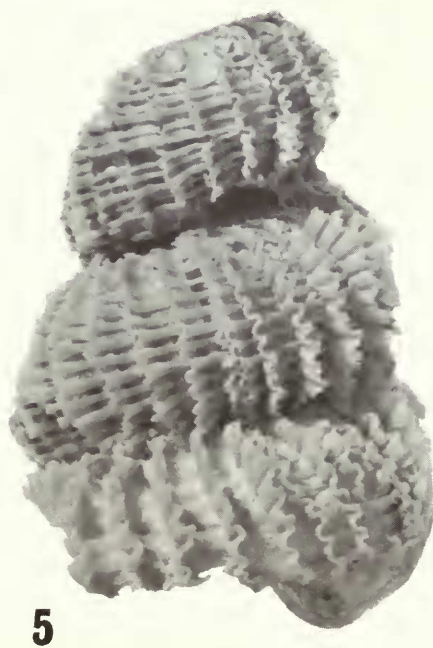
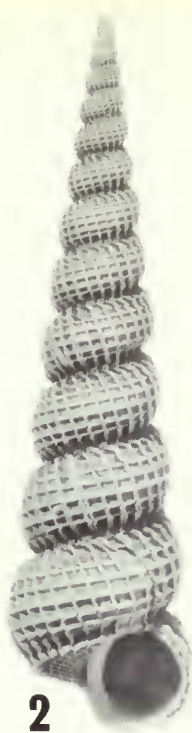
Fig. 2 *Amaea decussata* (Lamarck 1801) [= *Cirsotrema kieneri* (Tapparone-Canefri, 1876)]. Recent Mauritius, Indian Ocean; C. T. Trechmann coll. 1979252. $\times 2$. (Lacks varices, has rectangular ornament pattern). See also Fig. 7.

Fig. 3 *Cirsotrema varicosa* (Lamarck 1822), type species of *Cirsotrema*. Recent, collected under stones at low water, Bulusan, Province of Albay, Isle of Luzon, Philippines; Hugh Cuming collection 228/3. 1979253. $\times 2$.

Fig. 4 ? *Crossotrema* sp. [= '*Epitonium*' *kieneri* (Canefri); Cox in Weir 1938 : 65]. Pliocene, cliff at Tanga, Tanganyika (Tanzania); coll. G. M. Stockley, 1929. G 49523. $\times 2$. See also Fig. 8.

Fig. 5 *Crossotrema crebricostata* (Gardner 1876), holotype. Chalk, Upper Campanian, Mucronata Zone, Norwich, Norfolk; J. S. Gardner coll. G 19065, $\times 3$. (Opposite side to that figured by Gardner 1876: pl. 3, fig. 18). See also Fig. 9.

Fig. 6 *Claviscala clementina* (Michelin 1833). Gault, Albian, Folkestone, Kent; history unrecorded. G 71938. $\times 1.25$. (High-spined, elongate shell, narrow whorls). See also Fig. 10.



essentially spirally-ornamented species included in *Funis* by Gardner (1876 : 111) and Cossmann (1912 : 73). Furthermore, *crebricostata* cannot be included in the genus *Funis* Seeley 1861, for its whorls are not elongate nor are they separate.

Affinities with and separation from the living genus *Cirsotrema* and other Recent and fossil forms have been discussed above. A very small and little-known Recent species, *Discoscala edgari* Boury (1912 : 90-3), from Macclesfield Bank, China Sea, has closely similar frilled axial lamellae and the same general round-whorled shell. It is difficult to discern any spiral ornament on Boury's poor figure (1912 : pl. 7, fig. 3), but its possession of a marked basal disk would separate the two species.

Two specimens from the Pliocene of Tanzania, BM(NH) nos G 49522-3, Figs 4, 8, have considerable sculptural resemblance to *Crossotrema* in that their ornament is composed of lamellar axial ribs and both primary and secondary spiral cords. Their slender, high-spined shell and development of a strong basal cord also makes them very reminiscent of the Recent '*Cirsotrema kieneri*' (Tapparone-Canefri 1876) from the East Indies, NW Australia and Indian Ocean. This similarity led L. R. Cox (*in* Weir 1938 : 65, 68) to refer these two African fossils to that species. The structural components of the ornament in *kieneri* suggest a common ancestry with *Crossotrema*, while its multiple lamellar ribs also indicate some affinity with the North American Cretaceous genus *Striaticostatum* Sohl.

The confusion in epitoniid nomenclature is well illustrated by this example. '*Cirsotrema kieneri*' appears to be virtually indistinguishable from another Indo-Pacific species *Amaea decussata* (Lamarck 1801, 1804), Figs 2, 7. This species, in turn, can only be distinguished from the Panamic-Galapagan species *A. deroyae* Dushane and the eastern Atlantic species *A. retifera* Dall by its slightly more convex whorls and the smaller size of the two American species. The latter are essentially separated by their geographic occurrence (Clench & Turner 1950 : 245, Dushane 1974 : 54). Elsewhere, Wagner & Abbott (1978 : 08-204) have recognized two further species of Indo-Pacific epitoniids as synonyms of *kieneri*, but placed the species in the subgenus *Amaea (Elegantiscala)*.

Genus *FUNIS* Seeley, 1861

TYPE SPECIES. *Funis elongatus* Seeley 1861, by subsequent designation of Gardner 1876 : 10—see Figs 12, 13.

EMENDED DIAGNOSIS. Slender, very elongate imperforate shell with joined whorls. Narrow, elongate rounded whorls form a loosely-coiled spiral and are separated by an impressed and partly grooved suture. Spiral cords form dominant sculptural element; axial ornament reduced and when present restricted to collabral threads. Basal ridge present and may be accentuated by spiral furrow. Ovate aperture with simple outer lip and inner lip not recurved.

