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## Mollusca of the Selsey Formation (Middle Eocene): Conoidea, Turrinae.

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**Abstract:** Gastropods of the turrine genera *Eopleurotoma* Cossmann and *Gemmula* Weinkauff in the Middle Eocene Selsey Formation of the Hampshire Basin, southern England show limited stratigraphic and geographic ranges. Examination of the fauna has revealed previously undescribed taxa. These are described.

New species: *Eopleurotoma fowleri*, *E. hollowayi*, *E. fusellina*, *Gemmula* (G.) *veteratoris*, *G. (G.) pastoralis*, *G. (G.) wrigleyi*.

New names: *Gemmula* (G.) *jefferyi* for *Pleurotoma callifera* Edwards.

New combinations: *Eopleurotoma comma* (J. Sowerby), *Gemmula* (G.) *conifera* (Edwards), *G. (G.) acutisinuata acutisinuata* (Edwards), *G. (G.) acutisinuata stubbingtonensis* (Cossmann), *G. (Coroniopsis) monerma* (Edwards).

Neotype designated for *Pleurotoma comma* (J. Sowerby).

Lectotypes designated for *Pleurotoma callifera*, *P. conifera*, *P. gracilentia*, *P. monerma*, *P. moniligera* and *P. scalarata*, all of Edwards, 1861.

The genus *Eoturris* Finlay & Marwick is synonymised with *Eopleurotoma* Cossmann and *Coronia* de Gregorio is synonymised with *Gemmula* Weinkauff.

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### INTRODUCTION

The first comprehensive study of the English Palaeogene Conidae and Turridae was published in an exceptional monograph (Edwards, 1857; 1861) which is still the principal authority on the subject. The accurately drawn figures correspond well with the type material which is still preserved. Few species escaped Edwards' notice, and by his astute recognition of conoidean characters he avoided the confusion with other families which had dogged the work of some earlier authors. The data accompanying Edwards' material usually included little more than the name of the locality however, and this lack of precise stratigraphic data must to some extent have masked the small-scale variation in shell morphology that often occurs between one horizon and the next.

The present study reviews the taxonomy of the turrine genera *Eopleurotoma* Cossmann, 1889 and *Gemmula* Weinkauff, 1875 in the Selsey Formation of southern England, and makes necessary changes to the nomenclature. Examination of recently collected material from well-defined horizons in the Selsey Formation has shown that some taxa formerly referred to described species, or given varietal rank, should preferably be segregated as distinct species. Several previously unknown species are also described herein. A number of morphological variants, particularly of *Gemmula* are seen to occur at certain horizons. In view of their potential use in small-scale stratigraphy and evolutionary studies, those that differ from the nominal species in only small increments are described as Form A, Form B (etc.) until such time as further material might warrant giving them formal names.

### MATERIALS AND METHODS

A large number of specimens were examined in the collections of the Natural History Museum, London (NHM), representing most of the published records for the Selsey Formation and adjoining strata. An equally large amount of unrecorded material in the NHM and in private collections was also examined, together with material recently collected by, or donated to the author, of which a comprehensive representative series has been presented to the NHM. The synonymy and distributions given here are wholly based on this material.

Registration numbers refer to specimens in the NHM Department of Palaeontology unless otherwise indicated. Three of the species discussed here were described by J. de C. Sowerby in Dixon (1850). Each of these is represented in the NHM by a single figured specimen. As there is no indication that any other material was used in their original descriptions, these specimens are assumed to be the holotypes. The descriptions of Edwards' (1861) species however, were not usually based on single specimens, and sometimes more than one example was figured. As Edwards did not expressly specify holotypes, lectotypes for these taxa have been chosen, where relevant, from Edwards' own collection. This was unnecessary, however, in the case of the figured specimen of *Pleurotoma acutisinuata* and that of *P. crebrilinea* Edwards, 1861 (the latter renamed

*stubbingtonensis* by Cossmann, 1899), both of which were unique examples when they were first described. These specimens are therefore holotypes by monotypy.

Here particular emphasis is placed on the protoconch and ornament of the early whorls, whose greatest significance appears to be at the specific and infraspecific levels. In populations of Palaeogene turrine species examined there often appears to be a 'normal' maximum size for most shells of that species, which is reached without any significant loss of the characteristic ornament or whorl shape. Individuals that exceed that size tend to develop subscalariform last whorls and suffer severe reduction of ornament, particularly of the axial elements. The relative rarity of such individuals suggests that the condition may be gerontic. The irregular nature of the development and the resulting homeomorphy exhibited by the largest examples of different species makes these individuals less valuable as taxobases. For this reason holotypes have been selected in some cases from shells which retain their characteristic morphology, even if somewhat immature.

### CLASSIFICATION

There have been a number of proposals for the familial and subfamilial organization of toxoglossan gastropods. The history of these was given in a recent reclassification (Taylor *et al.*, 1993) which divided the group into six families within the superfamily Conoidea (=Toxoglossa), based largely on a phylogenetic analysis of anatomical characters. The genera formerly included in the family Turridae by Powell (1966) were redistributed between four of these families. At the same time the authors found insufficient anatomical differences to separate the Coninae from the Turridae at family level (Taylor *et al.*, 1993: 156). Although the genera covered in this paper are confidently referred to the Turrinae (presently included in the Turridae), these findings suggest that the subfamily might eventually be included in the Conidae.

### Included and excluded groups

The turrine genera *Eopleurotoma*, *Gemmula*, *Epalxis* Cossmann, 1889 and *Fusiturris* Thiele, 1929 have been recorded from the Eocene of England. Of these only the first two are known from the Selsey Formation.

Also occurring in this formation are such species as *Oxyacrum oblitteratum* (Deshayes, 1834) and "*Drillia*" *suffecta* (Pezant, 1909) (see Tracey *et al.*, 1996, this volume) with ornament resembling that of *Eopleurotoma* but with the sinus position somewhat variable, usually placed rather higher on the shoulder ramp. It seems more logical to refer these to the Crassispirinae and Clavatulinae respectively on the basis of their similarity to probable close relatives (S.T. in prep.).

### SHELL CHARACTERS

Shells of the Turrinae are moderately small to large, fusiform, typically with a long and narrow anterior canal, although basally truncated forms occur. The main character by which fossils have been referred to this subfamily is the position of the labral sinus, its apex being situated nearer the periphery than the suture. In Turrinae which have a sinus apex actually on the periphery this is a good enough character to distinguish them from all other groups except the clathrelline genus *Bathytoma* Harris & Burrows, 1891 and its subgenera, which have a peripheral sinus but differ in also having a columellar fold or swelling. In *Turris* Röding, 1798, type genus of the Turrinae, the sinus apex coincides with a narrow spiral cord just above the periphery, but in other genera such as *Gemmula* it is truly peripheral. As the periphery may occur anywhere between the shoulder ramp and mid-whorl, or even lower, the distance of the sinus from the adapical suture varies between taxa. In fact there is no clear dividing line between the various sinus positions seen in genera of the Turrinae (near the base of the shoulder ramp to peripheral in mid-whorl) and those of many Cochlespirinae and Clavatulinae (high to low on the shoulder ramp). Considering that the shape and position of the sinus may change during growth (see *Eopleurotoma* below), the referral of some fossil genera to particular subfamilies using this character may be problematic.

### Protoconch form

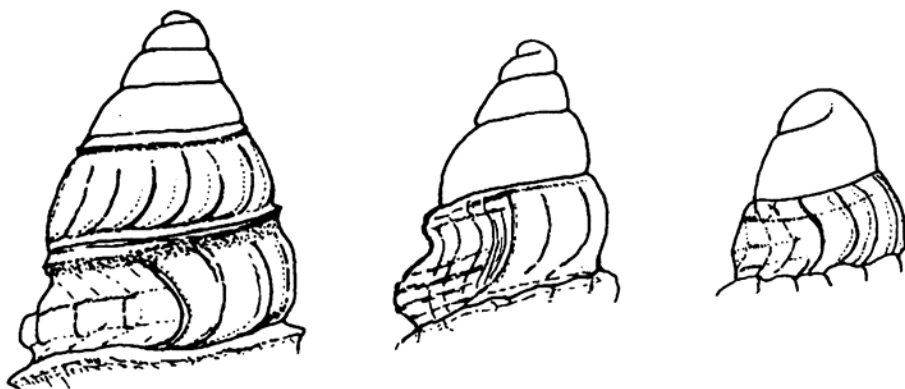
Many *Eopleurotoma* species have multispiral protoconchs of several variably inflated, smooth whorls followed by one, or part of one whorl of curved axial costellae. Other species of *Eopleurotoma* however, closely similar in their overall shell morphology, have smooth, blunt, paucispiral protoconchs of less than 2 whorls. Strathmann (1978) has provided evidence that the multispiral form in caenogastropods is an ancestral condition indicating planktotrophic larval development, while the paucispiral form is a derived condition in which the larval stage has been suppressed and the juvenile hatches directly from the egg. A number of recent studies (summarised by Jablonski & Lutz, 1980) have shown that there are many exceptions to this rule. The paucispiral form does not necessarily preclude a free-swimming larval stage, but nonetheless the inference that most taxa with paucispiral protoconchs are derived from ancestors with multispiral ones is now widely accepted. This change in mode of larval development has occurred independently in many genera within a number of gastropod families. Bouchet

(1990: 73) pointed out that such a change might occur more than once in a single lineage, and that the inclusion in a separate (sub)genus of all species sharing the apomorphy of a paucispiral protoconch could lead to the creation of polyphyletic genera. It has not yet been demonstrated that all *Eopleurotoma* with paucispiral protoconchs are more closely related to each other than to other *Eopleurotoma* with multispiral protoconchs, and so the conservative approach of considering both forms to be congeneric is adopted here. The possibility of two different modes of larval development, and hence two distinct forms of protoconch, occurring in individuals of a single species (poecilogony) is still debated (for summary of arguments see Oliverio, 1996). No such cases have been observed in the English forms discussed here, where it is always possible to separate species on more than this one criterion. In Lutetian faunas in the Paris Basin, however, Brébion (1992) recorded examples of taxa (described and undescribed) apparently differing from each other only in the possession of a multispiral or paucispiral protoconch. In other cases he considered such pairs to be varieties of a single species, e.g. *Eopleurotoma plicaria* (Deshayes, 1865) and *E. distinguenda* (de Boury, 1899). The phenomenon remains to be investigated in depth.

As far as can be determined, most if not all European Palaeocene *Eopleurotoma* had multispiral protoconchs. By the late Ypresian in France several *Eopleurotoma* species had developed paucispiral protoconchs, and this condition became common in the early Lutetian Middle Eocene (personal obs.). Paucispiral protoconchs are not found on English *Eopleurotoma* before the Selsey Formation when *E. obscurata* (J. de C. Sowerby in Dixon, 1850) appeared, followed by *E. fusellina* sp. nov. and *E. scalarata* (Edwards, 1861). These three species also share the character of a sinus centred on the periphery, unlike the Cuisian forms where the sinus was placed a little higher, but similar to that of *Eopleurotoma decussata* (Lamarck, 1804) in the middle Lutetian of France, which has a multispiral protoconch (see discussion of *E. scalarata*, below).

*Gemmula* has possessed a multispiral protoconch since its origins in the Late Cretaceous (C. L. Garvie, pers. comm.) and few if any species have adopted non-planktotrophic larval development. The southern U.S.A. Eocene *Trypanotoma longispira* Casey, 1904 and *Sinistrella americana* (Aldrich, 1885) both show a *Gemmula*-like ornament with a paucispiral protoconch, and might well be the result of such an event. These genera show respective additional differences, however; a much reduced aperture in one and sinistral coiling in the other.

Although not previously recorded in the Turrinae, examples of microsculpture have been observed on the protoconchs of three *Gemmula* species in the present study, and might prove to occur in other species if a larger selection of well-preserved shells were examined closely. Although sometimes visible under a x10 hand lens this ornament is easily overlooked, but is seen clearly under the SEM (Pl. 7). A well-preserved example (Pl. 7, fig. 71) shows close, oblique, raised, granular, filiform microstriae on at least the lower part of all protoconch whorls and along the axial costellae, with additional close spiral microstriae on the last half protoconch whorl. This form of ornament occurs in *G. acutangularis* (Deshayes, 1834) from soft limestones of the Calcaire Grossier, in *G. veteratoris* sp. nov. from silty clays in the New Forest, and in *G. pastoralis* sp. nov. from fine clay horizons (S8-S9) at Bracklesham Bay, but is absent from *G. plebeia* (J. de C. Sowerby in Dixon, 1850) at this last locality. It is not an ideal diagnostic character as its presence and extent may depend on the quality of preservation. It is also noted that the macro- and microsculpture on the protoconch of *G. pastoralis* is similar to that of the distantly related Oligocene clathrelline *Microdrillia vicksburgella* Casey, 1903 from Mississippi, U.S.A. (personal obs.).



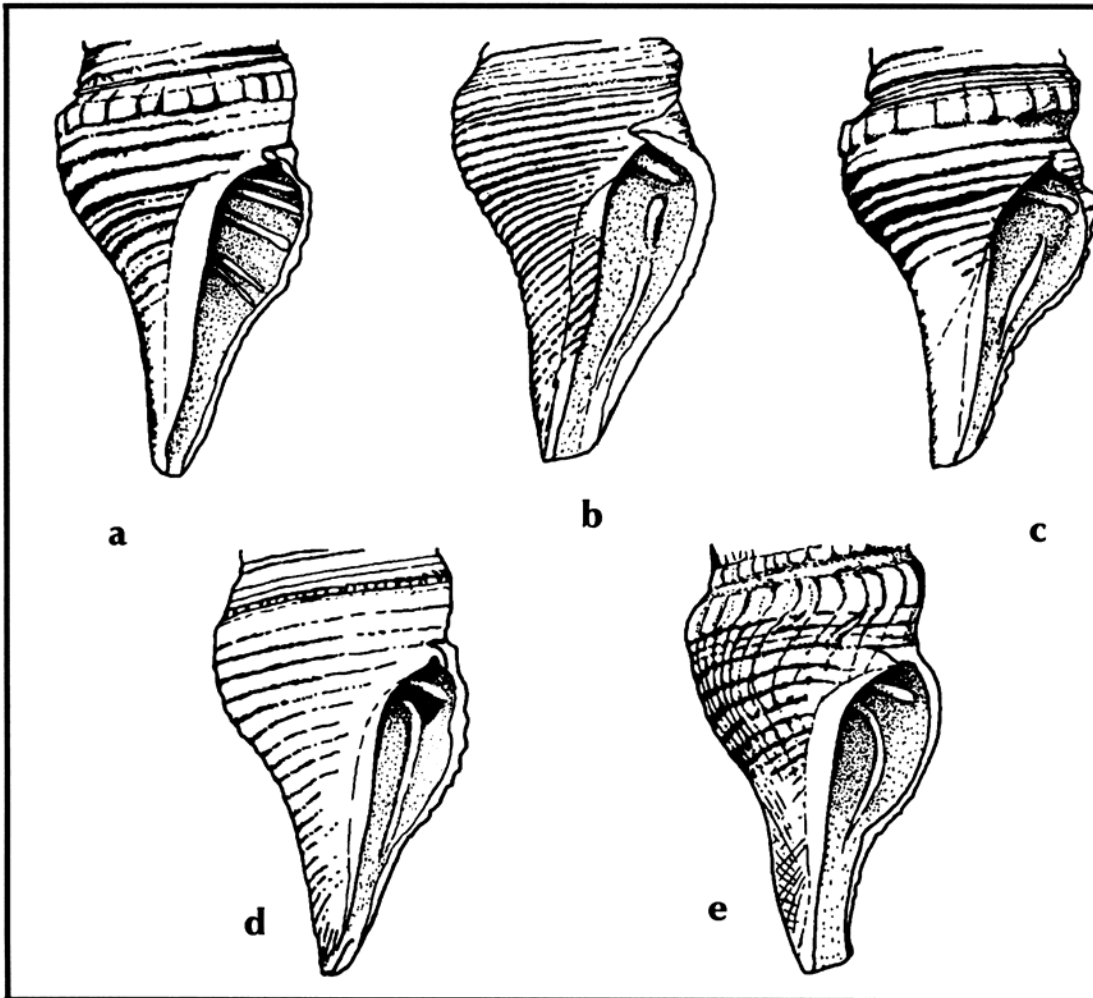
**Text-fig. 1.** Protoconch forms: **a.** multispiral (*Gemmula* s.s.); **b.** multispiral (*Eopleurotoma*); **c.** paucispiral (*Eopleurotoma*).

### Apertural processes

Two distinct forms of liration, on the inner face of the outer lip, occur in certain *Gemmula* species from the Middle Eocene onwards.

The first form (Text-fig. 2a, here termed 'multilirate') consists basically of 4 sharp and narrow, evenly spaced spiral lirae, the basal lira often doubled making 5 in all (although occasional examples show additional intermediary lirae). The adapical (posterior) 2 lirae correspond to the upper part of the exterior gemmulate keel and the 3rd and strongest lira corresponds to the lower part of it. The lirae are developed only where a sufficient thickness of enamel has been secreted inside the shell wall, so they terminate before reaching the thin outer lip. Although similar labral liration is commonly seen in many other gastropod genera, the only English species of *Gemmula* with this character are *G. pastoralis* sp. nov. in the Selsey Formation and the relatively distantly related Bartonian form *G. aspera* (Edwards, 1861). Other lirate *Gemmula*, apparently much closer to the former species, occur in the Palaeogene of the southern U.S.A. (see notes on *G. pastoralis*, below) and also from the Neogene onwards around the world.

The second form (Text-fig. 2b-d, here termed 'bilirate') involves a spiral ridge in the adapical part of the lip and another below it running more or less vertically, parallel to the edge of the lip, its top sometimes bent inwards. Between the two is a well-defined spiral channel corresponding to the external sinus trace. The bilirate condition is unusual in *Gemmula*, only being known in English Eocene species, although a similar arrangement of lirae also occurs in some populations of *Eopleurotoma scalarata* in the Selsey Formation (Text-fig. 2e). Edwards (1861) recognized this as the distinguishing character of his *Pleurotoma callifera* (see below), and other forms with this character (*raphium* and *moniligera* Edwards, 1861) were ranked as varieties of *callifera*. A similar



Text-fig. 2.

Apertural liration: a. multilirate: *Gemmula pastoralis* sp. nov.; b - e bilirate: b. *G. conifera* (Edwards); c. *G. veteratoris* sp. nov.; d. *G. traceyi* Tucker & Le Renard; e. *Eopleurotoma scalarata* (Edwards)..

development is sometimes present in the larger *Gemmula acutangularis* in England. In *G. conifera* (Edwards, 1861) where the vertical lira has a central depression (Text-fig. 2b), the condition may be a convergent character.

Both forms of liration are most easily seen when the thin part of the outer lip is broken away, which is often the condition in which bulk-sampled fossil *Gemmula* are found. The multilirate form can persist within the shell throughout growth, but the bilirate form is usually only visible within the last whorl, and may be indicated by no more than an indistinct furrow in immature or damaged shells.