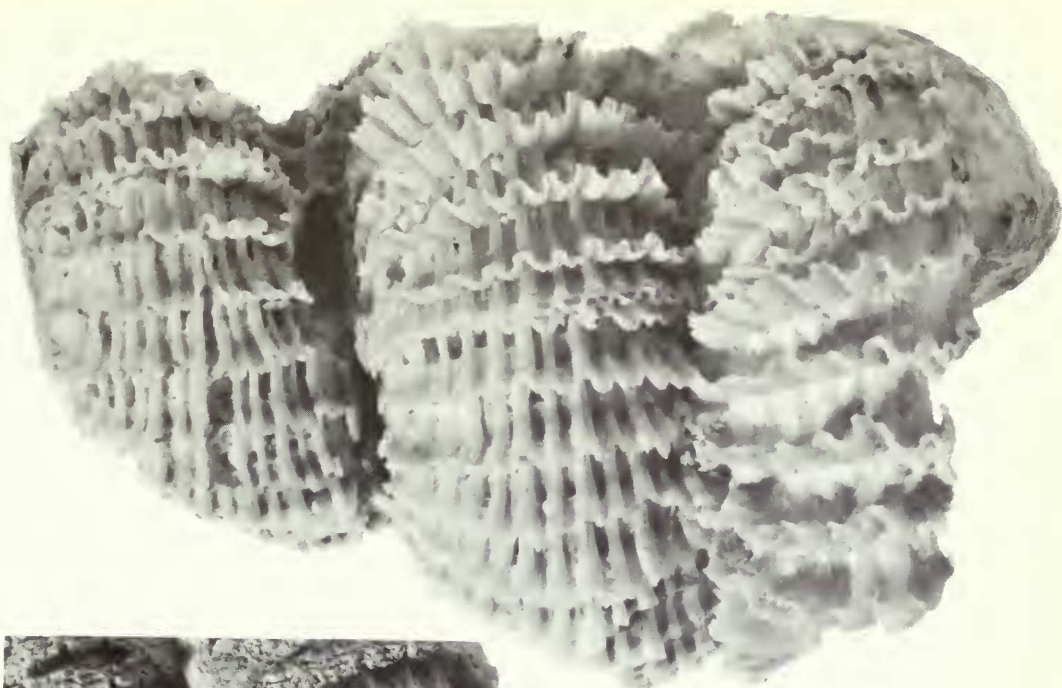
DISTRIBUTION. U.K.; *F. elongatus* Seeley: Upper Albian, Cambridgeshire; *F. spirornatus* sp. nov.: Albian, Bedfordshire.

REMARKS. Seeley when describing this genus placed it in the Melaniadae (*sic*; = Thiaridae) on the basis of a comparison with *Melania* and *Melanopsis*, though noting the similarity of its axial ribs to those of the 'Scalidae'. Gardner (1876 : 110) was the first to recognize that *Funis* belonged to the Epitoniidae. Cossmann (1912 : 23, 72) included the genus in his subfamily Clathrosalinae on the basis of supposed apertural and ornamental features, while he included *Amaea* in his

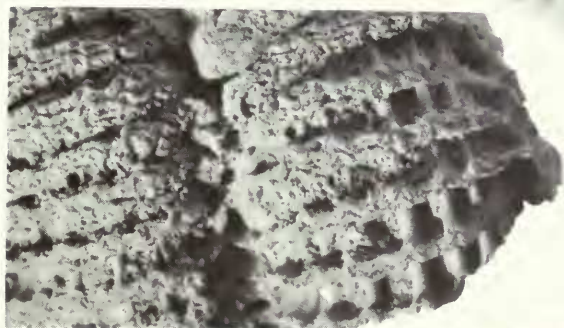
Fig. 7 *Amaea decussata* (Lamarck 1801). Same specimen as in Fig. 2, enlarged to show nature of axial ornament; note occasional close repetitive development of ribs. 1979252. $\times 5$.

Fig. 8 ? *Crossotrema* sp. [= '*Epitonium*' *kieneri* Cox 1938]. Same specimen as in Fig. 4, enlarged. Note composition of ornament and composite structure of axial ribs identical to Fig. 7. G 49523. $\times 3.6$.

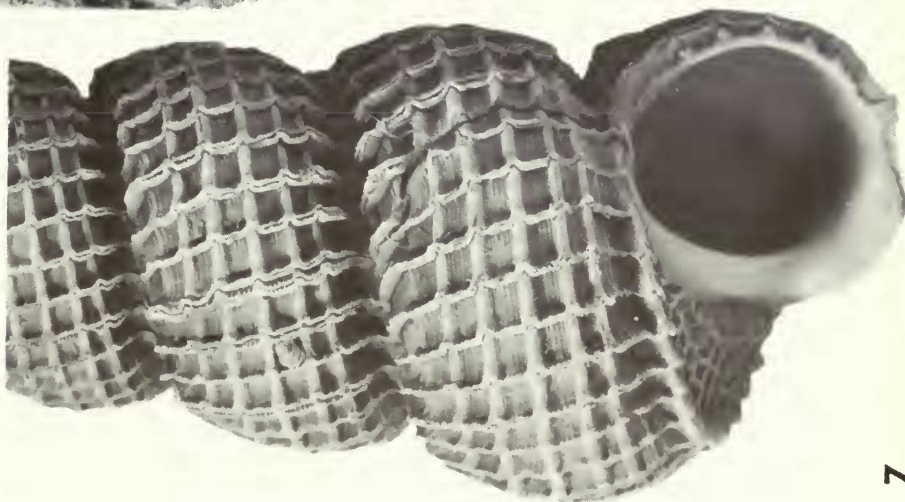
Fig. 9 *Crossotrema crebricostata* (Gardner 1876), holotype. Same specimen as in Fig. 5, enlarged to show detail of ornament; note occasional repetitive axial ornament, especially that at mid-whorl of central whorl. G 19065. $\times 5$.



9



8



7

Acrillinae. Later, Wenz (1939 : 803) incorporated *Funis* as one of sixteen subgenera listed under *Amaea* H. & A. Adams 1853, a position that reflects something of its true relationship even though many of the accompanying taxa have been re-assigned.

The inadequacy of the general characters originally used to define the genus was appreciated by both Gardner and Cossmann. The poorly preserved and incomplete material of the only species of which there were numerous examples, *F. elongatus*, contributed to that situation. The principal features in common with those of other Cretaceous Epitoniidae are its slender, elongate, imperforate shell, the rounded convex whorls, deeply impressed suture and ovate aperture.

The general shell morphology and the lack of strong axial ornament in *Funis* immediately relates it to *Amaea*. It can be distinguished from Recent *Amaea* s. str. by its more elongate whorls and smaller spiral angle. In comparison, the shell of *Funis* has a higher growth translation rate and lower expansion rate, while the generating curve is much closer to the axis of coiling. The resulting more loosely-coiled shell is further accentuated by a furrow occurring abapically at the suture, which may be described as 'grooved' rather than incised or impressed as in *Amaea*. Ornament in *Funis* is generally coarser than that of *Amaea*. Neither species of *Funis* appears to have a recurved inner lip as occurs in the type species *Amaea magnifica* G. B. Sowerby 1844 (Fig. 14). The apparent restriction of *Funis* to the Cretaceous, together with the morphological differences described above, would seem to warrant its consideration again as a full genus. However, several Cretaceous epitoniids described from Europe and north Africa indicate the contemporaneous existence of more-typical *Amaea*-like forms. A distinctive Recent Pacific-Galapagan species, *A. contexta* Dushane 1970, is shaped very similarly to the two *Funis* species and serves to emphasize the difficulties in classifying epitoniids on shell morphology.

From the species listed by both Gardner (1876 : 111) and Cossmann (1912 : 72), only the type species can still be accepted as a member of the genus. Gardner considered that *F. brevis* had to be regarded as a variety of *elongatus*; *F. crebricostatus* Gardner has now become the type species for the new genus *Crossotrema* (p. 237). The wider spiral angle and consequently broader and flatter whorls of *F. cancellatus* Gardner, from the Gault of Folkestone, suggests it would be better placed in *Amaea*.

Although cancellate ornament characterized those species originally placed in *Funis*, the distinctive ornamental trait of the genus would now appear to be the reduced significance of its axial component. Axial ornament is never dominant and in the new species described below it is limited to the collabral threads. The basal ridge or cord, although well-defined, is not as strong as that in *Amaea* and consequently *Funis* cannot be considered to have a true basal disk. Ornament below this ridge may differ from that on the whorl sides in the same manner or degree, as occurs in species of *Amaea*.

Funis spirornatus sp. nov.

Fig. 11

MATERIAL. Holotype (and only specimen), BM(NH) Dept. of Palaeontology no. GG 20892. Collected by R. J. Hogg.

LOCALITY AND HORIZON. Double Arches Pit (National Grid reference SP 939290), near Leighton Buzzard, Bedfordshire. Creamy-white limestone lenticle, Shenley Limestone, Cretaceous, Albian, Regularis Zone.

DIMENSIONS. Actual height of incomplete specimen	= 50.5 mm
Estimated height of complete spire	= 120 mm
Approximate height of last whorl	= 25.7 mm
Diameter of last whorl	= 19.3 mm
Height of aperture	= 14.5 mm
External spire angle	= 10°

DIAGNOSIS. Slender, very elongate shell characterized by ornament of dominant spiral cords and with axial component of ornament limited to collabral threads on its evenly biconvex whorls; whorls separated by an impressed suture which conceals a basal carina.

NAME. 'Ornamented with spirals'.

DESCRIPTION. This single, incomplete specimen shows four whorls of a moderately large, slender shell. The strongly convex whorls (widest at mid-whorl) are firmly joined, but separated by an impressed suture.

The whorl sides are ornamented by nine irregularly-spaced, spiral cords that vary in strength. The three mid-whorl cords are the strongest, while the first, third and seventh (from the adapical suture) are the weakest and are barely stronger than the intervening secondary cords. The secondary microscopic sculpture consists of irregularly positioned, very fine spiral threads lying between the primary cords. Fine opisthocyrt collabral growth lines cross the spirals and represent the only axial element; they are most apparent in the interspaces. The ninth primary spiral cord forms a basal angulation while the furrow between this and the eighth cord accentuates the suture.

The base of the whorl is ornamented by a further eight or nine spiral cords, of varying strength, which become progressively closer as they approach and virtually extend onto the inner lip. Neither the inner nor outer lip is preserved, but the aperture is distinctly ovate. An umbilicus is clearly not present.

REMARKS. Though attributed to the Epitoniidae, this species superficially exhibits features that are characteristic of the Turritellidae. The elongate, essentially spirally ornamented shell is reminiscent of the Turritellidae, which are more common than the Epitoniidae in the Upper Cretaceous. Yet the strongly inflated, convex whorls are quite distinct from the essentially flat-sided whorls of typical turritellids. The helical base of *Funis spirornatus* is clearly distinct from the relatively flat-bottomed whorls of 'Turritella'; and its opisthocyrt growth lines are more evenly curved than those present in Cretaceous turritellids. The occurrence of this fossil in an assemblage in which epifaunal species predominante and in which epitoniids are relatively rare (only twenty specimens in a collection of more than five hundred molluscs), suggests that it is unlikely to belong to the infaunal Turritellidae that generally occur and are collected as fossils in large numbers.