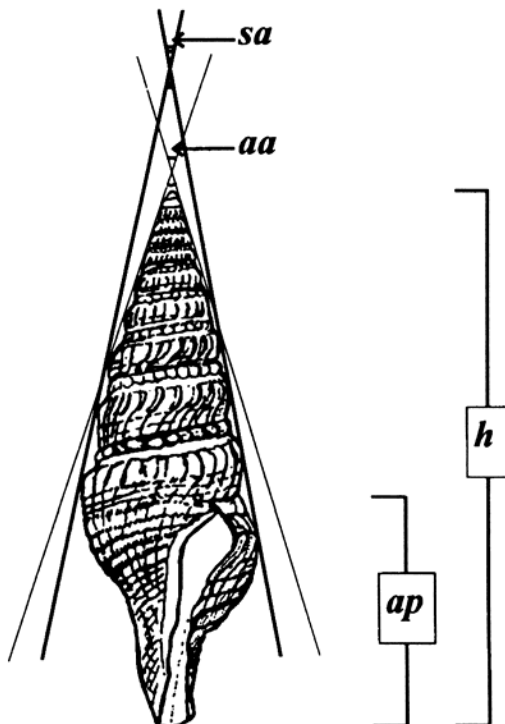
**Ornament**

The teleoconch ornament of most Turrinae (and some other conoidean subfamilies) occurs in 2-4 distinct spiral zones. For ease of description the spire whorl is here divided into 4 such zones, all or some of which may be distinguishable and may also be distinctly ornamented (Text-fig. 4):

1. **Subsutural**, often consisting of a single or double cord, ridge or collar at the top of the whorl immediately below the suture, which may be regularly beaded or irregularly nodular. Such nodules correspond with the tops of collabral ribs (costellae) seen on the periphery.
2. **Ramp** (=shoulder ramp), a non-nodulose zone separating the subsutural and peripheral bands; this may appear as a faint depression, a narrow sulcus or a tabulate or sloping platform. The spiral ornament of the ramp is often diagnostic in *Gemmula*.
3. **Peripheral**, on the widest part of the whorl, usually a combination of nodular thickening of growth lines to form costellae and subordinate spiral cords. In the Turrinae the lip sinus is centred on middle of the peripheral band or on its upper part.
4. **Subperipheral**, the lower part of the whorl which often shows a distinct development of spiral cords. Two further zones are visible only on the last whorl;
5. **Basal**, and 6. **Rostral**. These may be continuous in species where the base and rostrum are not sharply differentiated.

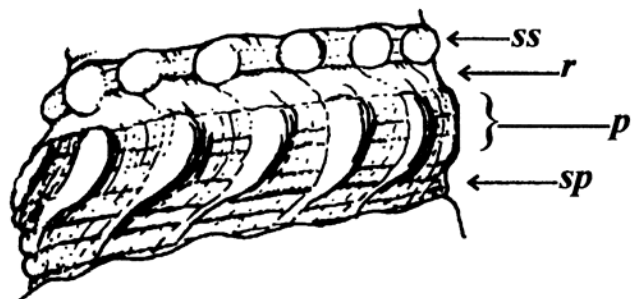
**DISCUSSION**

Loose-collected turrid material from mixed levels often give the impression that the species involved are particularly variable, but preliminary sampling of narrowly defined horizons has shown that the distribution of morphotypes is much more horizon-specific. A starting point for the present study involved a large bulk-sample collected from the New Forest locality of Coalmeer Gutter, bed B (see Localities and horizons, below) by Allan



**Text-fig. 3.**

Measurements: *aa* = apical angle; *ap* = aperture height; *h* = shell height; *sa* = spire angle, the term used herein for the incremental angle to the last 2 whorls. Where the whorls increase regularly the spire and apical angles are the same.



**Text-fig. 4.**

Zones of ornament on spire whorls: *p* = peripheral; *r* = ramp; *sp* = subperipheral; *ss* = subsutural.

Lawson and David Ward on a Tertiary Research Group Field-meeting. From this material several hundred turrids were sorted, comprising 25 species in all. The Subfamily Turrinae was represented by seven species (*Eopleurotoma gentilis*, *E. scalarata*, *Gemmula acutangularis*, *G. conifera*, *G. traceyi*, *G. veteratoris* and *G. pastoralis*, discussed under Systematics below) which were easily distinguished and showed little infraspecific variation. When compared with Turrinae collected by the author and others from specific horizons in the Selsey Formation at various Hampshire Basin localities, a similar assemblage of forms was usually found to be involved. Often, however, taxa that are herein segregated as discrete forms showed small but constant differences between horizons and between localities. It seems likely that most of the morphological variation in each lineage occurs stratigraphically throughout its range, and that comparable variation between geographically separated localities in the Hampshire Basin may largely be due to the discontinuity of small-scale stratigraphic units between those sites.

Most of the species discussed here have not been identified outside the Hampshire Basin. They may have been endemic in this area because suitable environmental conditions did not occur elsewhere in north-west Europe at the time, or perhaps such deposits were not preserved. Only three species have so far been identified as occurring outside the study area: *Eopleurotoma comma* (J. Sowerby, 1816) and *Gemmula acutangularis* in the Lutetian of the Paris Basin, and *Gemmula conifera* in the Lattorfian of Germany. Two other taxa are of interest in being closely similar to North American Palaeogene species (see *Gemmula pastoralis*, *G. monerma*, below).

A full review of the diverse conoidean faunas of northern France is overdue but outside the scope of the present study. Of the studies made in the latter half of the last century, probably the most accurate and comprehensive was the summary of de Boury (1899), who also erected numerous new species. These are not always easy to recognize from the life-size photographic figures, however. A more recent investigation of some Lutetian species (Brébion, 1992) restored the original meanings to several names that had subsequently been misapplied and revised the taxonomy of the species involved. These changes are followed here. Comparative material from the Paris Basin in the NHM, London (G. P. Deshayes coll., M. Cossmann coll. and others), has sometimes been found to contain mixtures and misidentifications which do not help to clarify the original authors' concept of the species concerned.

#### LOCALITIES AND HORIZONS

**Afton Brickyard** (Isle of Wight) SZ 367 863: clay and sand pit (since backfilled), formerly exposing a thick Eocene section. Fossiliferous horizons included the "*Corbula* bed" (equivalent to "Brook bed", upper part of the Selsey Formation) and the "*Rimella canalis*" and *Nummulites prestwichianus* beds (lower part of the Barton Clay Formation) (see Curry, 1942: 88).

**Barton to Highcliffe** (Hampshire) SZ 200 930 - 264 923: part of a continuous sea cliff section exposing fossiliferous Middle Eocene Barton Clay and Becton Sand Formations, beds A2 - K of Burton (1929; 1933)

**Bramshaw, Shepherds Gutter**, (Hampshire) SU 262 153 - SU 266 151: stream banks with discontinuous exposures of shelly clays in the upper part of the Selsey Formation, beds 1-5 of Stinton (1970); (see also Fisher, 1862).

**Coalmeer Gutter** (Hampshire): stream at the southern end of Kings Garn Gutter. Two principal fossiliferous sites (here termed **A** and **B**, pending a full description) are accessible and expose shelly clays: **A**. SU 267 133, equivalent to part of the "Brook bed" at Brook; **B**. SU 265 130, a higher horizon, similar to beds 2-4 at Shepherds Gutter.

**Dummer's Copse** (Hampshire) SU 465 153: temporary excavation for the M27 motorway north of Southampton which exposed Wittering and Earnley Formations, units DC1-10 of Kemp (1984). Molluscan fauna listed by Bone *et al.* (1991).

**Fawley Tunnel** (Hampshire) SW 477 028 - 041 501: temporary excavations for a transmission tunnel under the Solent between Fawley and Chilling. Fossiliferous horizons were recorded in the Marsh Farm Formation and most of the Selsey Formation, beds A - P of Curry *et al.* (1968).

**Gunville Brickyard** (Isle of Wight) SZ 479 886: former pit (since flooded) which exposed similar horizons to those at Afton, but including a fossiliferous unit equivalent to Whitecliff Bay FXVII (uppermost Selsey Formation) (see Curry, 1942: 98).

**Kings Garn Gutter** (Hampshire) SU 248 149 - SU 268 133: a New Forest stream with fossiliferous exposures in the 19th century, but the productive sites are now obscured. The stream banks showed a long section in the

Selsey Formation (see Fisher, 1862) which included equivalents of the beds at Shepherds Gutter and also the following two classic localities:

**Huntingbridge** SU 251 143: stream bank site, formerly exposing shelly clays of basal Barton Clay Formation (Elmore Member) overlying uppermost Selsey Formation (Studley Wood Member).

**Brook** SU 265 135: temporary excavation, formerly exposing shelly clays ("Brook bed") in the upper part of the Selsey Formation. (Note that NHM collections of turrids from Brook show an unusually large number of variants, confirming that more than one horizon may have been represented in the original excavation; see Fisher, 1862).

**Lee-on-the-Solent** (Hampshire) SU 551 013 - 562 002: almost continuous foreshore exposures of most of the Selsey Formation. The overlying Elmore Member of the Barton Clay Formation is exposed to the south-east. First described by Fisher (1862). Units L1-11 of Kemp (1985).

The lowest beds in this section crop out at the northern end, known as:

**Hill Head (= Stubbington)** SU 547 019: formerly a sea cliff (Fisher, 1862), later buried but since temporarily re-excavated. Units 1-8 of Kemp (1976) including the *Campanile* bed.

**Selsey Peninsula** (West Sussex), (see Curry *et al.*, 1977; Bone & Tracey, 1996; King, 1996; Tracey *et al.*, 1996, this volume) on which are the following main foreshore localities:

**Bracklesham Bay** comprising the entire western coast, the main fossiliferous interval cropping out between SZ 783 973 and SZ 847 927; exposing Wittering, Earnley, Marsh Farm and Selsey Formations.

**East Selsey** SZ 862 927 northeastwards, with foreshore exposures of shelly sands at the base of the Selsey Formation, now rarely exposed.

**Southampton Dock** (Hampshire) SU 393 125: temporary excavation of a graving dock at Millbrook exposing Earnley Formation. Virtually all the Mollusca recorded came from bed 3 of Wrigley (1934).

**Studley Wood** (Hampshire) SU 227 159: shelly clays in the banks of Latchmoor Brook, showing basal Barton Clay Formation (Elmore Member), units SW2-3, overlying uppermost Selsey Formation (Studley Wood Member) unit SW1 of Todd (1990).

**Whitecliff Bay** (Isle of Wight) SZ 639 858 - 645 865: sea cliff and foreshore sections showing a long Palaeogene succession. Beds I - XVII of Fisher (1862) (i.e. FI - FXVII) include the whole of the Bracklesham Group (Early-Middle Eocene).

Additional stratigraphic information and references for most of these localities were given by Curry (1958), Stinton (1975: 6-7) and Cooper (1976).

## SYSTEMATICS

### Taxa recognized from the Selsey Formation: Turrinae

#### *Eopleurotoma*

- E. gentilis* (J. de C. Sowerby in Dixon, 1850)
- E. inculta* (J. de C. Sowerby in Dixon, 1850)
- E. fowleri* sp. nov.
- E. comma* (J. Sowerby, 1816)
- E. hollowayi* sp. nov.
- E. cf. expedita* (Deshayes, 1865)
- E. obscurata* (J. de C. Sowerby in Dixon, 1850)
- E. scalarata* (Edwards, 1861)
- ~ Form A
- E. fusellina* sp. nov.

#### *Gemmula* (*Gemmula*)

- G. conifera* (Edwards, 1861)
- G. acutisinuata acutisinuata* (Edwards, 1861)
- G. acutisinuata stubbingtonensis* (Cossmann, 1899)
- G. plebeia* (J. de C. Sowerby in Dixon, 1850)
- ~ Form A
- G. acutangularis* (Deshayes, 1834)

- G. veteratoris* sp. nov.  
*G. traceyi* (Tucker & Le Renard, 1993)  
 ~ Form A  
*G. pastoralis* sp. nov.  
 ~ Forms A, B  
*G. wrigleyi* sp. nov.  
 ~ Form A

***Gemmula (Coroniopsis)***

- G. monerma* (Edwards, 1861)

Genus ***Eopleurotoma*** Cossmann, 1889

Cossmann, 1889: 269. Type by O.D: *Pleurotoma multicostata* Deshayes, 1834; Middle Eocene (mid Lutetian), Paris Basin. Range: Palaeocene to Oligocene, worldwide.

*Eoturris* Finlay & Marwick, 1937 (Type by O.D: *Turris complicatus* Suter, 1917.) Late Eocene, New Zealand.

**Characters:** Shells small to moderately large, mostly between 10 and 50mm high, fusiform, the aperture usually occupying 37-47% of the total height. Protoconch paucispiral of less than 2 whorls, or multispiral, conical of 2-4 smooth inflated whorls followed by 1 whorl or less of oblique costellae. Protoconch / teleoconch junction indistinct. Teleoconch ornament of more or less collabral costellae, often nodulose around the periphery, over subordinate spiral cords or striae. Sinus shallow to moderately deep, its apex either peripheral or situated at the base of the shoulder ramp shortly above the periphery.

**Notes:** Cossmann's choice of *multicostata* as type species poses some problems. This is a relatively rare species, moderately large c. 45 x 14mm, with numerous close collabral ribs running from suture to suture. On the spire whorls the sinus trace is very shallow, merely an angulation of the growth lines, rather high on the whorl and well above the periphery. By the time the adult lip is formed the sinus is still high but deeply and narrowly V-shaped. The overall morphology suggests that it is, however, congeneric with the species included here. The protoconch was said to be obtuse by Cossmann (1889: 269) although Deshayes (1834: 467) originally described the spire as very pointed.

The four species included in the New Zealand genus *Eoturris* by Powell (1966) were said by to differ from *Eopleurotoma* only by their possession of a multispiral protoconch, but many of the European Palaeogene species he listed under *Eopleurotoma* also have multispiral protoconchs. The shell morphology of *Eoturris complicatus* is very similar to that of *Eopleurotoma gentilis* while its protoconch (see Maxwell, 1992: 146, fig.9c) agrees well with other species such as *E. comma* (Pl. 5, fig. 54). The Australasian region is within the wide distribution area recorded for *Eopleurotoma* and the two genera are therefore considered to be synonymous.

***Eopleurotoma gentilis*** (J. de C. Sowerby in Dixon, 1850)

(Pl. 1, figs 1-3; Pl. 5, fig. 51)

*Pleurotoma gentilis* J. de C. Sowerby in Dixon, 1850: 103, 183, pl.6 fig.25; Edwards, 1854: 451; 1861: 280, pl.30, fig.1a-c; Lowry *et al.*, 1866: pl.3; Newton, 1891: 121

*Eopleurotoma gentilis* (J.de C. Sby); Curry, 1942: 95.

*Gemmula gentilis* (J.de C. Sby); Curry *et al.*, 1968: 202.

**Diagnosis:** A medium-sized *Eopleurotoma* with inflated whorls, moderately deep sutures, short and thick, more or less vertical ribs below mid-whorl, crossed by spiral cords that are strongest basally. Protoconch broad, multispiral.

**Types & type locality:** Holotype NHM G 66099 (F. Dixon coll.), a large adult from Bracklesham Bay, the preservation suggesting units S8/S9.



**Description:** Protoconch multispiral, conical with shallow impressed sutures, comprising one globular and eccentric nuclear whorl followed by  $3\frac{1}{2}$  smooth slightly convex whorls and rather less than one inflated whorl of curved brephic axials. The junction with the teleoconch is poorly defined, mainly indicated by the development of a subsutural ridge, concave ramp, V-shaped sinus and 2 peripheral spiral cords. Spire angle  $32^\circ$ . Teleoconch of up to 7 inflated whorls. Subsutural ridge formed from 2 fused cords bearing rounded nodules on the early whorls, becoming obsolete on later whorls. Ramp short, shelf-like with 2-4 faint, fine spiral threads. Peripheral ornament of 10-15 thick, rounded costellae per whorl forming blunt, elongate, vertical to slightly oblique nodules shortly below mid-whorl, scarcely reaching the ramp. Nodules crossed by 3 spiral cords which tend to truncate them above and below. 1-2 strong subperipheral cords first appearing in mid-growth, with 2 more on the base followed by numerous narrow cords on the rostrum. Sinus widely V-shaped, its rounded apex coinciding with the uppermost of the peripheral cords. Aperture 40% of the height of the shell, ovate and abruptly narrowed into a long and slender canal which is slightly bent near its end. Outer lip thin, without internal lirae.

**Size:** 29.3 x 9.5mm (holotype) up to 32.7 x 9.1mm (Bracklesham Bay); 31.8 x 9.4mm (Bramshaw).

**Variation:** The ribs may vary from vertical to slightly oblique on the spire of a single individual. The largest shells often show loss of ribs and flattening of spiral cords. Some shells from Bracklesham Bay S8 / S9 have a longer and more concave ramp, particularly in the later stages of growth. Examples from the *Rimella canalis* bed at Afton, NHM PI TG 2016 (D. Curry coll.) are rather broader and squatter, with a smooth ramp and 20-26 short ribs per whorl, occupying a narrower peripheral band, but these appear to intergrade with more typical forms.

**Range:** Middle Eocene of the Hampshire Basin, England.

**Distribution:** Middle and upper parts of the Selsey Formation: Bracklesham Bay units S7-S10; Lee-on-Solent units L9-L11; Shepherds Gutter, beds 1-4; Coalmeer Gutter beds A, B; Brook; Whitecliff Bay beds FXV-XVII.

Barton Clay Formation (Elmore Member): Huntingbridge; Afton brickyard *Rimella canalis* bed; a common species throughout its range.

Records from Barton (Newton, 1891: 121; Glibert, 1960:14) have not been substantiated. Shells from Barton bed C, NHM PI TG 2015 (E. St.J. Burton coll.), listed as *E. gentilis* by Burton (1933), are referable to *E. mixta* (Edwards, 1861).

**Notes:** The thick and nodular, semi-vertical ribs generally distinguish this from most others of the genus. Where *E. gentilis* coexists with *E. obscurata* (Bracklesham Bay) or with *E. scalarata* (e.g. New Forest and Afton) the pairs may exhibit strong homeomorphy, but *gentilis* can always be separated by its wider sinus and multispiral protoconch. The New Zealand Eocene *Eoturris complicatus* (Suter, 1917) can bear a particularly close resemblance to *gentilis* but differs in its narrower protoconch with deeper sutures (see Maxwell, 1992: 146, fig. 9c, pl.21, figs d-g).

### *Eopleurotoma inculta* (J. de C. Sowerby in Dixon, 1850)

(Pl. 1, figs 4, 5)

*Fusus incultus* J. de C. Sowerby in Dixon, 1850: 104, 185, pl.7, fig. 32.

*Pleurotoma zeta* Edwards, 1861: 284, pl.31, fig.16.

*Pleurotoma divisa* Edwards, 1861: 278, pl.31, fig.17a,b.

*Clavalithes incultus* (J.de C. Sby) Newton, 1891: 153

*Eopleurotoma inculta* (J.de C. Sby) Wrigley, 1934: 13; Glibert, 1960: 14; Powell, 1966: 45; Bone *et al.*, 1991: 134

**Diagnosis:** A medium-sized, broad-spined, stoutly fusiform turrinid with flush sutures, a shallow, open sinus just above the periphery, tripartite ornament of nodular cords on the earlier teleoconch, obsolete on the last whorl which is large and mostly smooth. Protoconch multispiral.

**Types & type locality:** Holotype NHM 71512 (F. E. Edwards coll.) a relatively large and somewhat damaged shell from Bracklesham Bay, probably from units E3-E4 of the Earnley Formation.

**Description:** Protoconch multispiral, rather broadly conical with more than 2 smooth whorls (only damaged examples known) followed by  $\frac{1}{2}$  whorl of curved brephic axial costellae. Teleoconch of up to 7 whorls. Spire broad, somewhat cyrtoconoid; apical angle  $45^\circ$ , lower spire angle  $26^\circ$ . Spire ornament strong, regular and distinctive: subsutural band initially composed of 3 close spiral cords bearing elongate orthocline nodules

which crimp the suture and developing up to 5 flattened spiral threads which persist throughout growth; ramp reduced to a narrow sulcus or depression in the whorl profile with 1-2 strong spiral cords; peripheral band of 3 moderately strong cords with projecting, oblique rounded nodules. Spiral cords over the whole whorl become more numerous but fainter on succeeding whorls. The nodules become obsolete by the 6th or 7th whorl. Last whorl barrel-like, relatively smooth, especially in mid-whorl, the subsutural edge thickened and clasping the previous whorl. Sinus broad, shallow, saucer-shaped, its apex situated on the lowest cord of the ramp, immediately above the peripheral nodules; on the last whorl the sinus may diminish to become a slight angulation in the growth line. Aperture ovate, gradually narrowing into a moderately long anterior canal. Columella gently convex, outer lip smooth within.