The unusual predominance of spiral cords combined with the narrow spiral angle, resulting in tall whorls and a slender shell, distinguish this species from all other epitoniids. In other Cretaceous epitoniids, axial ornament is generally dominant, but two examples with cancellate sculpture require consideration. The loosely coiled whorls, high spire and whorl shape of *Funis elongatus* Seeley 1861 (Figs 12, 13) described from the Cambridge Greensand resemble the features of *F. spirornatus*. Although the majority of the specimens of *elongatus* are preserved as internal phosphatic mould fragments, its cancellate sculpture is readily apparent. A few show the ornament is composed of primary and secondary cords and slightly raised prosocline axial costae. The strength of these various elements can be extremely variable, resulting in the ornament ranging from a fine network to a much coarser trellis. Worn specimens indicate that the costae might be crenulate and better-preserved examples show that these costae become blade-like and alternate with those of adjacent whorls at the suture. The spiral cords, even those at the coarse end of the range, appear to be finer than those that occur in *spirornatus*. The adapical cord does not form a carina as is exaggeratedly shown in Seeley's original illustration (1861 : pl. 11, fig. 7). In contrast to *F. spirornatus* the whorl of *F. elongatus* is widest below the mid-whorl line.

Shell morphology and ornament in the Epitoniidae

The presence of these two species in the Cretaceous demonstrates that a much wider range of shell ornament occurred within the Epitoniidae at that time than had previously been suspected. The high-spired shell and elongate whorls of *Funis spirornatus* are reminiscent of the Zygopleuridae from which Cossmann (1912 : 19-20) postulated the Epitoniidae may have been derived. As indicated above (p. 240), *Crossotrema crebricostata* with its elaborate sculpture is a probable ancestor of the later and more specialized forms of Recent *Cirsotrema*. At present, there is no link between the Lower Albian epitoniids, e.g. *Confusiscula* with relatively simple ornament (Fig. 1) and the Upper Chalk ornate *Crossotrema*. Nor is there any evidence concerning the development of the characteristic basal disk present in the Gault epitoniids.

Many authors have emphasized our inability to interpret the functional significance of shell geometry. Among them, Raup (1966) stressed that consideration of surface sculpture is also required to complete such understanding. Vermeij (1971*b*) provided a model for the expression of shell sculpture in geometrical terms, used this to show why particular sculpture developed and indicated its ecological benefits. The function of elaborate shell ornament, particularly in those cases where a secondary shell surface is developed as in *Cirsotrema dalli* Rehder 1945 (for description see Clench & Turner 1950 : 226; pl. 98, figs 1, 3), might be attributed to the protection it affords from predation, or possibly encrustation. Alternatively the two-layered shell ornament could be a method of strengthening the shell without involving any undue increase in weight.

The significance of the typical epitoniid varix has only recently been understood and, presumably, the multicellular varix is simply a structural modification. The textbook definition of a varix is generally given as 'a periodic growth resting stage, marked by a thickening of the outer lip' (Keen 1971 : 916, Arnold 1965). Vermeij (1978), in his research on patterns of adaptation in gastropods, illustrated several examples in which varices benefitted the mollusc, indicating that the structure had developed a more particular function.

Vermeij mentions the work of Palmer (1977), who concluded that the varices in the muricid *Ceratostoma foliatum* had a stabilizing function and afforded some degree of protection against predatory fish. Elsewhere, Vermeij (1977, 1978 : 42–50) and Zipser & Vermeij (1978) give the results of their work on the crustacean predation of gastropods. This revealed that strong sculpture was effective against crushing and that apertural thickening at the outer lip provided resistance against the lip-peeling sand crabs of the Calappidae. The measurements of shell thickness provided revealed that a very small margin marked the difference between protection and predation. Ankel (1938) is quoted by Dushane (1974 : 5) as suggesting that the costae are a defence against boring naticids; she noted in support that few epitoniids showed damage from such predators.

The varix needs to be examined as a significant evolutionary character within the Epitoniidae; it would appear to provide another instance of pre-adaptation, in which a particular feature has changed, or extended its function. cursory examination of Tertiary species suggests that typical epitoniid varices first occur in the Eocene, e.g. in *Cirsotrema gassinense* Sacco (1891 : pl. 2, figs 1–2), with more elaborate varices developing in Middle Miocene species, e.g. *Cirsotrema rusticum* (Defrance) and *C. miovaricosum* Sacco (1891 : pl. 2, figs 32, 35). An irregular widening of a rib occurs in some early Tertiary epitoniids, e.g. *Scalaria lamellosa* Brocchi [= *S. fimbriosa* S. V. Wood] and might represent a transitional stage.

As further support for the contention that only further biological research and observation of modern Epitoniidae will overcome the deficiencies of an existing classification based solely on shell shape, the observations of two Recent workers have contributed to our understanding of epitoniid shell morphology. Dushane (1974 : 7) classified living Panamic–Galapagan Epitoniidae with a height (i.e. length of shell) greater than 10 mm as being 'large'. A total of 36 of the 68 species she described fall within this category, but only nine species exceed 30 mm in height and not one attains 50 mm.

The initial impression gained from examining Cretaceous species is that early members of the family were exceptionally large and often exceeded 50 mm in height (see Table 1, p. 246).

Linsley (1977, 1978*a, b*) in his research on gastropod shell form, its evolution and influence on locomotion, concluded that modern Epitoniidae are, in his terminology, 'shell carriers', i.e. that they balance the shell at an angle above the body. This has enabled them to become relatively fast-moving gastropods (Linsley communication in seminar at BM(NH), 1978). On applying this to Cretaceous epitoniids, it seems very probable that those with long (i.e. 'high') shells, e.g. *Claviscala clementina* (Figs 6, 10) could only have been 'shell draggers' somewhat similar to modern *Terebra*. *Terebra*, however, is essentially infaunal, dragging its shell just below, or occasionally protruding through the surface of its habitat of clean sand (J. D. Taylor, personal communication). It seems unlikely that the Lower Albian epitoniids lived in the dark clay sediment in which they are found; presumably they occupied a more amenable neighbouring substrate. Yet, equally, it is difficult to conceive that such exceptionally high-spired shells were essentially epifaunal. It would appear that the small-sized animal occupying the limited space afforded by

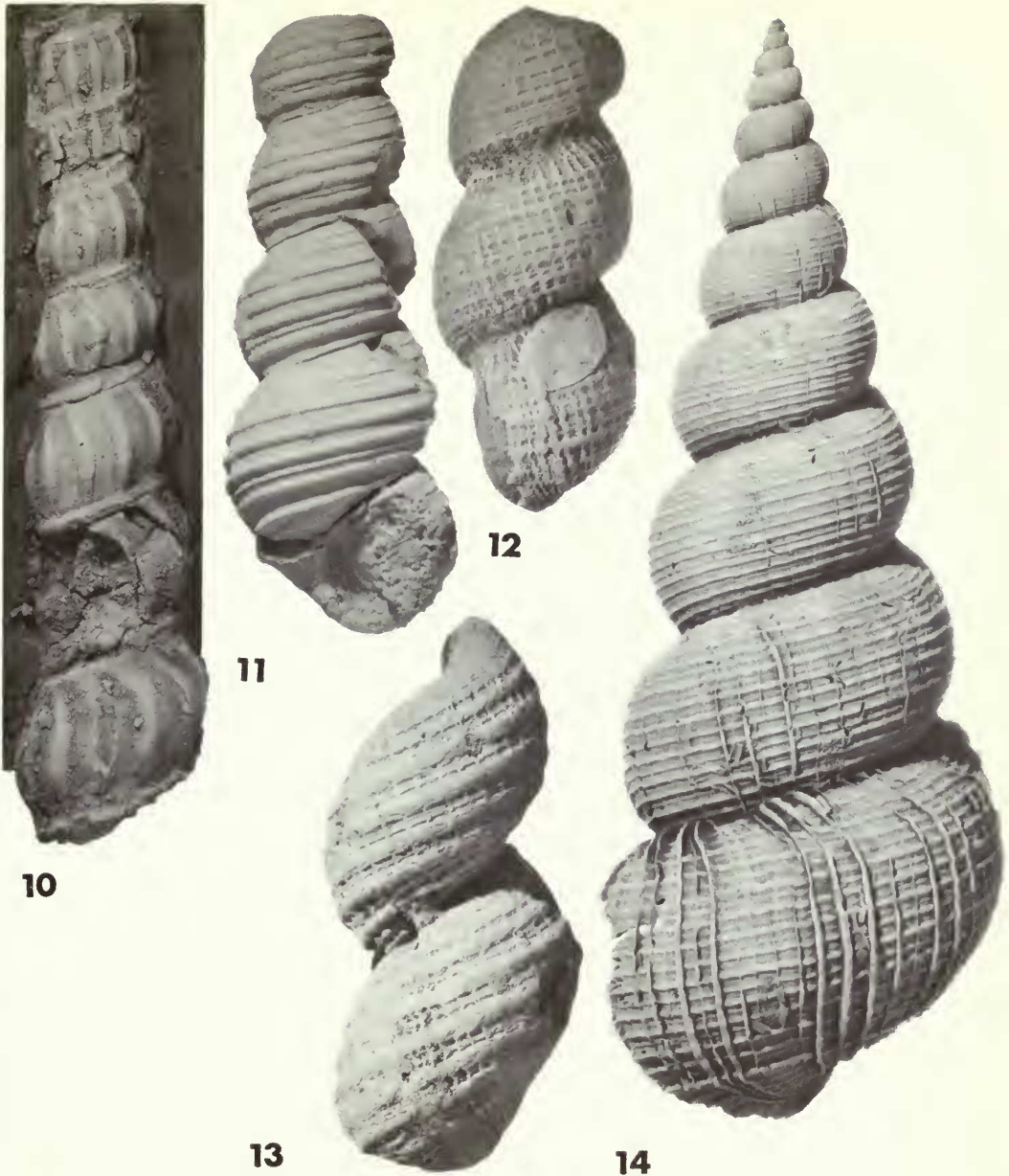


Fig. 10 *Claviscala clementina* (Michelin 1833). Gault, Albian, Folkestone, Kent; coll'd J. W. Butler. G 23792, $\times 1.7$. See also Fig. 6.

Fig. 11 *Funis spirornatus* sp. nov., **holotype**. Creamy-white limestone lenticle, Shenley Limestone, Albian, Regularis Zone; Double Arches Pit, near Leighton Buzzard, Bedfordshire; coll'd R. J. Hogg. GG 20892. $\times 1.4$.

Figs 12, 13 *Funis elongatus* Seeley 1861. Cambridge Greensand, Cenomanian, Cambridge; T. Jesson coll. Fig. 12, G 20745, $\times 2$; Fig. 13, G 8757a, $\times 2.9$.