**Size:** 26.8 x 8.9mm (holotype); 31.3 x 11.4mm; 25.3 x 11.0mm (Southampton Dock examples)

**Variation:** In adult individuals from any population, the last whorl can vary between subcylindrical and somewhat inflated. The subsutural border is variably thickened, sometimes swollen and detached or even slightly flaring. This feature is analogous to that occurring in species of the fasciolariid genus, *Clavilithes*.

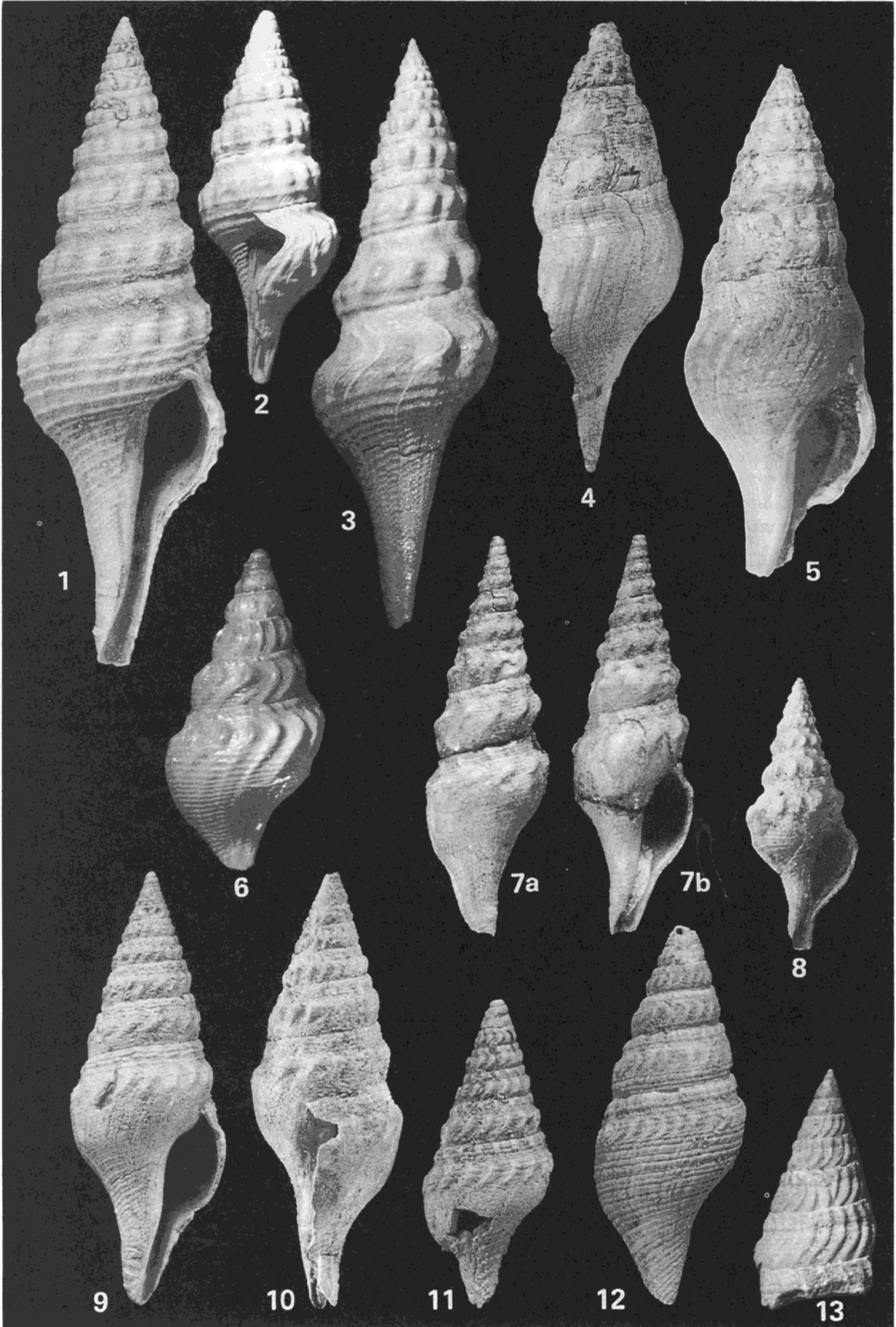
**Range:** Early Middle Eocene of the Hampshire Basin.

**Distribution:** Earnley Formation: Bracklesham (type) units E3-4 ; Southampton Dock (frequent); Dummer's Copse unit DC6. Marsh Farm Formation: Bracklesham Bay unit E10. Selsey Formation: East Selsey unit SL1 (frequent); Bracklesham Bay units S2, S4iii (uncommon).

**Notes:** Although the general aspect of *inculta* is not close to those of other *Eopleurotoma*, a shallow angular sinus also occurs in the type species *E. multicosata* (Deshayes). The smooth last whorl, while characteristic of the species, is not a significant enough reason to create a monotypic genus for *inculta*. Wrigley (1934) first pointed out that *Pleurotoma divisa* and *P. zeta* (Edwards) were synonyms of the present species, founded on a juvenile and a last whorl fragment, respectively. Presumably when first described these were not compared with *inculta* which was thought at the time to be a fasciolariid.

#### Plate 1. English Eocene *Eopleurotoma*

1. *Eopleurotoma gentilis* (J. de C. Sowerby), holotype, Bracklesham Bay. NHM G 66099 (F. Dixon coll.) (x 4): 29.3 x 9.5mm.
2. *Eopleurotoma gentilis* (J. de C. Sowerby), Coalmeer Gutter, bed B. NHM PI TG 2061 (S. Tracey coll.) (x 5): 12.9 x 5.0mm, labral view showing wide sinus.
3. *Eopleurotoma gentilis* (J. de C. Sowerby), Bracklesham Bay, units S8-S9. NHM PI TG 2062 (S. Tracey coll.) (x 4): 28.0 x 9.0mm.
4. *Eopleurotoma inculta* (J. de C. Sowerby), holotype, Bracklesham Bay. NHM 71512 (F. E. Edwards coll.) (x 3): 26.8 x 8.9mm, lateral view showing shallow sinus.
5. *Eopleurotoma inculta* (J. de C. Sowerby, 1850), Earnley Formation, Southampton Dock, bed 3. NHM PI TG 2063 (A. Wrigley coll.) (x 3): 31.7 x 11.9mm.
6. *Eopleurotoma fowleri* sp. nov., holotype, Bracklesham Bay, ex situ from units S8-S9. NHM PI TG 2017 (S. Tracey coll.) (x 7): 8.0 x 4.0mm.
7. *Eopleurotoma comma* (J. Sowerby), neotype, East Selsey, unit SL1. NHM PI TG 2018 (S. Tracey coll.) (x 4): 18.0 x 5.5mm, a. abapertural, b. apertural view.
8. *Eopleurotoma comma* (J. Sowerby), subadult, Earnley Formation, Southampton Dock. NHM PI TG 2019 (A. Wrigley coll.) (x4): 11.7 x 4.5mm.
9. *Eopleurotoma hollowayi* sp. nov., holotype, Stubbington. NHM 71280a (F. E. Edwards coll.) (x4): 19.8 x 7.2mm, recorded as *Pleurotoma undata* by Edwards (1861).
10. *Eopleurotoma hollowayi* sp. nov. paratype, Stubbington. NHM 71280d (F. E. Edwards coll.) (x 4): 19.7 x 6.9mm. Labral view showing position of sinus.
11. *Eopleurotoma hollowayi* sp. nov. juvenile paratype, Stubbington. NHM 71280f (F. E. Edwards coll.) (x 7): 8.1 x 3.4mm.
12. *Eopleurotoma* cf. *hollowayi* sp. nov. Stubbington. NHM 71280e (F. E. Edwards coll.) (x 4): 17.0 x 6.8mm, probable variant of *hollowayi* with more crowded ornament, from the same lot as the types.
13. *Eopleurotoma* cf. *expedita* (Deshayes), spire fragment, Bracklesham Bay, unit S10. NHM PI TG 2022 (S. Tracey coll.) (x 7.3) 6.0 x 3.0mm.



***Eopleurotoma fowleri* sp. nov.**

(Pl. 1, figs 6; Pl. 5, fig. 52)

**Diagnosis:** A broad-spired *Eopleurotoma* with inflated whorls and impressed sutures, roundly angled collabral costellae continuous across the whorls, rather regular spiral threads, fining upwards, and a relatively large multispiral protoconch.

**Types & type locality:** Holotype NHM PI TG 2017 (S.T. coll.) a unique juvenile from an *ex situ* shell concentrate near Broad Rife sluices, Bracklesham Bay, with the pyrite-fill and preservation that is characteristic of units S8/S9.

**Description:** Protoconch 2.7 x 1.7mm, large for the genus, multispiral, conical, of 4½ (tip missing) inflated whorls with impressed sutures. The first 3 are smooth, followed by 1½ whorls with low rib-like swellings growing into curved brephic axials and with faint spiral striae gradually developing into 17 distinct spiral threads. Junction with teleoconch abrupt, marked by the appearance of a deep sinus above a lip-trace that is strongly arched forward. Apical angle 40°. Teleoconch with 2¼ whorls preserved, evenly convex with deep sutures. Subsutural cord originating on the first teleoconch whorl, narrow, finely and obliquely beaded. Ramp narrow and rudimentary, with a single spiral thread. Axial ornament of spaced, roundly angular collabral costellae, 12-16 per whorl, raised and becoming distinctly nodular at the apex of the sinus angle. The costellae extend from suture to suture but are indistinct on the ramp. Peripheral band with c.8 fine, close and flattened threads visible between the nodular ribs. Subperipheral area with stronger spiral threads, 7 on the last whorls, continuous with a further 15 more closely spaced on the base. Sinus in the peripheral area, deeply U-shaped, its apex coinciding with the nodular upper part of the costellae shortly above mid-whorl. Last whorl half the total height. Aperture broadly ovate, narrowed into a slender canal, little of which is preserved.

**Size:** 8.0 x 4.0mm .

**Notes:** Although the specimen is clearly not a fully-grown shell, the broad spire, inflated whorls and singular protoconch (almost twice the size of the relatively large protoconch of *E. gentilis*) separate this from all other *Eopleurotoma* examined; nor does it resemble the apex of any other genera of large turrids in the Selsey Formation.

**Etymology:** Named in memory of the late Roy Fowler of East Wittering, whose hunting ground was the Bracklesham Bay foreshore and who collected much valuable material from the concentrates that also yielded this species.

***Eopleurotoma comma* (J. Sowerby, 1816) comb. nov.**

(Pl. 1, figs 7, 8; Pl. 5, fig. 54; Text-fig. 5)

*Pleurotoma comma* J. Sowerby, 1816: 105, pl.146, fig. 5; Edwards, 1861: 281, pl.30, fig.2.

*Pleurotoma bicatena* Lam. Cossmann, 1904 (in part), figs C, T [*non* Lamarck, 1804].

"*Pleurotoma bicatena* Lamk." Brébion, 1992: 13, pl.3, fig.18 [*sensu* Cossmann, 1904: figs C, T]

*Eopleurotoma bicatena* (Lamk.) Wrigley, 1934: 14.

**Diagnosis** (based on new material): A moderately small *Eopleurotoma* with a narrow spire, deep sutures and a somewhat inflated body whorl, ornamented with flattened spiral striae and projecting, spaced, nodular, curved collabral costellae in mid-whorl. Protoconch multispiral.

**Types and type localities:** The original unique specimen was reported lost by Edwards (1861) who repeated Sowerby's figure and description. The source horizon at the type locality of Stubbington may well have been the basal unit of the Selsey Formation at Hill Head. This bed is no longer accessible without deep excavation, which might have been a contributing factor to the shell's rarity. Although never rediscovered there, an approximately equivalent horizon at East Selsey has yielded several specimens that provide the best match for the figure and description of *comma*, particularly with regard to the characteristic shape of the costellae. It is felt necessary to provide a neotype for *E. comma* to settle the enigma of the species' identity, and so the most complete example is described below.

**Neotype** (herein designated): NHM PI TG 2018 (S.T. coll.) East Selsey, unit SL1 (Pl. 1, fig. 7).

**Additional material:** NHM PI TG 2074 (S.T. coll.) East Selsey, unit SL1, 1 juv. with protoconch (Pl. 5, fig. 54) + several fragments; NHM PI TG 2019 (A. Wrigley coll.) Southampton Dock, 1 probable subadult shell; NHM PI TG 2020 (S.T. coll.) Bracklesham Bay E10, 1 fragmentary example.

**Original description:** "Turreted, beaked, with acute transverse rising lines; volutions smooth in the middle, with many short curved costae; aperture ovate, canalculated; beak slightly curved. The costae extend only over the smooth part of the whorl, they are swelled at the upper part, curved and pointed below, something like a comma; the rising lines are few, sharp, even and most prominent near the middle of each turn: aperture about two-fifths the length of the shell. Stubbington has afforded this shell to Mr. Holloway, and I figure it at present as rare, not knowing that it has been found elsewhere." (J. Sowerby). Size: (from original figure) 15.5 x 5.0mm

**Description** (based on neotype and other East Selsey SL1 material): Protoconch multispiral, conical, of 4 smooth, inflated whorls with impressed sutures, followed by about  $\frac{1}{2}$  whorl of curved, brephic axials. Junction with teleoconch obscured in available specimens but curved costellae, subsutural beads and c.6 spiral threads appear abruptly on the first teleoconch whorl. Spire angle 29°. Teleoconch up to 8 whorls, spire narrowly conical to slightly opisthocyrat at first, the later whorls expanding rather more rapidly in height and width. Sutures impressed, well-marked. Subsutural band of 3 fine threads beaded on the early whorls by distantly spaced, narrow oblique nodules. Ramp narrow and concave continuing the spiral ornament of the subsutural band. Peripheral area with spaced, comma-shaped, collabral costellae, 9-10 per whorl, nodular and projecting strongly in mid-whorl but obsolete above and below, and a few faint spiral striae separating indistinct flat ribbons between the ribs in mid-whorl. Spiral threads mostly rather flattened, numbering c.15 in all on the penultimate whorl, continue as fine spiral striae from the subperipheral area onto the base and rostrum.

Sinus V-shaped, its rounded apex coinciding with upper part of the costellae shortly above mid-whorl. Last whorl slightly more than half the total height. Aperture narrowly ovate, 40% of the total height, distinctly narrowed into a moderately short canal. Lip internally smooth.

**Size:** 18.0 x 5.5mm (neotype); 11.7 x 4.5mm (Southampton Dock); 19.3 x 5.9mm (Grignon example, from figure of Brébion, 1992).

**Variation:** The last whorl of the Southampton Dock example (Pl. 1, fig.8), while probably immature, appears to be broadening rather more than the corresponding whorl of the East Selsey shell (Pl. 1, fig.7). The spire ornament, however, is very similar.

**Range:** Middle Eocene (early to middle Lutetian) of the Hampshire and Paris Basins.

**Distribution:** Earnley Formation: Southampton Dock (rare); Marsh Farm Formation: Bracklesham Bay unit E10 (rare); Lower part of the Selsey Formation: East Selsey unit SL1 (uncommon); Bracklesham Bay units S2, S4iii (uncommon); Stubbington (type, provenance uncertain). Calcaire Grossier, Grignon (Yvelines), France (J. L. M. Defrance coll.).

**Notes:** Until now the identity of the lost species *Pleurotoma comma* had not been satisfactorily established. Edwards (1861) noted that Sowerby's description of *comma* could apply to the Bracklesham species *Pleurotoma obscurata*, "...a species which may be reasonably expected to occur in the nearly synchronous deposit at Stubbington...", however *obscurata* appears to be restricted to Bracklesham Bay. The prominent subsutural nodules of *obscurata* are not a feature of *comma*, to judge from Sowerby's figure. The related *E. scalarata* is a



**Text-fig. 5.**

*Pleurotoma comma*; original figure of lost holotype from Stubbington. (J. Sowerby, 1816: pl.146, fig.5; actual height c.15mm), enhanced computer scan, x 4.

turreted species which occurs higher in the succession but still within Sowerby's "Stubbington" locality. While the spiral cords of *scalarata* are rather inconspicuous on the rib band, the ribs are hardly oblique and comma-shaped. An undetermined form, possibly of *E. hollowayi* (Pl. 1, fig.12) might also be considered a candidate, but the shell profile is broader and less turreted than in the original figure of *comma*.

The slender shape and deep sutures of the neotype distinguish it from *E. hollowayi* sp. nov., while the slender protoconch with its similarly deep sutures distinguish it from other English *Eopleurotoma* species. The closest relatives occur in the Lutetian of the Paris Basin. One of the shells of the Defrance coll. figured as *bicatena* by Cossmann (1904) bears a strong resemblance to the present species. This was again figured by Brébion (1992), who challenged Cossmann's identification, considering that the figured specimen did not match Lamarck's description of *bicatena* and was nearer to *E. multinoda* (Lamarck, 1804). Although referred incorrectly to *E. multinoda* and to *E. undata* (Lamarck, 1804) elsewhere (see Brébion, 1992), the figured form apparently has no valid name. On the basis of its overall morphology the specimen is referred to *E. comma* as interpreted here. *E. granifera* (Deshayes, 1834) differs only in its polished surface with fewer, wholly flat, spiral ribbons. Some forms of *E. decussata* (Lamarck, 1804), e.g. at Damery, are also of similar shape but have fewer spiral cords which are granulated by growth striae; (see Brébion, 1992 for re-interpretation and discussion of *bicatena*, *granifera* and *decussata*).

### *Eopleurotoma hollowayi* sp. nov.

(Pl. 1, figs 9-11; Pl. 5, fig. 55)

*Pleurotoma undata* Lamk.Edwards, 1861: 261, pl.29, fig.11a,b [non Lamarck, 1804]

**Diagnosis:** A moderately large, robust *Eopleurotoma* with a relatively broad spire, flattened whorls and shallow sutures, ornament of fine spiral threads coarsening at the top of the whorl and narrow oblique ribs on the periphery. Protoconch multispiral.

**Types & type locality:** Holotype NHM 71280a (Edwards coll.), a medium sized example from Stubbington, the preservation indicating the *Campanile* bed near the base of the Selsey Formation at Hill Head.

Paratypes NHM 71280b, c, d-n (Edwards coll.), the two shells figured by Edwards and 11 other specimens, all from the same locality and horizon as the holotype; NHM GG 8073a, b, c (F. C. Stinton coll.) an adult and 2 juveniles from bed C of the Fawley Tunnel excavation; NHM PI TG 2021 (A. Wrigley coll.) 1 adult from Bracklesham Bay "*Campanile* bed" (probably unit S4).

**Description:** Protoconch incomplete in all examples but multispiral with  $2\frac{1}{2}$  smooth whorls remaining, followed by  $\frac{1}{2}$  whorl of curved brepheic axials. The junction with the teleoconch is marked by the development of oblique costellae tracing an angular sinus in mid-whorl. Spire angle 33°. Teleoconch of up to 9 flattened whorls (8 on the holotype), concave above the periphery and somewhat cylindrical below it. Sutures only lightly impressed. Subsutural ridge wide with 3-4 coarse spiral threads bearing small, spaced beads on the early whorls, soon becoming obsolete. Ramp short and inclined with a few finer and fainter threads. Ornament in the peripheral area not strongly developed, of c.15 straight, narrow, oblique costellae per whorl, obsolete above and below the periphery, and very numerous fine, faint, raised spiral striae over the middle and lower parts of the whorl, thickening as they reach the rostrum. Sinus broadly V-shaped, its apex on the periphery and coinciding with the junction of the base of the ramp and the top of the ribs. Aperture ovate, 47% of the shell height in holotype (slightly less in the largest shells) distinctly narrowed into a moderately long canal. Outer lip gently sinuous as indicated by the growth lines, smooth internally.

**Size:** 19.8 x 7.2mm (holotype); 27.9 x 9.5mm, 27.0 x 8.3mm, 25.0 x 9.3mm (largest paratypes from Stubbington).

**Variation:** *E. hollowayi* has only been found in any numbers at the type locality where the known examples appear to be the product of a single horizon. Within this population there is considerable variation in details of the ornamentation, although evaluation of individual differences is hampered by the degree of damage and loss of surface detail suffered by shells at this horizon. A specimen here referred to *E. cf. hollowayi* from the type locality (Pl. 1, fig.12) has 18 closely placed, strongly curved costellae per whorl, increasing to c.24 on the last whorl, and spiral threads that are flatter and less numerous than in the typical form. Intergrading forms do seem to be present, however; a juvenile of *hollowayi* (Pl. 1, fig.11) for example, showing characters that could link both extremes.

**Range:** Middle Eocene of the Hampshire basin.

**Distribution:** Earnley Formation: Southampton Dock (rare); Bracklesham Bay unit E3(? fragmentary); Lower part of the Selsey Formation: Hill Head (type loc.- common); Fawley Tunnel bed C; Bracklesham Bay units S2, S4iii (uncommon).

**Notes:** As Edwards' figured specimens of "*undata*" are large examples with some loss of characteristic shape and ornament, a medium sized shell from the same lot is chosen as holotype of *hollowayi*. Although this taxon has previously been included under the much-misused name of *E. undata* (Lamarck, 1804), the true *undata* is longer and narrower with an early effacement of sculpture and has a paucispiral protoconch (Brébion, 1992). The morphology of *E. hollowayi* is close to that of several Lutetian *Eopleurotoma* in the Paris Basin and it may indeed occur there, although a valid prior name does not seem to be available for it. It resembles *E. plicaria* (Deshayes, 1865) which differs, however, in its longer, more inclined ramp and less shouldered whorls. It more closely approaches *E. albicans* Brébion, 1992 (a taxon that included in its original synonymy the earlier *E. houdasi* de Boury, 1899, founded on a juvenile shell and considered to be indeterminate). Although the original concept of *albicans* may include forms ornamented much like *hollowayi* (cf. Brébion, 1992: pl.4, fig.7), the typical form is distinctly different in having thicker, more orthocone ribs on the spire (Brébion, 1992: pl.4, fig.6 and J. Le Renard coll.). Some poorly-preserved and fragmentary shells from Bracklesham Bay S2 and S4iii are tentatively referred to *hollowayi*. "*E. aff. undata*" was recorded from the upper Bracklesham beds of Whitecliff Bay (Jackson, 1926: 359) but the material on which this record was based has not been examined.

**Etymology:** Named after the early 19th century collector, John Holloway of Portsmouth who pioneered collecting from the foreshore outcrops of Hampshire and Sussex and provided the types for the first Selsey Formation turrids to be described. His collection was left to the Portsmouth and Portsea Literary and Philosophical Society (Edwards, 1861: 281), although the fate of the turrid type specimens is uncertain.

***Eopleurotoma* cf. *expedita* (Deshayes, 1865)**

(Pl. 1, fig.13; Pl. 5, fig. 53)

[cf.] *Pleurotoma expedita* Deshayes, 1865: 371, pl.97, figs. 3,4.

[cf.] *Eopleurotoma expedita*; Cossmann, 1889: 269, pl.9, fig.29.

**Description:** Fragment consisting of a rather broadly conical spire with flattened whorls and nearly flush sutures. Protoconch multispiral, of 4 smooth conical whorls with almost flush sutures and waterworn traces of possible curved costellae on the last  $\frac{1}{4}$  whorl. Junction clear, marked by start of ribbed and beaded ornament. Teleoconch with 4 remaining whorls and part of a fifth, ornamented with 18-20 close, rather fine axial costellae per whorl. These reach from suture to suture and are shallowly curved on the upper half of the whorl, strongly opisthocline below. Spiral ornament of low ribbons separated by shallow striae, the top 3 on a wide flat subsutural ridge and 4 more below, subordinate to the ribs, increasing to 8 on the last remaining whorl. The true shape of the sinus is somewhat obscure, but if the costellae are assumed to be collabral then the sinus is broad and very shallow, occupying the upper half of the whorl.

**Size:** 6 x 3mm (fragment)

**Distribution:** *E. expedita*: late Ypresian, Cuise (type), Hérouval (Oise), Saint-Gobain (Aisne), France.

*E. cf. expedita*: upper part of the Selsey Formation, Bracklesham Bay unit S10: a unique fragmentary example, NHM PI TG 2022 (S.T. coll.)

**Notes:** This has a superficial resemblance to *Crassispira innexa* (Solander in Brander, 1766) or to *C. semicolon* (J. Sowerby, 1816) [= *inflexa*, sensu Edwards non Lamarck - see Tracey & Todd, 1996, this volume]. However, when directly compared with the latter, which also occurs at the same horizon, the present specimen has less turreted whorls with shallower sutures, a wider non-nodular subsutural band and a broader concave shoulder ramp. The protoconch is larger and more conical with shallower sutures than those of both *Crassispira* species. The sinus of this specimen is probably not fully developed on the spire whorls and its eventual position is therefore uncertain. There is a resemblance to *Eopleurotoma multicostata* (Deshayes, 1834) which also has a shallow sinus placed relatively high on the whorl although also possessing bifurcating ribs. Examples corresponding to the original description of *E. expedita* from Saint-Gobain (S.T. coll.) usually have fewer ribs, but in other respects the present specimen agrees closely with that species, and could well fall within its range of variation. Both *multicostata* and *expedita* were placed in the section *Eopleurotoma* (defined as having a blunt and paucispiral protoconch) by Cossmann (1889). It is worth noting that a card of 8 examples labelled *expedita*, NHM G 5056

(M. Cossmann coll.) from Cuise contains 2 species, one with a multispiral protoconch, the other paucispiral. More material is needed to clarify the relationships of this taxon.

***Eopleurotoma obscurata*** (J. de C. Sowerby in Dixon, 1850)

(Pl. 2, figs.14-16, Pl. 5, fig. 56)

*Pleurotoma obscurata* J. de C. Sowerby in Dixon, 1850: 103, 184, pl.7, fig.19; Edwards, 1854: 451; 1861: 296, pl.31, fig.1a-b.

**Diagnosis:** A medium-sized, narrowly fusiform *Eopleurotoma* with a long spire and rather short rostrum, moderately convex turreted whorls, dense spiral ornament, obliquely curved costellae most prominent around the periphery, a deep peripheral sinus and a somewhat globular paucispiral protoconch.

**Types & type locality:** Holotype NHM G 66110 (F. Dixon Coll.) a small example from Bracklesham Bay (horizon not indicated).

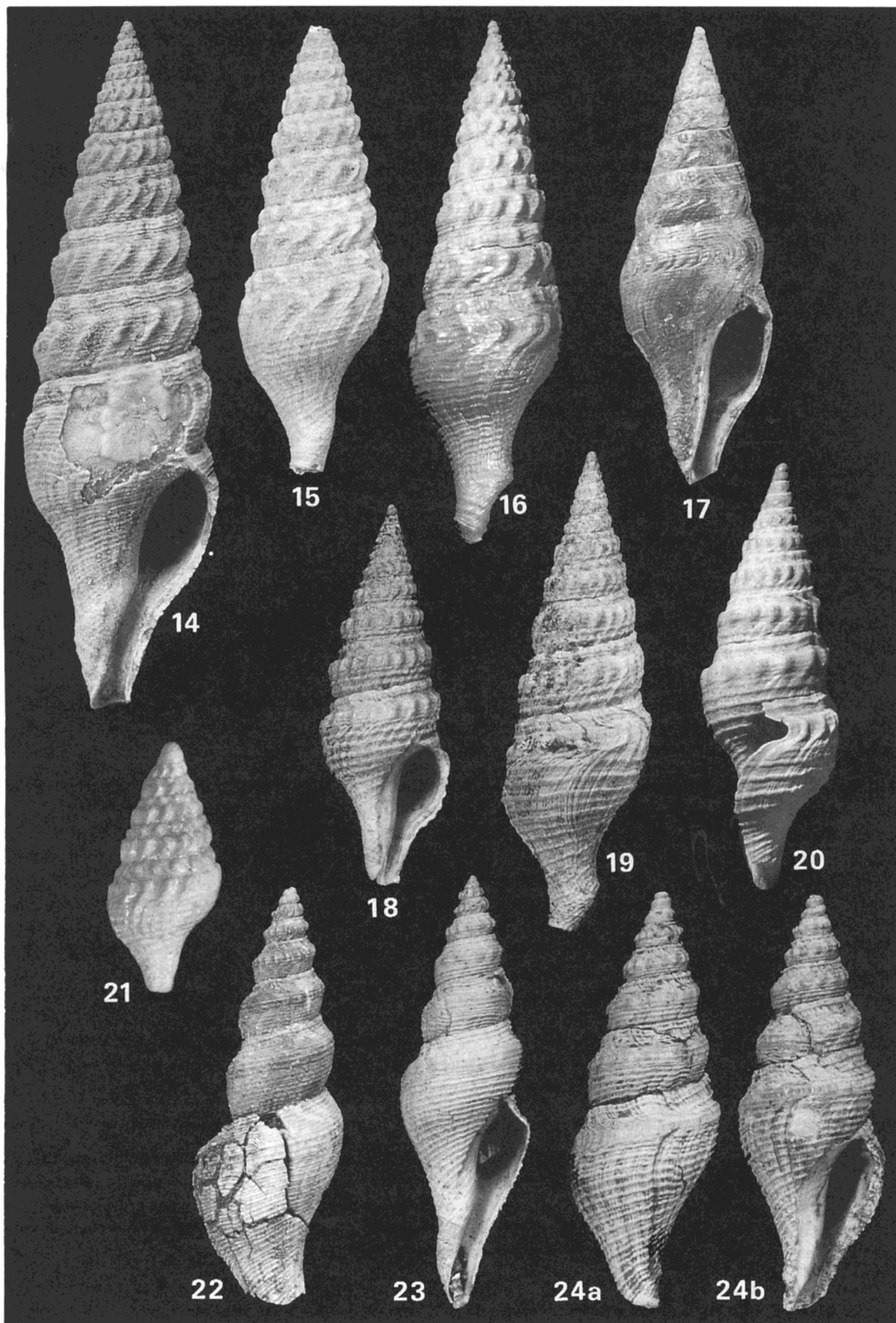
**Description:** Protoconch paucispiral, short and hemispherical, of  $1\frac{1}{2}$  smooth whorls and  $\frac{1}{2}$  whorl of slightly curved bryophic axials. The junction with the teleoconch is marked by the development of a beaded subsutural ridge, concave ramp and sharply curved collabral costellae. Apical angle  $36^\circ$ , spire angle narrowing to  $17^\circ$  on adult whorls. Teleoconch of up to 10 whorls, briefly concave above the periphery and gently convex below it. Subsutural ridge thick, formed of 2-4 undulating spiral threads bearing spaced, rounded nodules which persist to the last whorl in average sized adult shells. Ramp represented by a narrow constriction of the whorl at the top of the ribs. Peripheral ornament of 13-14 regular, curved, oblique costellae per whorl, nodular and prominent in mid-whorl, weakening abapically but continuing to the lower suture. Spiral ornament of regular, weak, fine cords over the whole whorl, 5-6 very faint on the first teleoconch whorls to 12-16 per whorl on the last. On the base the spiral cords are separated by finer, weaker intermediary threads. Sinus narrowly U-shaped, peripheral, its apex coinciding with the nodular part of the ribs, just above mid-whorl. Aperture lenticularly ovate, 45% of the shell height (to 37% in large shells), gradually narrowed into a relatively short canal which is swollen near its end. Outer lip without internal lirae.

**Size:** 19.8 x 6.8mm (holotype); 30.5 x 8.4mm, a large example (Pl. 2, fig.1), also figured by Edwards (1861).

**Plate 2. English Eocene *Eopleurotoma* and *Gemmula***

14. *Eopleurotoma obscurata* (J. de C. Sowerby), Bracklesham Bay. NHM 71329 (F. E. Edwards coll.) (x 4): 30.5 x 8.4mm; the original of Edwards (1861): pl.31, fig.1b.
15. *Eopleurotoma obscurata* (J. de C. Sowerby), holotype, Bracklesham Bay. NHM G66110 (F. Dixon coll.) (x 4): 19.8 x 6.8mm.
16. *Eopleurotoma obscurata* (J. de C. Sowerby), Bracklesham Bay, units S8-S9. NHM PI TG 2064 (S. Tracey coll.) (x 4): 25.0 x 7.5mm.
17. *Eopleurotoma fusellina* sp. nov., holotype, Bracklesham Bay, unit S7i. NHM PI TG 2023 (S. Tracey coll.) (x 4): 21.0 x 6.5mm.
18. *Eopleurotoma scalarata* (Edwards), lectotype, Bramshaw. NHM 71328c[R] (F. E. Edwards coll.) (x 4): 16.8 x 5.8mm.
19. *Eopleurotoma scalarata* (Edwards), paralectotype, Bramshaw. NHM 71328a[L] (F. E. Edwards coll.) (x 4): 21.2 x 6.8mm.
20. *Eopleurotoma scalarata* (Edwards), subadult, Coalmeer Gutter, unit B. NHM PI TG 2065 (S. Tracey coll.) (x 5): 14.7 x 4.8mm, labral view showing deep peripheral sinus.
21. *Eopleurotoma scalarata* (Edwards) Form A, juvenile, Barton Formation, Elmore Member, Studley Wood, "Huntingbridge bed". NHM PI TG 2066 (F. C. Stinton coll.) (x17): 6.6 x 3.1mm.
22. *Gemmula (G.) conifera* (Edwards), lectotype, Bracklesham Bay, probably from units S8-S9. NHM 71298c (F. E. Edwards coll.) (x 4): 19.3 x 7.0mm; the original of Edwards (1861): pl.31, fig.3a.
23. *Gemmula (G.) conifera* (Edwards), paralectotype, Bramshaw. NHM 71298b (F. E. Edwards coll.) (x 4): 20.4 x 6.2mm.
24. *Gemmula (G.) conifera* (Edwards), paralectotype, Bramshaw. NHM 71298a (F. E. Edwards coll.) (x 4): 18.5 x 6.6mm; the original of Edwards (1861): pl.31, fig.3b, a. abapertural, b. apertural view.





**Variation:** The degree of obliquity and curvature of the ribs may vary a little but in other respects the morphology is quite constant. The largest examples show irregularity or loss of the collabral ornament on the last whorl.

**Range:** Middle Eocene of the south-eastern Hampshire Basin.

**Distribution:** Selsey Formation: Bracklesham Bay units S5-S6 (rare), S8-S9 (common).

**Notes:** Most of the known specimens have incomplete apertures owing to the mode of preservation at the S8-S9 level where the species is commonest. Its range at Bracklesham Bay does not overlap that of the closely related *E. scalarata* which occurs in the overlying bed. *E. scalarata* is a smaller species, readily distinguished by its more numerous, shorter ribs and fewer, coarser, granulated spiral cords. *E. fusellina* has much weaker and finer ornament and no subsutural ridge (see remarks below). *E. hollowayi* has a very similar ornament which can cause confusion with regard to fragmentary material, but is distinguished by its broader, shorter spire and multispiral protoconch.

***Eopleurotoma scalarata*** (Edwards, 1861)

(Pl. 2, figs 18-21; Pl. 5, fig. 58; Text-fig. 2e)

*Pleurotoma scalarata* Edwards, 1861: 295, pl.31, fig. 6a-b; Lowry *et al.*, 1866: pl.3.

*Eopleurotoma scalarata* (Edw.); Curry, 1942: 95; Curry *et al.*, 1968: 202.

**Diagnosis:** A small, narrowly fusiform *Eopleurotoma* with a rather short rostrum, moderately convex turreted whorls, impressed sutures, short slightly curved costellae crowded around the periphery, strong spaced and beaded spiral cords below the peripheral area, and a small, bluntly conical, paucispiral protoconch.

**Types & type locality:** Lectotype (herein designated) NHM 71328a (F. E. Edwards coll.), the specimen depicted in Edwards' fig.6a, from Bramshaw (horizon not indicated). The shell is a relatively large example for this locality and shows a reduction in the strength of the collabral ribs on the last whorl (Pl. 2, fig.19).

Paralectotypes NHM 71328b,c (F. E. Edwards coll.) also from Bramshaw (Pl. 2, fig.18), 2 smaller examples (fixed to a card with the lectotype), that are more representative of the species as commonly found. Neither of these correspond well to the specimen shown in Edwards' figure 6b which has not been recognized with any certainty.

**Description:** Protoconch paucispiral, small and narrowly conical, of  $1\frac{1}{2}$  smooth whorls and  $\frac{1}{2}$  whorl of brephic axial costellae. The junction with the teleoconch is marked by the development of a subsutural ridge, concave ramp and sharply curved collabral costellae. Spire angle 25-30°. Teleoconch of up to 9 whorls, briefly concave above the periphery, somewhat flat-sided below it and nested with canaliculate sutures, giving a turreted profile to the shell. Subsutural ridge of 1-2 thickened spiral threads with moderately distinct small beads on the early whorls, later becoming obsolete. Ramp narrow, inclined, smooth. Peripheral band of numerous, close, orthocone to slightly opisthocline, short nodular costellae, becoming curved on later whorls; 18-22 per whorl, with 3-4 weak, subordinate spiral threads visible between them. Subperipheral area with 2 strong spiral cords (emerging from the lower suture on the early whorls) and a further 6 or so evenly spaced on the base. These cords are interspersed by weaker single intermediaries and are strongly and obliquely granulated by the regular, raised growth striae, prominent over the whole shell. Sinus narrowly U-shaped, peripheral, its rounded apex coinciding with the band of costellae in mid-whorl or shortly above. Aperture lenticularly ovate, 40-45% of the shell height, gradually narrowed into a relatively short canal which is swollen near its end. Outer lip thin, sometimes bilirate within, the vertical lira strongly curved (Text-fig.2e).

**Size:** 21.2 x 6.8mm (holotype); most examples from the Selsey Formation smaller, commonly up to c.17 x 6mm.

**Variation:** The short ribs can vary from vertical to slightly oblique and from straight to gently curved, often on the spire of a single individual. The granulation of the lower spirals may be less developed on juveniles and much diminished on gerontic shells. Occasional examples have fewer, more nodular ribs (e.g. the juvenile from Coalmeer Gutter, Pl. 2, fig.20, where this seems to be a traumatic phenomenon following shell breakage in early life). The internal lirae are strongly developed on Studley Wood unit SW1 examples.

***E. scalarata* - Form A:** a later variant with fewer (c.15) ribs per whorl, more oblique and sharply truncated apically (Pl. 2, fig. 21). In some ways this approaches *obscurata* but the granulated spirals link it with the present species. More material is required to establish whether or not these differences are constant. Examples from Studley Wood units SW2-3 are occasionally rather large, up to 29.3 x 9.2mm.

**Range:** Middle Eocene of the Hampshire Basin.

**Distribution:** Upper part of the Selsey Formation: Bramshaw (type loc.); Shepherds Gutter, beds 1-5 (abundant); Coalmeer Gutter, bed B (abundant); Brook (Newton, 1891); Bracklesham Bay, unit S10 (rare); Lee-on-the-Solent units L9-11; Whitecliff Bay beds FXV(?), FXVII; Studley Wood unit SW1.