Fig. 14 *Amaea magnifica* (G. B. Sowerby 1844), type species of *Amaea*. Recent, Awaji, Japan; C. T. Trechmann coll., ex Y. Hirase coll. 1964471. $\times 1.7$

Table 1 Height (mm) of specimens of Cretaceous Epitoniidae in the Dept. of Palaeontology, BM(NH). *Estimated height

<i>'Scalaria' canaliculata</i> d'Orbigny [= <i>Confusiscalca</i>]		
Aptian, Isle of Wight		
	28247	72
	G 9297	66
<i>Claviscalca clementina</i> (Michelin)		
(i)	Albian, Gault, Folkestone	G 71938
	several others exceed	70
(ii)	,, Regularis nodules, Arnold's Pit, Leighton Buzzard	GG 5984
	others in excess of	70
(iii)	,, Double Arches Pit, Leighton Buzzard	GG 20938
		42*
<i>Confusiscalca dupiniana</i> (d'Orbigny)		
(i)	Albian, Gault, Folkestone	G 71944
		70*
(ii)	,, Upper Greensand, Blackdown	G 71071
		49
(iii)	,, ,, Sidmouth	G 44
		53

such a narrow shell would certainly not be able to carry such a burden, but the lack of any indication of wear that could be associated with dragging, on the few complete fossils available, does not support this view.

Other studies provide confirmation that shell dragging locomotion is adopted by some epitoniids. In her analysis of locomotion in prosobranch gastropods, Miller (1974a, 1974b) recorded that *Opalia wroblewskii* progresses by means of indistinct arhythmic locomotion, with only the most anterior part of the foot moving forward before dragging the remainder passively along. She included this locomotory method in her category of 'discontinuous locomotion' (type 1), in which the shell is pulled forward by means of contraction of the columellar muscles. This type of locomotion is found in gastropods with augur-shaped shells having a long, narrow spire and a relatively small aperture, which is identical to the shell of the Cretaceous *Claviscalca clementina*.

Applying Miller's evidence that the locomotion type is directly related to the habitat, habits and substrate as a consequence of the speed required for the gastropod's activities, Perron (1978) conducted a laboratory study of the feeding behaviour of *Epitonium greenlandicum*. He established that this species also moved by discontinuous locomotion and was extremely slow. Its vulnerability to predation as a result of such slow movement and its inherent limited adhesion indicated it had to be essentially an infaunal gastropod. His observations confirmed this and demonstrated that its locomotion contributed to its facultative ectoparasitic predation of sea-anemones.

The diversity of shell form occurring within the fossil Epitoniidae suggests that a variation of locomotory types existed among them comparable with, or even greater than, that found in Recent species, and that the examples mentioned above are not therefore contradictory.

Linsley (1978a : 435), in referring to the parameters for expressing the properties of shell coiling provided by Raup (1961, 1966), pointed out that the major differences in shell form resulted from an alteration in the translation rate of the generating curve down the axis of coiling. Other important factors were attendant differences in the rate of expansion of the generating curve and in the distance of that curve from the axis. It is generally accepted that the greater the translation rate, the less the whorl expansion rate, the closer the whorls become to the axis of coiling and the less the degree of overlap of successive whorls. The high-spired shells of the earlier epitoniids are a product of these factors.

I suspect that one of the general trends in the evolution of the Epitoniidae has been to overcome the limitations presented by the elongate, tightly-coiled shell. In doing so, they have become more efficient and competitive molluscs and have been able to extend their habitat range considerably. Forms comparable with the earlier species still exist, but many later forms are shorter-spired and have more inflated whorls. Such shells have been produced by increasing the expansion rate of the generating curve and by increasing the distance of this curve from the axis. It is also

possible that the development of the basal disk may well have initially assisted in overcoming the disadvantages of the lengthy shell. This would have been achieved by ensuring the overlap of the whorls (see function of overlap, Raup 1966 : 1189), and perhaps by altering the centre of gravity, a point which requires verification by measurement. The development of strong varices, sometimes overlapping, and axial ornament has almost certainly made the shell stronger and provided resistance to crushing predators.

Confirmation of this view is provided by Vermeij's (1971*a*) utilization of three of Raup's parameters in an analysis of conispirally-coiled gastropods. This demonstrated the effective exploitation of shell morphology for evolutionary development and ecological expansion within the Class. By using the angular orientation of the coiling relative to the plane of the generating curve, Vermeij produced a table of representative values for comparison of Recent gastropods. Among these, the figure obtained (Vermeij 1971*a* : 18) for the Recent *Epitonium fucatum* serves to demonstrate the improved position occupied by some modern epitoniids when compared with that of their high-spired relatives.

The two new Cretaceous forms described in this paper contribute to an understanding of the evolution of the Epitoniidae. A clearer picture can only be obtained by close examination of the total fossil record of the family.

Acknowledgements

I must first record my gratitude to R. J. Hogg and P. R. Payne for drawing my attention to their find of a rich fossiliferous lenticle in the Shenley Limestone, from which they obtained the unique specimen of *Funis*. My thanks are due to many colleagues at the British Museum (Natural History) for helpful discussion.