(Form A): Barton Clay Formation (Elmore Member), Studley Wood, units SW2-3; Afton brickyard, *Rimella canalis* bed.

**Notes:** The numerous short ribs and granulated spirals of *scalarata* are usually quite distinctive. When these are not so strongly developed there may be a close superficial resemblance to *E. gentilis*, but the deeply U-shaped peripheral sinus and the paucispiral protoconch of *scalarata* clearly distinguish it. *E. scalarata* bears a close resemblance to some forms of the French Lutetian *E. decussata* (Lamarck, 1804) [= *rudiuscula* (Cossmann, 1889), see Brébion, 1992: 13] particularly the form in the Calcaire Grossier at Fercourt (Oise). This has a similar granulated ornament and U-shaped sinus with its apex on the periphery, but differs in lacking internal lirae and having a multispiral protoconch. The protoconch is, however, a small and short (3½ whorls) example of its kind, which supports the possibility that the two species may be closely related.

***Eopleurotoma fusellina* sp. nov.**

(Pl. 2, fig.17; Pl. 5, fig. 57)

**Diagnosis:** A small, evenly fusiform *Eopleurotoma* with long, flattened whorls and nearly flush sutures. Ornament minimal, of flat spiral ribbons separated by shallow striae and crossed by strongly curved growth lines, emphasised along the narrow sinus band in mid-whorl. Subsutural cord weakly defined apically, absent on rest of shell. Apex slender, protoconch paucispiral.

**Types & type locality:** Holotype NHM PI TG 2023 (S.T. coll.), Bracklesham Bay, near base of unit S7i, unique.

**Description:** Protoconch small, globular, paucispiral, of one smooth whorl. Spire angle approximately 30° after allowance is made for some dorso-ventral compression in the holotype. Teleoconch of 9 evenly but slightly convex whorls separated by very shallow sutures. First 3 whorls somewhat decorticated but with indications of low, curved collabral costellae and of a subsutural cord beaded by weak axial plicae, which is completely absent from the last few whorls. Ramp long, comprising the whole adapical part of the whorl with 1 or 2 fine spiral threads, increasing to 6 by the last whorl. Peripheral ornament of growth lines, slightly thickened around the sinus at regular intervals to form short, close, strongly curved costellae, scarcely raised above the surface of the whorl, and 4 flattened spiral threads crossing them. Subperipheral area with up to 8 very close and fine, flattened spiral threads separated by weak, shallow striae, continuing onto the base and rostrum. Sinus deeply and narrowly U-shaped, its apex situated on the periphery in mid-whorl. Aperture 41% of shell height, narrow, lenticular, tapering gradually into the anterior canal. Columella more or less straight, outer lip (indicated by growth lines) deeply and narrowly notched, smooth within.

**Size:** 21.0 x 6.5mm; height of aperture 8.5mm.

**Distribution:** Middle of the Selsey Formation, Bracklesham Bay, unit S7i.

**Notes:** This recalls the original figure of *E. wetherellii* (Edwards, 1861: pl. 29, fig.16), however the ribs of that species are more prominent than illustrated and when directly compared the two species show little resemblance. The subdued ornament of *fusellina* and the virtual absence of a subsutural ridge seem to ally it to *E. undata* (Deshayes) from the Lutetian of Grignon, France. However, *undata* is a much larger species with more inflated, contoured whorls, deeper sutures, the body whorl shorter than the spire which has prominent short axial ribs until mid-growth, (Deshayes, 1833: 456; Brébion, 1992: 11). It is interesting to find *fusellina* occurring within the range of *E. obscurata*, and apparently replacing it at this horizon. Their significant differences in shape and ornament preclude the one being a geographical subspecies of the other, however. All the available material of *obscurata* suggests that its prominent ornament is a constant character throughout its range.

**Etymology:** Latin adj. *fusellinus*, shaped like a small spindle.

Genus *Gemmula* Weinkauff, 1875 (s.s.)

Weinkauff, 1875: 287. Type by SD - Cossmann, 1896: *Pleurotoma gemmata* Hinds in Reeve, 1843; (= *Gemmula hindsiana* Berry, 1958); living, tropical West America. Range: Maastrichtian, U.S.A. to Recent, worldwide.

*Hemipleurotoma* Cossmann, 1889: 264 (Type by O.D: *Pleurotoma archimedis* Bellardi, 1877; Middle Miocene, Italy).

*Coronia* de Gregorio, 1890 (Type by S.D.- Gardner, 1945: *Pleurotoma acutirostra* Conrad, 1835; (= *P. childreni* Lea, 1833 var., for Harris, 1937); Middle Eocene, Alabama, U.S.A.

**Characters:** Shells small to moderately large for the family, narrowly to broadly fusiform. Protoconch multispiral, conical to somewhat pupoid, comprising 2-4 smooth whorls followed by 1-3½ whorls of brephic axial costellae which trace the development of the sinusigera lip. Teleoconch ornament beginning abruptly at the start of the first whorl, with the appearance of a nodular peripheral keel. Subsutural cord sharp and unornamented. Ramp flat to concave with one or more spiral threads. Peripheral keel formed from 2 more or less fused spiral cords, crenulated by a regular series of nodules (i.e. 'gemmulate') which range from discrete raised points to undulations like the teeth of a cog-wheel. Subperipheral area with spiral cords and threads which continue on to the base. Apart from the crenulations on the keel, axial ornament is limited to subordinate, very fine collabral growth lines which are sometimes regularly spaced and raised. Sinus generally deep, roundly V-shaped, its apex situated on the peripheral keel, often deeper and narrower in the adult lip. Aperture ovate, usually occupying 30-50% of the total shell height. Internal lirae may be present.

**Notes:** This is a large, distinctive genus of somewhat homeomorphic species. Glibert (1960) attempted to split the Cenozoic species into three groups on the basis of carination and apertural dentition: 1. with a prominent keel and strong internal lirae, as in *G. gemmata* (Hinds); 2. with a prominent keel and weak or inconstant internal lirae, as in *G. carinata* (Gray), and 3. with a feeble keel and without internal lirae, as in *G. turrifera* (Nyst). The scheme has not been generally accepted, however, perhaps partly due to the artificial nature of the second category, in which several *Eopleurotoma* were incidentally included. No allowance was made for species with weak keel and internal lirae, such as *G. traceyi* (see below). The obsolescence of the gemmulate keel in particular is another character that has appeared many times in various lineages and is unlikely to signify a major subdivision.

Glibert (1954: 5; 1960: 4) also directly compared the type species of *Gemmula* with that of *Hemipleurotoma* and concluded that the two were congeneric.

*Coronia* was originally proposed to accommodate the present group of turrids in the Cenozoic of North America, but did not gain wide acceptance at first. It was considered to be a synonym of *Hemipleurotoma* by Cossmann (1896: 78) and of *Gemmula* by Harris (1937: 32). Gardner (1945: 240) sought to re-establish *Coronia* as a separate taxon, and wrote, "The nucleus [of *Gemmula*] ... is relatively smaller and more acute, the canal is decidedly longer, and the fasciolar notch a peripheral slit". Only the last of these characters would appear to have any great significance, but examination of several Recent species of *Gemmula* shows that a deep, narrow notch only tends to occur on the lip of fully grown adult shells, the sinus trace on the spire being similar to those of Palaeogene forms whose adult lip is seldom preserved. Gardner continued, "The close relationship of *Gemmula* Weinkauff, typified by a Recent Pacific species, to a group of lower Tertiary Gulf turrids is extremely dubious, and *Coronia* has been retained to include most species referred by various workers to *Gemmula* ...", but chronological or geographical separation alone does not require the use of different genera. The history of *Gemmula* in fact exemplifies the longevity, wide distribution and overall constancy of characters that may occur in a genus with planktonic larval development. Harris & Palmer (1947: 417, 418) considered that the English Middle Eocene species too should be referred to *Coronia*. In support of its use they remarked, "...when we consider the long fusiform outline, the strong centrally located carination whereupon the deep fasciole is located and marked with its characteristic row of beading, there seems reason to believe typical *Gemmula* to be a specialized, end-development of some more generalized Tertiary ancestor", and also "...*Coronia* is in general less regularly spindle-shaped than *Gemmula* s.s., its spire being generally much longer than its aperture, and the riblike crenulae may seem coarser and longer than in typical *Gemmula*". But these distinctions do not apply, even to many American species. The spire of the Recent *G. hindsiana* (type species of *Gemmula*) is longer than its aperture and the crenulations on its keel are much coarser and longer than those of *G. childreni* (type species of *Coronia*; compare Harris, 1937: pl. 1, figs 22 and 33). Also some Eocene species, (e.g. *G. acutangularis*, below) are so close to *hindsiana* that detailed specific separation is required. Nonetheless *Coronia* was maintained as a genus by Powell (1966: 46) and by Palmer & Brann (1966: 605-613), the latter

authors using it for all Palaeogene *Gemmula* of the south-eastern U.S.A. The taxon would appear to be neither easily defined nor particularly useful and is herein synonymised with *Gemmula* (s.s.).

***Gemmula* (*G.*) *conifera*** (Edwards, 1861) comb. nov.

(Pl. 2 figs. 22-24; Pl. 6, fig. 68; Text-fig. 2b)

*Pleurotoma conifera* Edwards, 1861: 274, pl.31, fig.3a, b.

[?] *Pleurotoma conifera* Edwards.; von Koenen 1890: 343, pl. 26, figs 9-11.

[?] *Turris* (*Fusiturris*) *conifera* (Edw.); Glibert, 1960: 19.

*Fusiturris conifera* (Edw.) Powell, 1966: 49.

**Diagnosis:** A small fusiform *Gemmula*, with a bulky body-whorl, spire ranging from scalariform to squat and relatively short, prominent gemmulate keel on the early whorls tending to become obsolete later, and numerous fine but strong, regular spiral cords. Protoconch multispiral, broadly conical, decussately ribbed towards its lip.

**Types & type locality:** Lectotype (herein designated) NHM 71298c (F. E. Edwards coll.) Bracklesham Bay, probably from units S8-S9, the original of Edwards' (1861): pl.31, fig.3a.

Paralectotypes NHM 71298a (F. E. Edwards coll.) Bramshaw, the original of Edwards (1861): pl.31, fig.3b; NHM 71298b (F. E. Edwards coll.) Bramshaw.

**Description:** Protoconch broadly conical with impressed sutures, of 2½ remaining smooth whorls (tip missing) followed by 1½ whorls of gently curved brephic axials. A subsutural ridge and 5-7 strong flat spiral cords develop on the last ½ whorl, crossing the curved costellae and losing the polished texture of the early protoconch in the process. Junction with teleoconch distinct, indicated by a strongly curved terminal rib following the adult sinus, and the appearance of a gemmulate keel formed from the 3rd and 4th cords below the subsutural ridge. Spire angle 30-32°. Teleoconch typically attenuated and subscalariform, of up to c.6 bluntly angulate whorls with deeply indented sutures. Subsutural cord becoming double and then obsolete on adult whorls. Ramp becoming steeper on later whorls, with 2 spiral cords continuing from the protoconch, often increasing to 5 or so with growth. Peripheral keel prominent with cog-like gemmules for the first 2-3 whorls, subsequently becoming obsolete and marked only by the 2 spaced cords which formed it. Numerous sharp, narrow cords cover the subperipheral area, base and rostrum. Sinus roundly V-shaped, its apex on the periphery. Last whorl about half the shell height in dorsal view, typically slender. Aperture 44-49% of shell height, lenticular, gradually narrowing into the anterior canal. Columella slightly concave above, convex below, normal for the genus but obliquely crossed by 8 or so of the external spiral cords which persist on the columella as very fine pleats throughout growth. Outer lip internally bilirate a short distance back from its edge. The vertical lira has a small, approximately central depression.

**Size:** 19.3 x 7.0mm (lectotype); 20.4 x 6.2mm; 18.5 x 6.6mm (paralectotypes).

**Variation:** The finely ornamented, scalariform lectotype and the more sparsely corded, squat paralectotype (Pl. 2, figs. 22 & 24) seem quite different at first sight. Examples of both forms are found in populations from Bracklesham Bay and from Bramshaw, however, together with intergrading forms. The gemmulate keel persists to the last whorl in some shells from later populations at Studley Wood, where the slender form is not known to occur.

**Range:** Middle Eocene of the Hampshire Basin; (?)Middle Eocene - Oligocene, Latdorfian) of Germany and Belgium.

**Distribution:** Selsey Formation: Bracklesham Bay units S6-S9 (probable type horizon units S8/S9); Shepherds Gutter, beds 1-5 (common); Coalmeer Gutter bed B (common); Lee-on-the-Solent unit L11; Whitecliff Bay beds FXIV-XVII; Studley Wood unit SW1 (common). Barton Clay Formation (Elmore Member): Studley Wood units SW2-3. "Lattorfian": Lattorf, Calbe a/S, Atzendorf, Unseburg and Helmstadt, Germany; also Belgium (*vide* von Koenen, 1890)

**Notes:** The distinctive teleoconch shape of *conifera* resembles that of *G. aspera* (Edwards, 1861) from the Barton Clay Formation, but the number of other individual characters in common are too few to segregate these two species from *Gemmula* (*G.*) at subgeneric level.

The general aspect of *conifera* is unlike that of most *Gemmula* and raises the possibility that it may belong to the Borsoniinae (i.e. Clathurellinae - see Taylor *et al.*, 1993). A spirally corded end to the protoconch, a peripheral sinus and a gemmulate keel occur in some species of *Bathytoma*, e.g. *B. hantoniensis* (Edwards,

1861), while a fine plication of the columella by continuation of external spirals also occurs in *Domenginella conoides* (Solander in Brander, 1766) and *D. newtoni* Tucker & Le Renard, 1993 [= *dissimilis* Edwards], all referred to the Borsoniinae (Powell, 1966). However the bilirate lip process, non-beaded subsutural ridge and the simple gemmulate keel are a combination of characters only found in *Gemmula* (s.s.).

Von Koenen gave a description of the protoconch of German examples which closely matches that of the present species. His figures show a very similar morphology; the gemmules persist until the last whorl on some of the shells, although examples from Studley Wood units SW2-3 sometimes share this character. Plication of the columella and liration of the lip were not mentioned, and so the record is included here with a query. Although considered Lower Oligocene by von Koenen, the mollusc fauna of German "Latdorfian" localities has been shown to range from NP15 to NP21 (see Ritzkowski, 1981). A probable Middle Eocene date for *G. conifera* in Germany is suggested by the appearance in the same beds of *Turricula attenuata* (J. Sowerby, 1816), a singular turrid restricted to a very narrow interval in the Selsey Formation in England (von Koenen, 1890: 312, pl.30, fig.9; Tracey et al., 1996).

***Gemmula* (*G.*) *acutisinuata acutisinuata* (Edwards, 1861) comb. nov.**

(Pl. 3, fig. 25)

*Pleurotoma acutisinuata* Edwards, 1861: 306, pl.32, fig.5a-b.

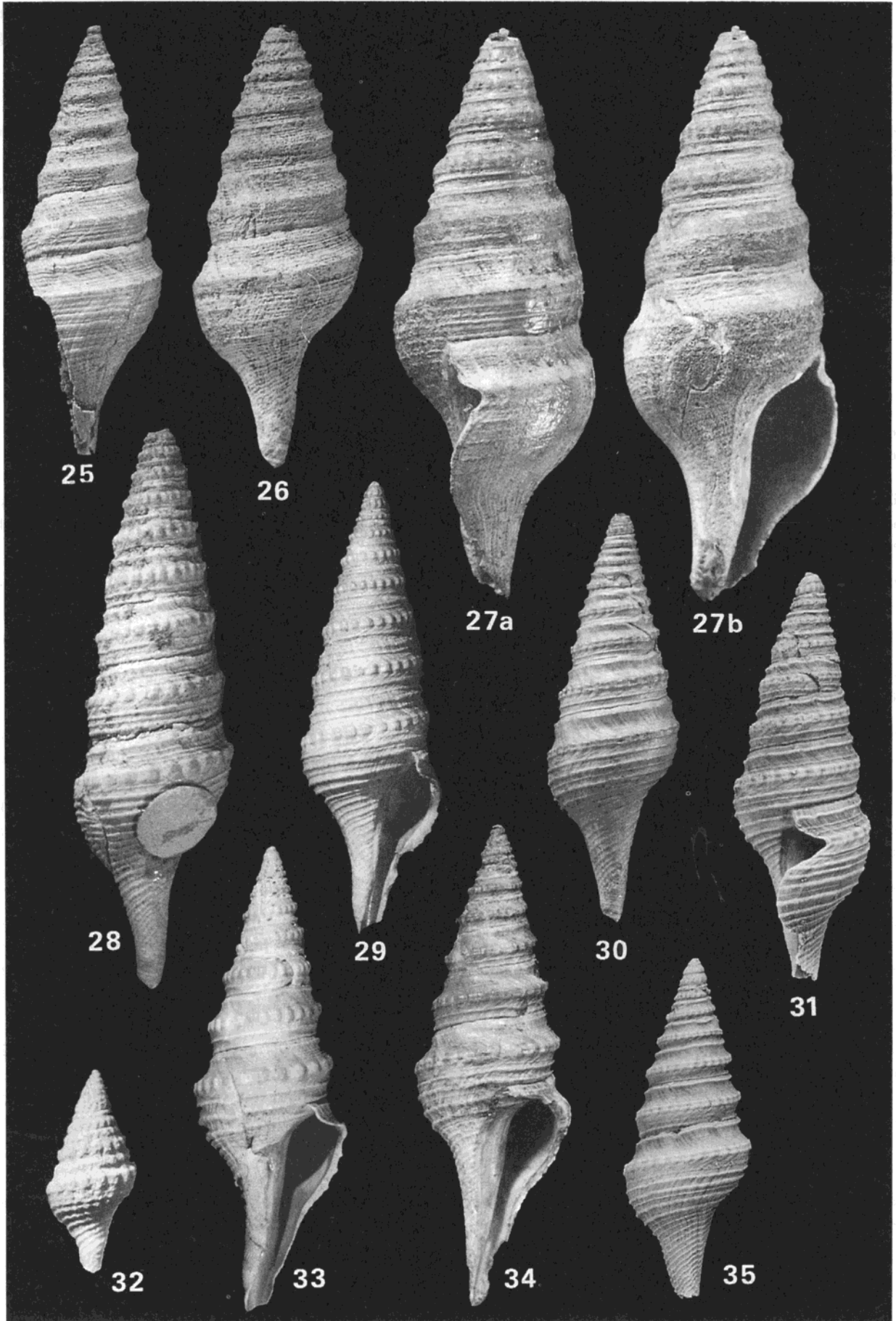
**Diagnosis:** A medium-sized *Gemmula* with close, fine spiral ornament of flattened threads and a weak subsutural ridge. Peripheral gemmules fading away on the early teleoconch leaving a smooth angulate keel which is reduced to a narrow carination on later whorls.

**Type & type locality:** Holotype NHM 71341 (F. E. Edwards coll.) Bracklesham Bay (horizon not recorded), unique.

**Description:** Apex eroded and worn, but showing a thick median keel with an uneven surface that could indicate the former presence of nodules. Apical angle 33°, spire angle narrowing to c.26° on later whorls. Teleoconch with c.8 remaining medially carinate whorls with moderately shallow sutures. Subsutural ridge very weak, formed from 2 fused threads. Ramp wide, concave with up to 9 fine, flattened spiral threads. Periphery of the last whorl angulated by a single narrow cord, which is clearly thicker on the earlier whorls, although obscured by wear. Subperipheral area with 4 flattened spiral cords, the lowest strongest and most prominent.

**Plate 3. English Eocene *Gemmula***

25. *Gemmula* (*G.*) *acutisinuata acutisinuata* (Edwards), holotype, Bracklesham Bay. NHM 71341 (F. E. Edwards coll.) (x4): 19.5 x 6.3mm.
26. *Gemmula* (*G.*) *acutisinuata stubbingtonensis* (Cossmann), Stubbington. NHM 71321 (F. E. Edwards coll.) (x4): 20.0 x 7.7mm; holotype of *Pleurotoma crebrilinea* Edwards / *stubbingtonensis* Cossmann.
27. *Gemmula* (*G.*) *acutisinuata stubbingtonensis* (Cossmann), Stubbington. NHM PI TG 2024 (history not recorded) (x4): 26.3 x 9.8mm, a. labral, b. apertural.
28. *Gemmula* (*G.*) *plebeia* (J. de C. Sowerby), holotype, Bracklesham Bay. NHM G 66107 (F. Dixon coll.) (x 4): 25.7 x 7.4mm.
29. *Gemmula* (*G.*) *plebeia* (J. de C. Sowerby), Bracklesham Bay, units S8-9 NHM PI TG 2068 (S. Tracey coll.) (x 4): 20.7 x 6.4mm.
30. *Gemmula* (*G.*) *plebeia* (J. de C. Sowerby) Form A, Brook. NHM 71319d (F. E. Edwards coll.) (x4): 18.6 x 6.1mm. Variant with wide and smooth ramp, recorded as *Pleurotoma odontella* by Newton (1891).
31. *Gemmula* (*G.*) cf. *plebeia* (J. de C. Sowerby) Brook. NHM 71313a (F. E. Edwards coll.) (x 4): 18.4 x 6.3mm. Labral view.
32. *Gemmula* (*G.*) sp., Fawley Tunnel, unit C, "Campanile bed". NHM PI TG 2067 (F. C. Stinton coll.) (x7): 5.1 x 2.2mm; possibly a juvenile of *G. acutisinuata stubbingtonensis* (Cossmann).
33. *Gemmula* (*G.*) *acutangularis* (Deshayes), Coalmeer Gutter, unit B. NHM PI TG 2026 (S. Tracey coll.) (x 4): 22.0 x 7.1mm.
34. *Gemmula* (*G.*) *acutangularis* (Deshayes), Brook. NHM 71313a (F. E. Edwards coll.) (x 4): 21.7 x 7.2mm, recorded as *Pleurotoma denticula* by Newton (1891).
35. *Gemmula* (*G.*) *acutangularis* (Deshayes), subadult, Brook. NHM 71313b (F. E. Edwards coll.) (x 4): 15.3 x 5.9mm, recorded as *Pleurotoma denticula* by Newton (1891).



Strong cords continue on to the base, developing finer intermediary threads until fine ornament reappears on the rostrum. Sinus V-shaped, as for the genus. Aperture ovate, gradually narrowed into a moderately long anterior canal.

**Size:** 19.5 x 6.3mm

**Range & distribution:** Middle Eocene: Bracklesham Bay, from an unspecified horizon; the preservation of the unique type suggests that the origin was either the Earnley or the Selsey Formation.

**Notes:** Although the characteristic gemmules are not preserved, it is more reasonable to assume that they were present and to accept this as a *Gemmula* close to *stubbingtonensis*. The similarity suggests that only one species is involved, but no firm conclusions about infraspecific variation can be drawn in this case from comparing the unique example of one taxon with 2 presumed examples of the other. In view of the differences in profile, *acutisinuata* and *stubbingtonensis* are maintained as subspecies pending the discovery of further material.

***Gemmula (G.) acutisinuata stubbingtonensis*** (Cossmann, 1899) comb. nov.

(Pl. 3, figs. 26-27)

*Pleurotoma crebrilinea* Edwards, 1861: 290, pl.30, fig.8a-c [non *P. teretrium* var. *crebrilinea* Edwards, 1857: 210]  
*Pleurotoma stubbingtonensis* Cossmann, 1899: 139 [nom.subst. for *P. crebrilinea* Edwards, 1861]

**Diagnosis:** A moderately large, broad, robust *Gemmula* ornamented with numerous close, fine spiral threads and raised growth striae on the adult whorls, and a thick gemmule band on the early teleoconch which becomes a smooth keel on later whorls.

**Types & type locality:** Holotype NHM 71321 (F. E. Edwards coll. as *crebrilinea*) Stubbington. This was the formerly unique adult shell figured by Edwards (1861).

**Additional material:** NHM PI TG 2024 (history not recorded) Stubbington, a large example;

NHM 71313f1 (F. E. Edwards coll. as *denticula*) Stubbington, 2 probable juveniles c.15mm; NHM PI TG37 (F. C. Stinton coll.) Fawley Tunnel, "Campanile bed" unit C, probable juvenile.

**Comparison:** The two known adult examples are broader than *acutisinuata* s.s. as a result of a more rapid increase in the early whorls (apical angle 40-45°) but the later spire angle is a similar 26°. The spiral threads are slightly finer and the growth lines more prominent. The shell base is rounder than that of *acutisinuata* s.s. and more abruptly narrowed into the rostrum. Both examples of *stubbingtonensis* show a gemmulate keel which fades out shortly before or shortly after mid-growth; the corresponding point is obscured in *acutisinuata* s.s. but must have been before mid-growth.

**Size:** 20.0 x 7.7mm (holotype); 26.3 x 9.8mm (PI TG 2024).

**Variation:** The spiral ornament on the ramp of the larger example begins with a single thread and increases whorl by whorl to become more than 8 threads. If this is the case with the holotype, the increase must have taken place much earlier. The crisp, decussate nature of the striae on the type are not evident on the larger shell which is more waterworn. While the spiral ornament on the spire whorls of the type is closer to that of *acutisinuata* s.s. than that of the larger example, the reverse is true in respect of the basal ornament.

A broadly biconic juvenile, NHM PI TG 2025 (F. Stinton coll.) from the Fawley Tunnel, 5.1 x 2.2mm (Pl. 3, fig. 32) has a small, regularly conical protoconch (worn), thick subsutural and peripheral bands, a condensed tabulate ramp, and basal cords beaded by the growth lines. Two similarly biconic juveniles from Stubbington, c.14mm with strongly gemmulate keels, have 3 initial threads on the ramp, increasing in number with growth. All of these are tentatively referred to *stubbingtonensis*, although more material is needed to establish a pattern of development of the ornament in this subspecies.

**Range & distribution:** Middle Eocene: Selsey Formation, Stubbington; probably from the *Campanile* bed near the base of the formation at Hill Head (rare); Fawley Tunnel unit C (one ? juvenile).

**Notes:** The broad and robust shell, close and fine ornament on later whorls, and early obsolescence of ornament on the keel distinguish this from other Eocene *Gemmula* (s.s.).



***Gemmula (G.) plebeia*** (J. de C. Sowerby, 1850)

(Pl. 3, figs 28-31; Pl. 6, figs 59-61)

*Pleurotoma plebeia* J. de C. Sowerby in Dixon, 1850: 103, 184, pl. 6, fig.23; Edwards, 1854: 451.*Pleurotoma denticula* Bast. Edwards, 1861: 286 (in part), pl. 30, fig. 7a, b; Lowry *et al.*, 1866: pl.3; [non Basterot, 1825].[?] *Hemipleurotoma plebia* (Sow.); Jackson, 1926: 359; Wrigley, 1934: 13.*Gemmula plebeia* (J. de C. Sowerby); Castell & Cox, 1975: pl.27, fig.6.Not *P. (Hemipleurotoma) plebeia* of Cossmann, 1889: pl.9, fig.34 [= *Gemmula acutangularis* (Deshayes, 1834)]; nor *P. plebeia* of Morris in Forbes, 1856: pl.5, fig.1 [= *Gemmula odontella* (Edwards, 1861)].**Diagnosis:** A moderately large and slender *Gemmula* with a long spire and relatively short aperture, slightly convex whorls, shallow sutures, a moderately but variably wide and low, closely gemmulate keel in midwhorl, a steeply inclined shoulder ramp with 2-4 irregularly spaced, fine spiral threads, and aperture without internal processes. Protoconch multispiral, large and somewhat pupoid, as for the genus but with the addition of spiral cords and a subsutural ridge which develop towards its lip.**Types & type locality:** Holotype NHM G 66107 (F. Dixon coll.), a large adult of 8½ whorls (apex missing), from Bracklesham Bay (horizon unknown). The shell wall is fragile and has been mostly lost from the apertural side. Some grey glauconitic sand matrix is preserved internally. This specimen does not precisely match any other of the many examples examined, but appears to be most similar in form to Bracklesham Bay specimens collected by A. Wrigley from the *Campanile* bed (probably part of unit S4) and to NHM GG 6936 (F. E. Edwards coll., figured by Castell & Cox, 1975) with an olive glauconitic sand matrix, suggesting the same horizon. These in turn are hardly separable from the slightly less strongly ornamented form commonly found *in-* and *ex situ* on outcrops of units S8/S9.**Description:** Protoconch large, multispiral, cyrtoconoid with very shallow sutures, comprising c.3 smooth conical whorls (of which 2½ remain in the best example) followed by 2 whorls of curved brephic axials, fine and oblique at first, becoming stronger and straighter, below a distinct subsutural cord. On the last half-whorl c.4 spiral threads are developed, equalling the axial costellae in strength, the adapical 2 continuing onto the teleoconch as the gemmulate keel, the 3rd (at least) ending at the sinusigera lip of the protoconch. No microsculpture apparent on protoconch. Junction with the teleoconch indistinct, marked by the termination of the protoconch ornament. Apical angle 28°, spire angle narrowing to 17° on later whorls. Teleoconch of up to 8 rather flattened and turreted whorls. Subsutural ridge sharply carinate. Ramp concave and steeply inclined, smooth on the early whorls developing 2-4 irregular and often faint, fine threads on later whorls. Peripheral keel persistent but not prominent in mid-whorl, typically moderately thick, divided by a weak median sulcus and bearing 20-25 cog-like projections per whorl. Subperipheral spiral cords 1 on early whorls increasing to a maximum of 3 on the penultimate whorl, continuing onto the base where a few single intermediary threads may also develop. Sinus deep, narrowly V-shaped as for the genus. Aperture 35-40% of the height of the shell, narrowly ovate and abruptly contracted into a relatively short and slender canal. Outer lip without internal processes.**Size:** 25.7mm x 7.4mm (incomplete holotype); 20.7 x 6.4mm (PI TG 2068); 17.1 x 7.7mm (GG 6936).**Variation:** Rarely juvenile shells occur with the characteristic protoconch of *plebeia* but with weak paired lirae inside the lip of the first teleoconch whorl (e.g. at Bracklesham Bay units S8-9). This feature does not appear to continue with growth, however. The spiral ornament on the ramp and the thickness of the keel varies between individuals without greatly affecting the overall appearance, although one particular morphotype is distinctive:**G. plebeia** - Form A: (Pl. 3, fig. 30; Pl. 5, fig. 61). Shell size and shape as in the typical form but gemmulate keel weak, initially narrow or very narrow, soon becoming a distinctly bifid cord, not prominent on spire, obsolescent on final whorls. The shoulder ramp is concave on the spire whorls, smooth or with 1 to 3 fine faint threads, and often becomes steep and elongated on later whorls. Protoconch as in typical form, last protoconch whorl with 3-4 flattened spiral cords between axial costellae. Form A may be the dominant morphotype in some populations but as examples transitional to more typical *plebeia* often occur with it, it is not considered to represent a distinct subspecies.**Range:** Middle Eocene of the Hampshire Basin.**Distribution:** Earnley Formation: Bracklesham Bay unit E3; Southampton Dock (*vide* Wrigley, 1934); Selsey Formation: Bracklesham Bay unit ?S4 (uncommon); units S6-9 (common), Lee-on-Solent units ?L4-5 & L7-9;

Whitecliff Bay beds FXIV-XVII; Brook; Shepherds Gutter bed 4 (rare protoconchs only). Barton Clay Formation (Elmore Member) Studley Wood units SW2-3 (frequent).

Form A: Brook (NHM 71319d, F. E. Edwards coll.); Bracklesham Bay, unit S9; Lee-on-the-Solent units L7, L9 (NHM PI TG 2102-2108, S.T. coll.), (common).

Identification of material from the Earnley and Barton Clay Formations could not be verified as no protoconchs are preserved; attribution is here based on gross morphology.

**Notes:** Brébion (1992) placed *plebeia* in the synonymy of *Pleurotoma acutangularis* Deshayes, a common French Lutetian species whose identity had long been misinterpreted. *G. plebeia* in fact differs from *acutangularis* in its shorter aperture, less angular whorls, longer ramp and larger protoconch, but *plebeia* is largely replaced in the upper part of the Selsey Formation of the New Forest with a form agreeing closely with the French species (see below).

### *Gemmula (G.) acutangularis* (Deshayes, 1834)

(Pl. 3, figs 33-35; Pl. 6, fig. 62; Pl. 7, fig. 69)

*Pleurotoma acutangularis* Deshayes, 1834: 459, pl. 64, figs. 24, 25; Deshayes, 1865: 384; de Boury, 1899: 84  
*Pleurotoma denticula* Bast.; Edwards, 1861: 286; Newton, 1891: 120 [in part, Brook and Bramshaw records only; non Basterot, 1825].

*Pleurotoma plebeia* Sow.; Cossmann, 1902: 72, pl. 4, fig. 35; Cossmann & Pissarro, 1913: pl. 51, fig. 224-10. [non J. de C. Sowerby in Dixon, 1850].

*Gemmula plebeia* (J. de C. Sow.); Curry, 1942: 95.

*Gemmula (Hemipleurotoma) acutangularis* (Desh.); Brébion, 1992: pl. 4, fig. 15.

Not *Drillia acutangularis* (Desh.); Cossmann, 1902: 94, pl. 6, fig. 5; *Drillia (Tripia) acutangularis* (Desh.); Cossmann & Pissarro, 1913, pl. 52, fig. 225-25 [= *P. acuticinctus* de Boury, 1899].

**Diagnosis:** A moderately large and slender *Gemmula*, evenly fusiform with a relatively long aperture, convex whorls with impressed sutures, a strongly projecting gemmulate keel in midwhorl, an inclined concave shoulder ramp with up to 5 close, very fine spiral striae, aperture bilirate or with a weak channel inside the lip, or more commonly smooth. Protoconch multispiral, medium-sized, conical, slightly pupoid.

**Material:** NHM 71313a, b (F. E. Edwards coll. as *plebeia*) from Brook; NHM PI TG 2026 (S.T. coll.) from Coalmeer Gutter bed B; several other examples from Bramshaw and Coalmeer Gutter, Villiers-St.-Frédéric and Montmireil (S.T. coll.).

**Description** (English material): Protoconch not seen in an unworn state, but medium sized, more or less conical. Spire angle c.28°. Teleoconch of up to 8 angularly convex whorls with strongly indented sutures. Subsutural ridge weak and narrow. Ramp wide, concave and sloping, covered by very fine, very close spiral striae. Peripheral keel moderately thick, weakly or distinctly bifid, strongly projecting in mid-whorl, bearing 25-30 cog-like gemmules per whorl. Subperipheral ornament sparse, of 1-2 distant spiral cords, with or without faint and irregular, fine intermediaries. Base with 1-2 more strong cords, becoming finer and more regular on the rostrum. Sinus V-shaped, as for the genus. Aperture lanceolate with a peripheral angulation, gradually narrowing into a long and narrow anterior canal. Columella straight, outer lip sometimes clearly bilirate within but more often smooth or with a weak canaliform depression corresponding to the sinus.

**Size:** 22.0 x 7.1mm (Coalmeer Gutter); 21.7 x 7.2mm (Brook).

**Variation:** The shell ornament varies in detail within material from any one locality, but much more so in the Calcaire Grossier than in the Selsey Formation. English populations, however, vary to a similar extent from one locality to another. The ramp may have as few as (0-)1 or 2 fine threads, or may be covered by them. Under the SEM, well-preserved protoconchs of French shells show a microsculpture of scattered granules later becoming crowded spiral threads (Pl. 7, fig. 69), but this has not yet been shown to be present in English examples. Material of medium-sized *Gemmula* (s.s.) in the NHM collections from Brook (and perhaps from more than one horizon) show a particularly great variation in ornament, often in shells which lack the protoconch. Although some of these are referable to the present species, others are more equivocal and require better material to resolve.

**Distribution:** Selsey Formation: Shepherds Gutter, beds 2-5; Coalmeer Gutter beds A, B; Barton Clay Formation (Elmore Member): Studley Wood units SW2-3 (apex not seen); Afton Brickyard *Rimella canalis* bed (frequent).

Calcaire Grossier, Paris Basin: Parnes (type), Damery, Vaudancourt, Gomerfontaine, Boisset (de Boury, 1899); Chaumont, Mouchy, Chambors, St-Félix, L'Orme, Beynes, Montainville (Brébion, 1992); Villiers-St.-Frédéric, Montmireil (S.T. coll.).

Also recorded from Middle Eocene of La Palarea (Nice), Bos d'Arros and Bassin de Nantes at Coislin, La Close (see Brébion, 1992).

**Notes:** A misleading figure given by Deshayes (1834), resembling *Pleurotoma turrella* Lamarck, 1804, caused a debate between subsequent revisers (Cossmann, 1889; 1902; de Boury, 1899) as to the identity of *P. acutangularis* and the provenance of its holotype. The original description was considered to best fit the present *Gemmula* by de Boury (1899) and Brébion (1992). The Recent *G. hindsiana* Berry, 1958 is rather similar but is more slender with a relatively longer spire and often has a multirate lip.

The larger proportions and stronger ornament of *acutangularis*, noticeable even in juveniles distinguishes it from *G. traceyi* which tends to be somewhat homeomorphic where the two species occur together. In the absence of the protoconch it is often hard to separate *acutangularis* from the similarly sized *plebeia*, both species being rather variable. More complete material is required to investigate the relationship of these two species.

While internal lirae have not been recorded in French *acutangularis*, the occurrence of this character in Selsey Formation examples is inconstant and is not considered a good enough reason to segregate the English form.

***Gemmula (G.) veteratoris* sp. nov.**

(Pl. 4, figs 36-38; Pl. 6, fig. 64; Pl. 7, fig. 70; Text-fig. 2c)

*Pleurotoma callifera* var. *moniligera* Edwards, 1861: 292; Newton, 1891: 119 [in part, Brook records only]

**Diagnosis:** A rather small, moderately broad, turreted *Gemmula* with the lip internally bilirate, early whorls wide and condensed, a shelf-like shoulder ramp with at least 3 strong spiral threads, a prominent and persistent gemmulate keel and a small protoconch which is in proportion to the spire.

**Types & type locality:** Holotype NHM PI TG 2027 (S.T. coll.) Coalmeer Gutter unit B, a complete subadult shell of average size.

Paratypes NHM PI TG 2028-2037 (S.T. coll.) 10 shells from the type locality and horizon; NHM 71324b (F. E. Edwards coll.) 2 examples from Brook; A further 30 paratypes from the type locality and horizon (S.T. coll.) to be distributed to various institutions.

**Description:** Protoconch multispiral, small and conical with shallow sutures, increasing regularly within the profile of the spire, the first 3 whorls smooth, the next 1½ whorls with curved brephic axials. Microsculpture of protoconch (visible under SEM) of short, oblique raised microstriae just above the suture and numerous spiral microstriae on the last protoconch whorl. Traces of a gemmulate keel begin on the last protoconch whorl, somewhat obscuring the junction. Spire angle 40°. Teleoconch of up to 6 short, wide whorls. Subsutural ridge sharp. Ramp tabulate, shelf-like, near-horizontal, bearing 3-4 strong, close spiral threads. Peripheral keel persistent, projecting, thick and bifid with 18-20 cog-like nodules per whorl. Subperipheral area with 1(-2) variably strong, smooth spiral cords, continuing closely on to the base and rostrum, more or less interspersed with finer single intermediaries. Sinus V-shaped, as for the genus. Aperture c.45% of the height of the shell, ovate and abruptly contracted into a rather short canal. Columella almost straight. Outer lip thin, internally bilirate; lirae well-defined, forming a channel which terminates before reaching the lip. Traces of this channel are usually recognisable at all growth stages.