References

- Abbass, H. L. 1953. A monograph on the Egyptian Cretaceous gastropods. *Monograph geol. Mus. U.A.R.*, Cairo, Palaeont. ser. 2: 1-146, 12 pls.
- Adams, H. & Adams, A. 1853-58. *The genera of Recent mollusca: arranged according to their organization*. 1, xi+484 pp.; 2, 661 pp.; 3, atlas 138 pls. London.
- Ankel, W. E. 1938. Beobachtungen an Prosobranchiern der Schwedischen Westküste. *Ark. Zool.*, Stockholm, 30A (9): 1-27.
- Arnold, W. H. 1965. A glossary of a thousand-and-one terms used in conchology. *Veliger*, Berkeley, Cal., 7 (Suppl.), iii+49 pp.
- Berry, S. S. 1910. [Review of] 'Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province' by W. H. Dall. *Nautilus, Philad.* 23(10): 130-132.
- Boury, see De Boury, E.
- Briart, A. & Cornet, F. L. 1870-87. Description des fossiles du Calcaire Grossier de Mons. Gasteropodes. Parte III. *Mém. Acad. r. Sci. Lett. Belg.*, Brussels, 43: 1-73, pls 13-18.
- Burch, J. Q. 1956. Family Epitoniidae. Key to genera. *Minut. conch. Club Sth. Calif.*, Los Angeles, 158: 2-6.
- Clench, W. J. & Turner, R. D. 1950. The genera *Sthenorytis*, *Cirsotrema*, *Acirsa*, *Opalia* and *Amaea* in the western Atlantic. *Johnsonia*, Cambridge, Mass., 2 (29): 221-248, pls (text-figs) 96-107.
- 1951-52. The genus *Epitonium* [&c.] in the western Atlantic. Part 1. *Johnsonia*, Cambridge, Mass., 2 (30): 249-288, pls 108-130 (1951). Part 2. *loc. cit.* 2 (31): 289-386, pls 131-177 (1952).
- Conrad, T. A. 1865. Catalogue of the Eocene and Oligocene Testacea of the United States. *Am. J. Conch.*, Philadelphia, 1 (1): 1-35.
- Cossmann, M. 1912. *Essais de Paléoconchologie comparée*, 9, 215 pp., 10 pls. Paris.
- Dall, W. H. 1908. Reports on the Dredging Operations . . . carried on by the . . . steamer 'Albatross' . . . [&c.]. Mollusca and Brachiopoda. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., 43 (6): 205-487, pls 1-22.
- De Boury, E. 1890*a*. Révision des Scalidae miocènes et pliocènes de l'Italie. *Boll. Soc. malac. ital.*, Pisa, 14 (for 1889): 161-326, pl. 4.
- 1890*b*. Étude critique des Scalidae Miocènes et Pliocènes d'Italie. *Boll. Soc. malac. ital.*, Pisa, 15: 81-213, pl. 4.

- 1909. Catalogue des sous-genres de Scalidae. *J. Conch. Paris* **57**: 255–258.
- 1912–13. Description de Scalidae nouveaux ou peu connus. *J. Conch. Paris* **60**: 87–107; 169–196; 269–322, pls 7–11.
- 1917. Revision critique de l'étude des scaliars faite par M. Cossmann dans les 'Essais de Paléoconchologie'. *J. Conch. Paris* **63**: 13–62.
- Dixon, F.** 1850–52. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. xvi + 422 + xvi pp., 45 pls. London. (Description of the fossils of the Chalk formation . . ., by J. de C. Sowerby).
- Durham, J. W.** 1937. Gastropods of the family Epitoniidae from Mesozoic and Cenozoic rocks of the west coast of North America. *J. Paleont.*, Menasha, **11** (6): 479–512, pls 56–57.
- Dushane, H.** 1970. Two new Epitoniidae from the Galápagos Islands. *Veliger*, Berkeley, Cal., **12** (3): 330–332, pl. 51.
- 1974. The Panamic-Galapagan Epitoniidae. *Veliger*, Berkeley, Cal., **16** (Suppl.): 1–84, 15 pls.
- Fitton, W. H.** 1836. Observations on some of the strata between the Chalk and the Oxford Oolite in the southeast of England. *Trans. Geol. Soc. Lond.* **4** (2): 103–389.
- Gardner, J. S.** 1876. On Cretaceous Gasteropoda: Family Scalidae. *Geol. Mag.*, London, (2) **3**: 75–78, 105–114, pls 3–4.
- Hertlein, L. G. & Strong, A. M.** 1951. Eastern Pacific expeditions of the New York Zoological Society. Mollusks from the west coast of Mexico and Central America. Part X. *Zoologica, N. Y.* **36**: 67–120, pls 1–11.
- Keen, A. M.** 1971. Glossary, in: *Sea shells of Tropical West America*, 2nd edit. xiv + 1064 pp. Stanford, Calif.
- Lamarck, J. B. P. A. de M. de** 1812 (?1811). *Extrait d'un cours de zoologie du Muséum d'histoire naturelle, sur les animaux sans vertèbres*. 127 pp. Paris.
- 1822. *Histoire naturelle des animaux sans vertèbres*, **6** (2): 223. Paris.
- Linsley, R. M.** 1977. Some 'laws' of gastropod shell form. *Paleobiol.*, Menlo Park, **3** (2): 196–206.
- 1978a. Shell form and the evolution of gastropods. *Am. Scient.*, New Haven, **66**: 432–441.
- 1978b. Locomotion rates and shell form in the Gastropoda. *Malacologia*, Ann Arbor, **17** (2): 193–206.
- Michelin, H.** 1833. In: Classe V, Mollusques. *Magasin Zool. Paris*, (ser. 1) **3**: pl. 29 (with description).
- Miller, S. L.** 1974a. Adaptive design of locomotion and foot form in Prosobranch gastropods. *J. exp. mar. Biol. Ecol.*, Amsterdam, **14**: 99–156.
- 1974b. The classification, taxonomic distribution, and evolution of locomotor types among prosobranch gastropods. *Proc. malac. Soc. Lond.* **41**: 233–272.
- Mörch, O. A. L.** 1852–53. *Catalogus cochyliorum quae reliquit D. Alphonso d'Aquirra et Gadea Comes de Yoldi. Fasc. Prim.: Cephalophora*. vi + 170 pp. Copenhagen (Hafniae).
- Orbigny, A. D. de** 1842–43. *Paléontologie française. Terrains crétacés II. Gastéropodes*. 2 vols. 456 pp., pls 149–236. Paris.
- Palmer, A. R.** 1977. Function of shell sculpture in marine gastropods: hydrodynamic destabilization in *Ceratostoma foliatum*. *Science, N.Y.* **197**: 1293–1295.
- Raup, D. N.** 1961. The geometry of coiling in gastropods. *Proc. natn. Acad. Sci. U.S.A.*, Washington, **47** (4): 602–609.
- 1966. Geometric analysis of shell coiling: general problems. *J. Paleont.*, Tulsa, **40** (5): 1178–1190.
- Rehder, H. A.** 1945. Two new species of *Cirsotrema* (Epitoniidae) from Florida. *Proc. biol. Soc. Wash.* **58**: 127–129.
- Perron, F.** 1978. The habitat and feeding behavior of the wentletrap *Epitonium greenlandicum*. *Malacologia*, Ann Arbor, **17** (1): 63–72.
- Robertson, R.** 1971. Biological systematics of marine bivalves and gastropods (abstr.). *Rep. Am. malac. Un. AMU Pacif. Div.*, Buffalo, **37** (for 1970): 62–63.
- Sacco, F.** 1891. Naticidae, Sculariidae e Aclidae. In Bellardi, L. & Sacco, F., *I Molluschi dei terreni terziarii del Piemonte e della Liguria*, **9**. 102 pp., 2 pls. Turin.
- Seeley, H.** 1861. Notes on Cambridge Palaeontology II. Some new gasteropods from the Upper Greensand. *Ann. Mag. nat. Hist.*, London, (3) **7**: 281–295, pl. 11.
- Sohl, N. F.** 1964. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek and Prairie Bluff Formations. *Prof. Pap. U.S. geol. Surv.*, Washington, **331-B**: 153–344.
- Sowerby, G. B.** (2nd) 1844. Descriptions of new species of *Scalaria* collected by Hugh Cuming, Esq. . . [&c.]. *Proc. zool. Soc. Lond.* **12**: 10–14, 26–31.
- Sowerby, J. de C.** See Dixon, F. (1850–52), Fitton, W. H. (1836).
- Tapparone-Canefri, C. M.** 1876. Rectifications dans la nomenclature de quelques espèces du genre *Scalaria*. *J. Conch. Paris* **24** (2): 152–156.