**Size:** 15.9 x 5.8mm (holotype); 12.1 x 4.8mm; 14.1 x 5.4mm (paratypes NHM PI TG 2028-9); up to 15.0 x 4.9mm (Studley Wood unit SW1) and up to 12.4 x 4.9mm (units SW2-3).

**Variation:** In some fully grown examples from Studley Wood units SW1-3 and at Afton, the shoulder ramp begins to lose its tabulate aspect and approaches the inclined form seen in *moniligera*. Unlike that species, however, the basal spirals are smooth.

**Range:** Middle Eocene of the Hampshire Basin.

**Distribution:** Upper part of the Selsey Formation: Shepherds Gutter, beds 2-5 and Coalmeer Gutter beds A, B (common); Bracklesham Bay top of unit S9; Whitecliff Bay bed FXVII; Lee-on-the-Solent units L9-11; Studley Wood, unit SW1 (common). Barton Clay Formation (Elmore Member): Studley Wood units SW2-3 and Afton brickyard *Rimella canalis* bed (common).

**Notes:** This approaches *G. pastoralis* in general form and prominence of the gemmulate keel, but constantly differs in the smaller protoconch, bilirate lip processes and 3 or more strong and close threads on the ramp. It differs from the larger *G. moniligera* and related forms in having deeper sutures, a more shelf-like ramp, a relatively much shorter and less cyrtocoid spire, and in lacking the strong granulation of the spiral cords on the lower part of the whorl.

**Etymology:** Latin, genitive of *veterator*, 'the wise old fox'. Named for Dr. Jacques Le Renard of the Muséum National d'Histoire Naturelle, Paris.

***Gemmula (G.) traceyi* Tucker & Le Renard, 1993**

(Pl. 4, figs 41-45; Pl. 6, fig. 67; Text-fig. 2d)

*Pleurotoma denticula* var. *gracilentata* Edwards, 1861: 287, pl.30, fig.7f; Newton, 1891: 121 [*non P. gracilentata* Reeve, 1843].

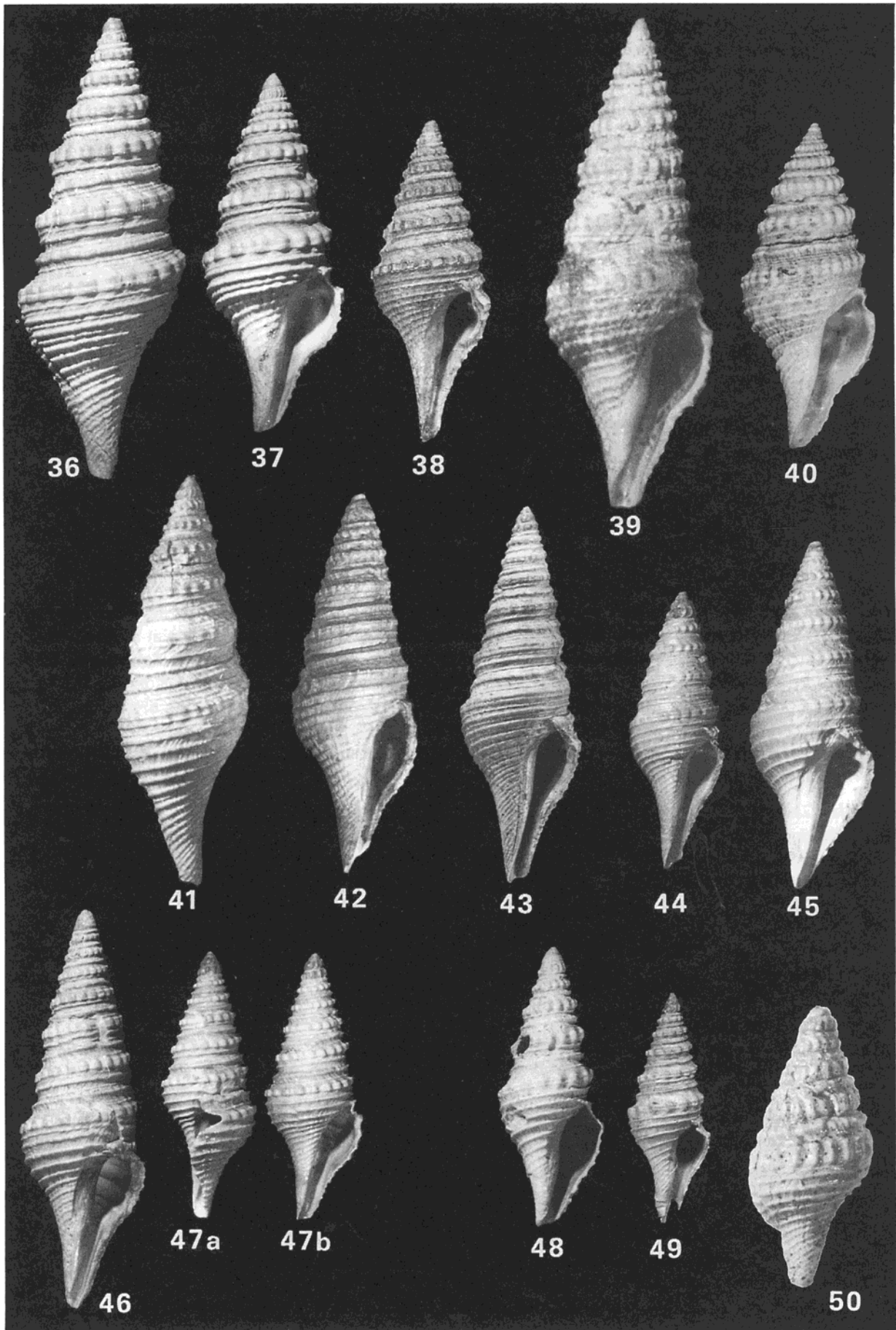
*Pleurotoma denticula* var. *odontella* Edwards; Newton 1891: 121 [in part, Brook record only]

*Gemmula traceyi* Tucker & Le Renard, 1993: 2, 50 [*nom.subst.* for *P. gracilentata* Edwards]

Not *Pleurotoma gracilentata* Edw. of Cossmann, 1902: pl.5, fig.3; nor *Gemmula traceyi* of Le Renard & Pacaud, 1995: 124.

**Plate 4. English Eocene *Gemmula***

36. *Gemmula (G.) veteratoris* sp. nov., holotype, Coalmeer Gutter, unit B. NHM PI TG 2027 (S. Tracey coll.) (x 5): 15.9 x 5.8mm.
37. *Gemmula (G.) veteratoris* sp. nov., paratype, Coalmeer Gutter, unit B. NHM PI TG 2028 (S. Tracey coll.) (x 5): 12.1 x 4.8mm.
38. *Gemmula (G.) veteratoris* sp. nov. paratype, Brook. NHM 71324b (F. E. Edwards coll.) (x 4): 14.1 x 5.4mm, recorded as *Pleurotoma callifera* var. *moniligera* by Newton (1891).
39. *Gemmula (G.) moniligera* (Edwards), lectotype, Barton Clay Formation, Barton. NHM PI TG 2055 (F. E. Edwards coll.) (x 5): 18.1 x 6.1mm, a species with granular ornament, not occurring in the Selsey Formation.
40. *Gemmula (G.) jefferyi* *nom.nov.*, lectotype of *Pleurotoma callifera* Edwards *non* Conrad, Barton Clay Formation, Highcliffe. NHM 71322b (F. E. Edwards coll.) (x 4): 14.7 x 6.1mm.
41. *Gemmula (G.) traceyi* (Tucker & Le Renard), lectotype of *Pleurotoma gracilentata* Edwards *non* Reeve, Brook. NHM 71317b1 (F. E. Edwards coll.) (x 5): 13.7 x 4.5mm; the interior of the aperture (not shown) is smooth in this example.
42. *Gemmula (G.) traceyi* (Tucker & Le Renard), paralectotype of *Pleurotoma gracilentata* Edwards *non* Reeve, Brook. NHM 71317b2 (F. E. Edwards coll.) (x 5): 12.8 x 4.3mm, an example from the type lot with weakly developed horizontal and vertical liriation within lip.
43. *Gemmula (G.) traceyi* (Tucker & Le Renard), Brook. NHM 71319d (F. E. Edwards coll.) (x 4): 16.0 x 5.1mm, specimen recorded as *Pleurotoma odontella* by Newton (1891).
44. *Gemmula (G.) traceyi* (Tucker & Le Renard), Bracklesham Bay, units S8-9. NHM PI TG 2069 (S. Tracey coll.) (x 5): 9.4 x 2.35mm.
45. *Gemmula (G.) traceyi* (Tucker & Le Renard), Studley Wood, unit SW1. NHM PI TG 2070 (S. Tracey coll.) (x 5): 11.8 x 6.2mm, variant with strong channel inside lip.
46. *Gemmula (G.) pastoralis* sp. nov., paratype, Coalmeer Gutter, unit B. NHM PI TG 2039 (S. Tracey coll.) (x 5): 13.7 x 4.4mm; a large example.
47. *Gemmula (G.) pastoralis* sp. nov., holotype, Coalmeer Gutter, unit B. NHM PI TG 2041 (S. Tracey coll.) (x 5): 9.7 x 3.5mm, an average sized example; a. labral, b. apertural view.
48. *Gemmula (G.) wrigleyi* sp. nov., holotype, Bracklesham Bay *ex situ*, probably from unit S4iii. NHM PI TG 2042 (S. Tracey coll.) (x 5): 9.3 x 3.6mm.
49. *Gemmula (G.) wrigleyi* sp. nov. Form A, Whitecliff Bay, unit FXIV. NHM PI TG 2071 (A. Wrigley coll.) (x 4): 10.6 x 3.8mm; a form apparently transitional to *pastoralis*.
50. *Gemmula (Coroniopsis) monerma* (Edwards), juvenile, Studley Wood, unit SW1. NHM PI TG 2072 (F. C. Stinton coll.) (x 7): 7.2 x 3.1mm.



**Diagnosis:** A small, slender *Gemmula* with slightly convex rounded whorls, a steep ramp with 1-3 fine threads, a narrow inconspicuous gemmulate keel on the early whorls, its ornament reduced or lost on later whorls, and outer lip weakly and inconstantly to strongly bilirate within. Protoconch small to medium sized, slightly pupoid.

**Types & type locality:** Lectotype (herein designated) NHM 71317b1 (F. E. Edwards coll.) Brook (Pl. 4, fig. 41)

Paralectotypes NHM 71317a, a specimen similar to the lectotype and labelled as being the one figured by Edwards (1861: pl.30, fig. 7f), but now badly damaged; NHM 71317b2, a shell close to lectotype in shape and ornament, but interior of lip weakly bilirate; (both from Brook, F. E. Edwards coll.).

**Additional material:** NHM 71317d, e (F. E. Edwards coll.) Brook, 2 shells recorded as *odontella* (Newton, 1891); NHM PI TG 2069 (S.T.coll.) Bracklesham Bay units S8-9; NHM PI TG 2070 (S.T.coll.) Studley Wood unit SW1; numerous examples from various localities in NHM and private collections.

**Description:** Protoconch moderately small, somewhat pupoid with shallowly impressed sutures, of more than 3 small conical smooth whorls followed by  $1\frac{1}{2}$  whorls of curved brephic axials of more or less constant width, ending in a sinusigera lip. Junction with teleoconch abrupt, marked by the expansion of a subsutural ridge and appearance of a gemmulate keel in mid-whorl. Spire angle  $30^\circ$ . Teleoconch of up to 6 gently convex whorls. Subsutural ridge sharp. Ramp wide, steeply inclined, with 1-3 spaced, fine spiral threads. Peripheral keel narrow, not prominent, formed from 2 fine cords bearing 15-30 small cog-like gemmules on the early whorls, which are reduced or lost on later whorls. Subperipheral area typically with one fine and two strong spiral cords and a further c.15 strong cords covering the base and rostrum. Sinus roundly V-shaped, as for the genus. Columella almost straight. Aperture lanceolate, gradually narrowed into a moderately long anterior canal. Outer lip internally smooth in the lectotype and one paralectotype but weakly bilirate in another paralectotype probably from the same horizon.

**Size:** 13.7 x 4.5mm (lectotype); 12.8 x 4.3mm (paralectotype NHM 71317b2); up to 17.0 x 5.6mm (NHM 71319e).

**Variation:** In examples from Bracklesham Bay and Studley Wood (Pl. 4, figs. 44, 45) the 2 lirae inside the lip are strongly developed to form a thickly walled channel but the strength of the lirae is variable at most horizons and so is not an infallible distinguishing character. The absence of internal lirae in the lectotype and its weak presence in one paralectotype from the same lot (Pl. 4, fig. 42) shows that this character alone cannot be used for specific separation in this case. On the protoconch of occasional examples (Pl. 6, fig. 67) the brephic axial costellae are closer and more numerous than in the usual form (Pl. 4, fig. 41). A form probably from the same lineage as *traceyi* but of uncertain relationship occurs in the Elmore Member, Afton brickyard, *Rimella canalis* bed, in which the gemmulate keel has a paedomorphic tendency to persist to the last whorl.

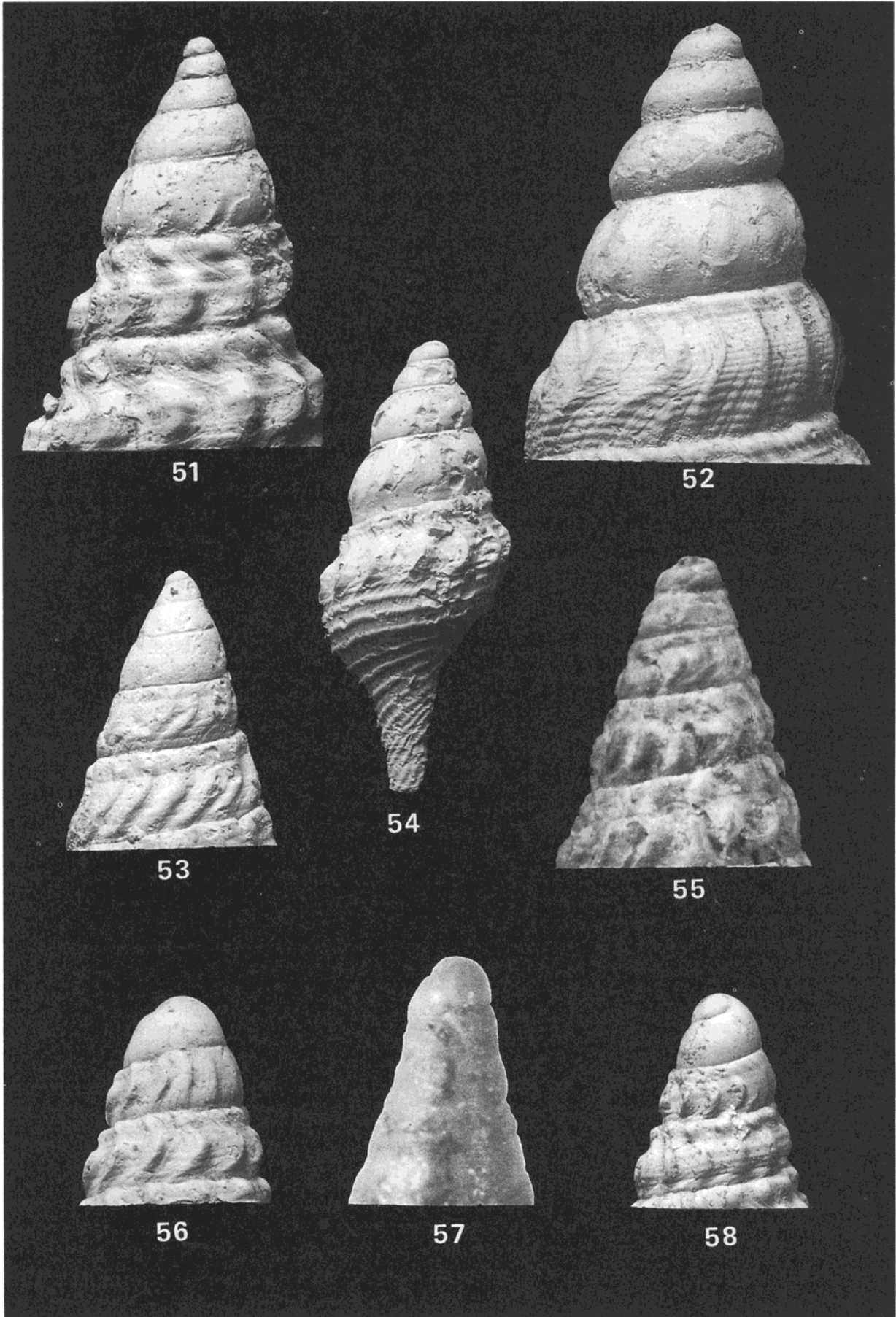
***Gemmula (G.) traceyi* Form A:** NHM PI TG 2097-2101 (S.T. coll.) Lee-on-the-Solent bed L9. This morphotype differs in having a much larger protoconch than the typical form, although not so large as that of *G. plebeia*, and it lacks any spiral cords on the last protoconch whorl. The form occurs exclusively at some horizons, but mixed with typical examples at others.

**Range:** Middle Eocene of the Hampshire Basin.

#### Plate 5 Protoconchs of *Eopleurotoma*

All figures approximately x 28 with an undetermined margin of error of c.  $\pm 5\%$ . Figures 51-54, 56 and 58 are scanning electron micrographs of uncoated specimens using an ISI ABT-55 microscope with environmental chamber. Figs 55 and 57 are conventional light microphotographs.

51. *Eopleurotoma gentilis* (J. de C. Sowerby), Bracklesham Bay, units S8-9. NHM PI TG 2073 (R. Fowler coll.)
52. *E. fowleri* sp. nov., Holotype, Bracklesham Bay, units S8-9 (ex situ). NHM PI TG 2017 (S. Tracey coll.)
53. *E. cf. expedita* (Deshayes), Bracklesham Bay, unit S10. NHM PI TG 2022 (S. Tracey coll.)
54. *E. comma* (J. Sowerby), East Selsey, unit SL1. NHM PI TG 2074 (S. Tracey coll.)
55. *E. hollowayi* sp. nov., Fawley Tunnel, *Campanile* bed. NHM PI TG 2075 (F. Stinton coll.) juvenile, early protoconch whorls missing.
56. *E. obscurata* (J. de C. Sowerby), Bracklesham Bay, units S8-9. NHM PI TG 2076 (R. Fowler coll.)
57. *E. fusellina* sp. nov. Holotype, Bracklesham Bay, unit S7i. NHM PI TG 2023 (S. Tracey coll.)
58. *E. scalarata* (Edwards), Coalmeer Gutter, bed B. NHM PI TG 2077 (S. Tracey coll.)



**Distribution:** Selsey Formation: Brook (type loc.); Shepherds Gutter, beds 2-5; Coalmeer Gutter units A, B; Bracklesham Bay units S7-9; Whitecliff Bay beds FXIV-XVII; Studley Wood unit SW1 (common).

**Form A:** Lee-on-the-Solent unit L7-11; Whitecliff Bay beds FXIV-XVII;

**Notes:** Similar and possibly ancestral forms to *traceyi* from the lower part of the Selsey Formation at Stubbington, Bracklesham Bay and East Selsey are referred to *G. wrigleyi* sp. nov. in view of their smaller size and spiky nodular ornament. *G. traceyi* has a close resemblance to the variable *G. nilssoni* (Deshayes, 1865) from the Early Eocene Sables de Pierrefonds in the Paris Basin, agreeing in protoconch morphology, steep ramp and in having a broadly similar spiral ornament. The only constant difference is that *G. nilssoni* has a much thicker gemmulate keel on the spire (obsolete on the later whorls) and also lacks any indication of internal lirae. *G. nilssoni* occurs in the Earnley Formation, Bracklesham Bay unit E3 (personal obs.) and may well belong to the same lineage.