- Tate, R.** 1890. The gastropods of the older Tertiary of Australia (Part II). *Trans. R. Soc. S. Aust.*, Adelaide, **13** (2): 185–235, pls 5–13.
- Thiele, J.** 1928. Über ptenoglosse Schnecken. *Z. wiss. Zool.*, Leipzig, **13**: 73–94.
- Vermeij, G. J.** 1971a. Gastropod evolution and morphological diversity in relation to shell geometry. *J. Zool., Lond.* **163**: 15–23.
- 1971b. The geometry of shell sculpture. *Forma Functio*, Oxford, **4**: 319–325.
- 1977. Patterns in crab claw size: the geography of crushing. *Syst. Zool.*, Washington, **26** (2): 138–151.
- 1978. *Biogeography and Adaptation. Patterns of marine life*. xi+332 pp. Cambridge, Mass.
- Wagner, R. J. & Abbott, R. T.** 1978. *Standard Catalog of shells*. 3rd edit. (1 vol., unpagged, looseleaf). Greenville, Del. [Epitoniacea: pp. 08-201–08-216].
- Wanner, J.** 1902. Die Fauna der Obersten weissen Kreide der libyschen Wüste. *Palaeontographica*, Stuttgart, **30** (2): 91–151, pls 13–19.
- Weir, J.** 1938. Additions to the Neogene molluscan faunas of Kenya. *Monogr. geol. Dep. Hunter. Mus.*, Glasgow, **5** (4): 61–81, pls 5–7.
- Wenz, W.** 1938–44. Gastropoda. Allgemeiner Teil und Prosobranchia. In: Schindewolf, O. H. (ed.), *Handbuch der Paläozoologie*, **6**. 7 vols, 1639 pp., 4211 figs. Berlin. [Scalidae, Teil 1: 787–815].
- Wollemann, A.** 1908. Nachtrag zu meinen Abhandlungen über die Bivalven und Gastropoden der Unteren Kreide Norddeutschlands. *J. preuss. geol. Landesanst.*, Berlin, **29** (2): 151–193, 5 pls.
- Zipser, E. & Vermeij, G. J.** 1978. Crushing behaviour of tropical and temperate crabs. *J. exp. mar. Biol. Ecol.*, Amsterdam, **31**: 155–172.

Postscript

Further to my remark (p. 235) that since the Eocene Epitoniid species are generally represented by relatively few individuals, at late proof stage I learn (Amy Breyer, personal communication) that *Epitonium (Nitidiscala) tinctum* Carpenter 1865 occurs in considerable numbers at suitable habitats near Bodega Bay, California.

Regarding the unusual preservation of the holotype of *Crossotrema crebricostata* (p. 238), it may be relevant that in the Maastrichtian Chalk the calcite of some invertebrate fossils is found to be locally and incompletely replaced by chalcedonic quartz at many horizons (Håkansson, Bromley & Perch-Nielsen 1974: 226–7). Extremely rarely specimens have been found with delicate replacement of the shell by chalcedony. These showed no traces of distortion, unlike normally preserved specimens, suggesting the silicification had occurred early in diagenesis.

Håkansson, E., Bromley, R. & Perch-Nielsen, K. 1974. Maastrichtian chalk of north-west Europe—a pelagic shelf sediment. *Spec. Publs int. Ass. Sedimentol.*, Oxford, **1**: 211–233.