***Gemmula (G.) pastoralis* sp. nov.**

(Pl. 4, figs 46, 47; Pl. 6, figs 65, 66; Pl. 7, fig. 71; Text-fig. 2a)

*Pleurotoma denticula* Bast. Edwards, 1861: 288, 290 [in part, non Basterot, 1825].

**Diagnosis:** A small, slender, biconic *Gemmula* with a single median spiral thread on the ramp, a prominent and persistent gemmulate keel, 4-8 distinct spiral lirae inside the outer lip, and a small and pointed protoconch that ends in an inflated, turban-shaped last whorl.

**Types & type locality:** Holotype NHM PI TG 2038 (S.T. coll.) Coalmeer Gutter unit B, a complete subadult shell of average size.

Paratypes NHM PI TG 2039 a relatively large adult shell with scars from repeated lip breakage during growth, and NHM PI TG 2040, 2084, 2088-2096 (S.T. coll.) 12 examples from the type locality and horizon; NHM PI TG 2041 (E. M. Venables coll.) Bracklesham Bay S8-S9, 1 juvenile; NHM 71317c (F. E. Edwards coll.), 3 examples from Bramshaw labelled *gracilentia* Edw.; A further 30 paratypes from the type locality and horizon (S.T. coll.) to be distributed to various institutions.

**Description:** Protoconch multispiral, coeloconoid, trochiform with impressed sutures expanding rapidly; first whorl globular, slightly eccentric, the next  $2\frac{1}{2}$  whorls small, smooth with shallow sutures, then one depressed whorl of fine curved brepheic axials followed by a wide and deep whorl of stronger, spaced, curved costellae. The last  $\frac{1}{2}$  whorl is as wide as the preceding whorl with thicker costellae, a subsutural cord and a sinusigera lip. Microsculpture over whole protoconch consists of oblique, filiform, raised microstriae, most evident just above the sutures and on the edges of the costellae. Junction with the teleoconch sharp, marked by the abrupt start of a median gemmulate keel and V-shaped sinus. Spire angle  $25^\circ$ . Teleoconch of 5-7 slightly convex whorls with little depth. Subsutural ridge sharply carinate. Ramp concave, short, somewhat shelf-like with a median, single, fine spiral thread, originating between teleoconch whorls 1 and 3. Peripheral keel narrow, situated in mid-whorl, divided by a weak median sulcus and bearing 20-25 prominent cog-like projections per whorl, persistent throughout growth. One subperipheral spiral cord below the keel, several more similar strong cords on the base becoming finer and weaker on the rostrum. Sinus V-shaped, as for the genus. Aperture 40-45% of the height of the shell, ovate and abruptly contracted into a moderately long and slender canal. Outer lip thin, internally multiliriate with 4-5 (rarely up to 8) strong, narrow spiral lirae, the basal lira usually being doubled. Typically these lirae persist internally from the start of the teleoconch to a point a short distance before the lip.

**Size:** 9.7 x 3.6mm (holotype); up to 13.7 x 4.4mm (paratype NHM PI TG 2039), the usual maximum size being around 10.0 x 3.6mm.

**Variation:** At the type horizon in the New Forest and approximate equivalents elsewhere, *G. pastoralis* is particularly constant in its morphology, the main diagnostic characters of internal lirae, prominent keel, single thread on the ramp and turban-like protoconch being present in virtually all uneroded shells examined. Large shells occasionally show the beginnings of a second spiral thread on the ramp of the last whorl, or internal lirae ceasing almost half a whorl back from the lip, although these seem to be gerontic features. Three intermediary internal lirae are developed in one shell from Shepherds Gutter (bed 5) making a total of 8 lirae. Two morphotypes have been noted from slightly older strata than the typical form:



**G. pastoralis** - Form A: typical in most respects but having a smooth ramp on the early teleoconch whorls, the single spiral thread appearing around mid-growth.

**G. pastoralis** - Form B: with typical shape and ornament but the internal lirae are generally weaker, sometimes absent, the protoconch is slightly narrower and its last whorl less inflated.

**Range:** Middle Eocene of the Hampshire Basin.

**Distribution:** Middle and upper parts of the Selsey Formation: Shepherds Gutter, beds 1-5 and Coalmeer Gutter beds A, B (abundant); Bracklesham Bay, units S8-10; Whitecliff Bay beds FXV-XVII; Lee-on -Solent, units L7-11.

**Form A:** Bracklesham Bay *ex situ*, preservation suggesting a horizon within units S8-S9; Whitecliff Bay bed FXV.

**Form B:** Bracklesham Bay unit S7; Whitecliff Bay bed FXIV.

**Notes:** Edwards observed the internal lirae on specimens which he considered to be juveniles of *denticula* (i.e. *plebeia*). However, *plebeia* is distinguished at all growth stages by its fatter, spirally corded protoconch, broader spire and usual lack of internal structures. The multirate lip of *pastoralis* separates it from all other English *Gemmula* except the Bartonian *G. aspera*, which is very different in other respects, having a shape closer to that of *G. conifera* (see above). There are, however, some very similar species in the Palaeogene of North America and Neogene of Europe. Both *Gemmula* (*G.*) *amica* (Casey, 1903) from the Oligocene of Mississippi and the closely similar *G. (G.) denticula borealis* (Glibert, 1954) from the Miocene of northern Europe share comparable internal lirae and a similar profile, but have a shorter anterior canal, 2-5 threads on the ramp, and a longer protoconch with almost orthocline costellae (that of *G. amica* may have as many as  $3\frac{1}{2}$  whorls of costellae). An undescribed form (cf. *amica*) from the Middle Eocene of Texas (C. Garvie coll.) has an almost identical profile and ornament to *pastoralis*, but has a more evenly expanding, conical protoconch, similar to that of *G. traceyi*, but with orthocline costellae. The living *G. (G.) hindsiana* Berry, 1958 and *G. (G.) ryukyuensis* MacNeil, 1960 may also have multirate apertures, but both are larger and more slender with longer protoconchs, denser spiral ornament and fewer gemmules per whorl.

**Etymology:** Latin, *pastoralis*, of the shepherd, from the type horizon, the Shepherds Gutter bed, where the species is characteristically common.

### ***Gemmula (G.) wrigleyi* sp. nov.**

(Pl. 4, fig. 48; Pl. 6, fig. 63)

*Hemipleurotoma* [aff.] *gracilentata* (Cossmann, non Edwards); Wrigley & Davis, 1937: 212.

**Diagnosis:** A very small, slender, biconic *Gemmula* with a smooth interior, rather steeply inclined subsutural ramp with 1-5 fine spiral threads, and a peripheral row of discrete pointed nodules which spread beyond the double cord on which they are placed. Protoconch moderately narrow, proportionate.

**Types & type locality:** Holotype NHM PI TG 2042 (S.T. coll.) Bracklesham Bay, *ex situ* near Broad Rife sluices, probably from unit S4iii.

Paratypes NHM PI TG 2049 (A. Wrigley coll.) Whitecliff Bay bed FIV; NHM 71313f1 (F. E. Edwards coll. as *denticula*) Stubbington, 2 juveniles; NHM PI TG 2043-2048 (S.T. coll.) East Selsey unit SL1, 6 juvenile and fragmentary examples.

**Description:** Protoconch multispiral, conical with shallow sutures, c.  $2\frac{1}{2}$  smooth, regularly increasing whorls and  $2\frac{1}{2}$  with fine curved brephic axials. No microsculpture observed in the types. Junction with the teleoconch sharp, marked by the abrupt start of a median keel and V-shaped sinus. Spire angle  $33^\circ$ . Teleoconch of up to  $4\frac{1}{2}$ -5 rather angulated whorls. Subsutural ridge fine and sharp. Ramp concave, moderately steeply inclined, typically with a median, single, fine spiral thread. Peripheral keel narrow formed from 2 fine, close cords passing through a row of 14-16 small, discrete, rounded but pointed nodules per whorl, whose bases spread beyond the 2 cords and which diminish in prominence on later whorls. One subperipheral spiral cord below the keel, c.7 more similarly strong cords on the base but fading on the rostrum. Sinus V-shaped, as for the genus. Aperture

45% of the height of the shell, ovate and gradually contracted into a moderately narrow canal. Outer lip thin, without internal lirae.

**Size:** 9.3 x 3.6mm (holotype).

**Variation:** Although the peripheral nodules are relatively strong on the spire of the holotype, in other examples the nodules are less pronounced and much diminished by the last whorl, which has a more rounded profile as a result. Juvenile material from East Selsey suggests that the size of the protoconch may vary, but lack of adult shells prevents a full understanding of this. The holotype has a single thread on the ramp, while the earlier Wittering Formation shell has 2, increasing to 5 threads.

**Gemmula (G.) wrigleyi** Form A: NHM PI TG 2050 (A. Wrigley coll.) 10.6 x 3.8mm (Pl. 4, fig. 49) has features in common with the holotype but the nodules on the earlier teleoconch whorls are rather more cog-like, the ramp is smooth and the protoconch has deeper sutures. This may be transitional to *pastoralis*, but is referred to *wrigleyi* in view of its nodular ornament. Little material from this horizon is presently available for further study.

**Range:** Early to Middle Eocene of the Hampshire Basin.

**Distribution:** Wittering Formation: Whitecliff Bay bed FIV; Lower part of the Selsey Formation: Stubbington; East Selsey unit SL1; Bracklesham Bay probably unit S4iii (type). Form A: Whitecliff Bay FXIV (i.e. a horizon within the "Brook bed" of Fisher, 1862).

**Notes:** The general proportions of the holotype with a single thread on the ramp and strong basal cords suggest that this may be an earlier representative of the *pastoralis* lineage with the Form A morphotype showing some transitional features. However, it lacks most of the diagnostic characters of typical *pastoralis*, having a narrower protoconch, a nodular ornament exceeding the bounds of the two peripheral cords, and an absence of internal lirae. Some paratypes resemble *G. traceyi* but are smaller and have the characteristic nodular periphery. A lack of well-preserved material from the lower part of the Selsey Formation and earlier horizons in England prevents a full assessment of the variability apparently present among the examples here referred to *G. wrigleyi*.

Wrigley & Davis (1937) compared their Whitecliff Bay specimen to the French Cuisian "*gracilenta* Edw." of Cossmann, but none of the *Gemmula* from France have this form of nodular ornament. The closest in general shape is the larger *G. nilssoni* (Deshayes, 1865) which has a much thicker band of cog-like gemmules.

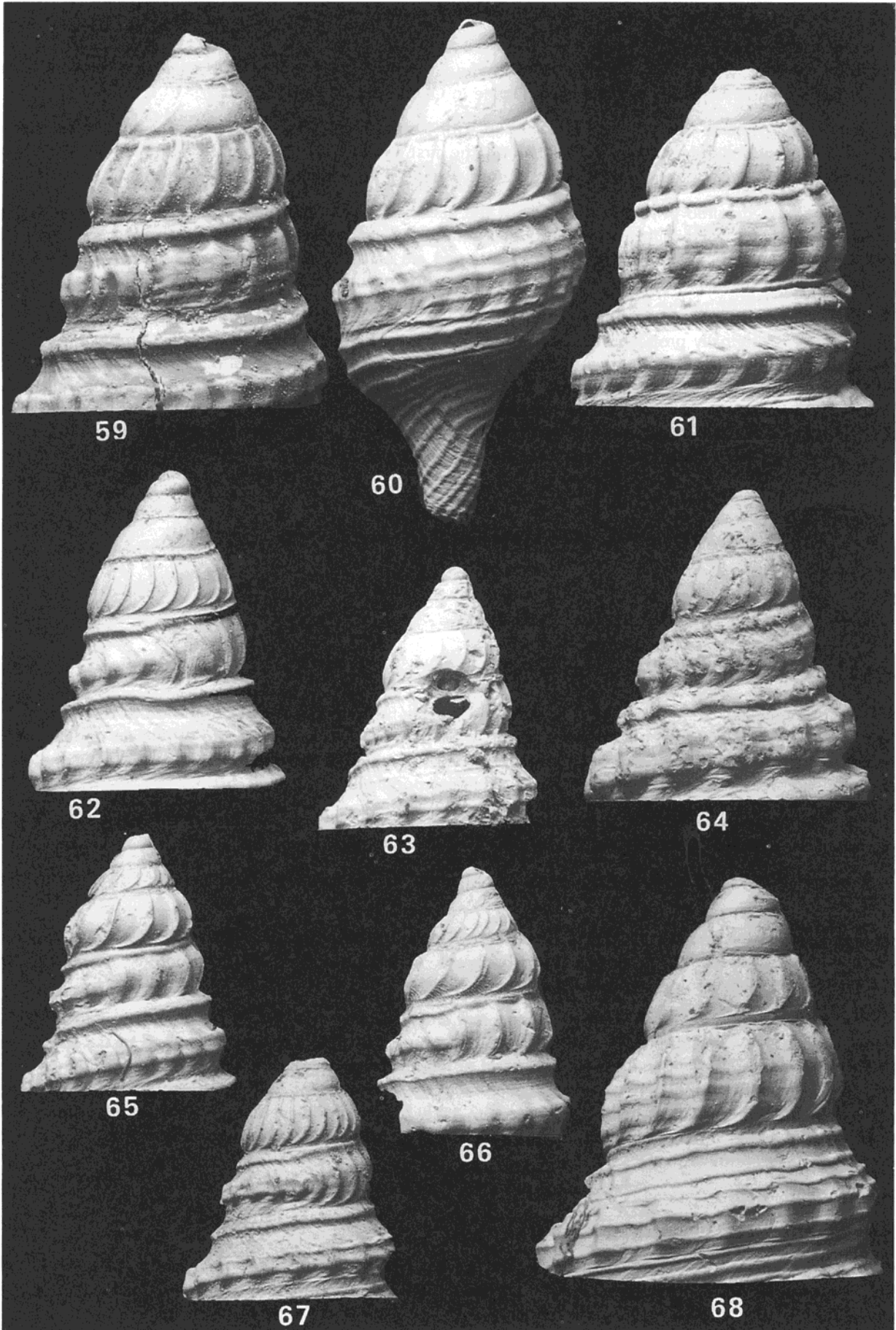
A similar spiky ornament to that of *wrigleyi* is also characteristic of subgenera *Clavogemmula* Long, 1981, and *Ptychosyrinx* Thiele, 1925 (see Hickman, 1976; Kilburn, 1983), but these both have a rather short and twisted anterior canal.

**Etymology:** Named after the late Arthur Wrigley, a leading authority on English Palaeogene molluscs.

#### Plate 6. Protoconchs of *Gemmula*

All figures x 28 ( $\pm 5\%$ ) and are scanning electron micrographs (see Pl. 5).

59. *Gemmula (G.) plebeia* (J. de C. Sowerby), Bracklesham Bay, units S8-9. NHM PI TG 2078 (S. Tracey coll.)
60. *Gemmula (G.) plebeia* (J. de C. Sowerby), Bracklesham Bay, units S8-9. NHM PI TG 2079 (S. Tracey coll.), juvenile showing sinusigera lip of protoconch.
61. *Gemmula (G.) plebeia* Form A., Bracklesham Bay, units S8-9. NHM PI TG 2080 (S. Tracey coll.)
62. *Gemmula (G.) acutangularis* (Deshayes), Middle Lutetian, wood at Villiers-St.-Frédéric (Yvelines), France. NHM PI TG 2081 (S. Tracey coll.)
63. *Gemmula (G.) wrigleyi* sp. nov., East Selsey, unit SL1. NHM PI TG 2082 (S. Tracey coll.)
64. *Gemmula (G.) veteratoris* sp. nov., Coalmeer Gutter, bed B. NHM PI TG 2083 (S. Tracey coll.)
65. *Gemmula (G.) pastoralis* sp. nov., Coalmeer Gutter, bed B. NHM PI TG 2084 (S. Tracey coll.)
66. *Gemmula (G.) pastoralis* sp. nov., Bracklesham Bay, units S8-9 (*ex situ*), NHM PI TG 2085 (S. Tracey coll.)
67. *Gemmula (G.) traceyi* (Tucker & Le Renard), Studley Wood, unit SW1. NHM PI TG 2086 (S. Tracey coll.)
68. *Gemmula (G.) conifera* (Edwards), Coalmeer Gutter, bed B. NHM PI TG 2087 (S. Tracey coll.)



Subgenus: *Coroniopsis* MacNeil in MacNeil & Dockery, 1984.

MacNeil & Dockery, 1984: 174. Type sp. by OD *Pleurotoma tenella* Conrad, 1848; Oligocene of Mississippi, U.S.A. Range: Middle Eocene of Europe, Late Eocene to Oligocene of North America.

**Characters:** Resembling *Gemmula* (*Gemmula*) and with a similar protoconch, but apical angle moderately to very broad, subsutural ridge distinctly beaded on the first few whorls, peripheral band wide with elongate orthocline nodules degenerating on later whorls and a wide, slightly asymmetrical U-shaped sinus.

**Notes:** Pending a detailed phylogenetic study of the genus, it might be justified to include in *Gemmula* (*s.s.*) this small group of species with a wide peripheral gemmule band and beaded subsutural ridge, particularly as species exist with seemingly intermediate characters and are hard to place. However, as a suitable subgenus already exists, usage of it will serve to draw attention to the occurrence of some closely related taxa on both sides of the Atlantic during the Palaeogene.

*Coroniopsis* was originally proposed as a subgenus of *Coronia*, herein synonymised with *Gemmula* (*s.s.*). The American Oligocene species, *Gemmula* (*Coroniopsis*) *tenella* (Conrad, 1848) and *G. (C.) ancilla* (Casey, 1903), are very closely related to *Pleurotoma monerma* Edwards (Middle to Late Eocene of England). The subgenus is also considered to include *P. nodulina* Casey from the Late Eocene of Mississippi. A similar peripheral ornament occurs in *Gemmula crenulata* (Lamarck, 1804) [= *uniserialis* Deshayes] from the Middle Eocene of France, but this lacks any subsutural beading and is otherwise close to *Gemmula* (*s.s.*).

***Gemmula* (*Coroniopsis*) *monerma* (Edwards, 1861) comb. nov.**

(Pl. 4, fig. 50)

*Pleurotoma monerma* Edwards, 1861: 292, pl.32, figs.1a-c

*Eopleurotoma monerma* (Edw.); Burton, 1933: 156.

*Gemmula* sp. cf. *monerma* (Edw.); Curry, 1942: 95.

**Diagnosis** (of species): A medium-sized, broadly and variably fusiform *Gemmula* with a wide to very wide apical angle, beaded subsutural cord on the early whorls, wide peripheral band of elongate orthocline nodules which degenerates on the later whorls to a more or less smooth band with raised growth lines following the sinus, resulting in a great variety of gerontic ornament within any population.

**Types & type locality:** Lectotype (herein designated) NHM PI TG 2051 (F. E. Edwards coll.) Highcliffe, a large example, the original of Edwards' (1861) pl. 32, fig. 1b.

Paralectotype NHM PI TG 2052 (F. E. Edwards coll.) Highcliffe, a young shell, the original of Edwards' (1861) pl. 32, fig. 1a.

**Additional material:** NHM PI TG 2053 (F. C. Stinton coll.) Studley Wood, "Nummulites bed", (unit SW1) juvenile; NHM PI TG 2054 (D. Curry coll.) Afton brickyard *Rimella canalis* bed; Numerous examples from Highcliffe/Barton bed A3 in private collections.

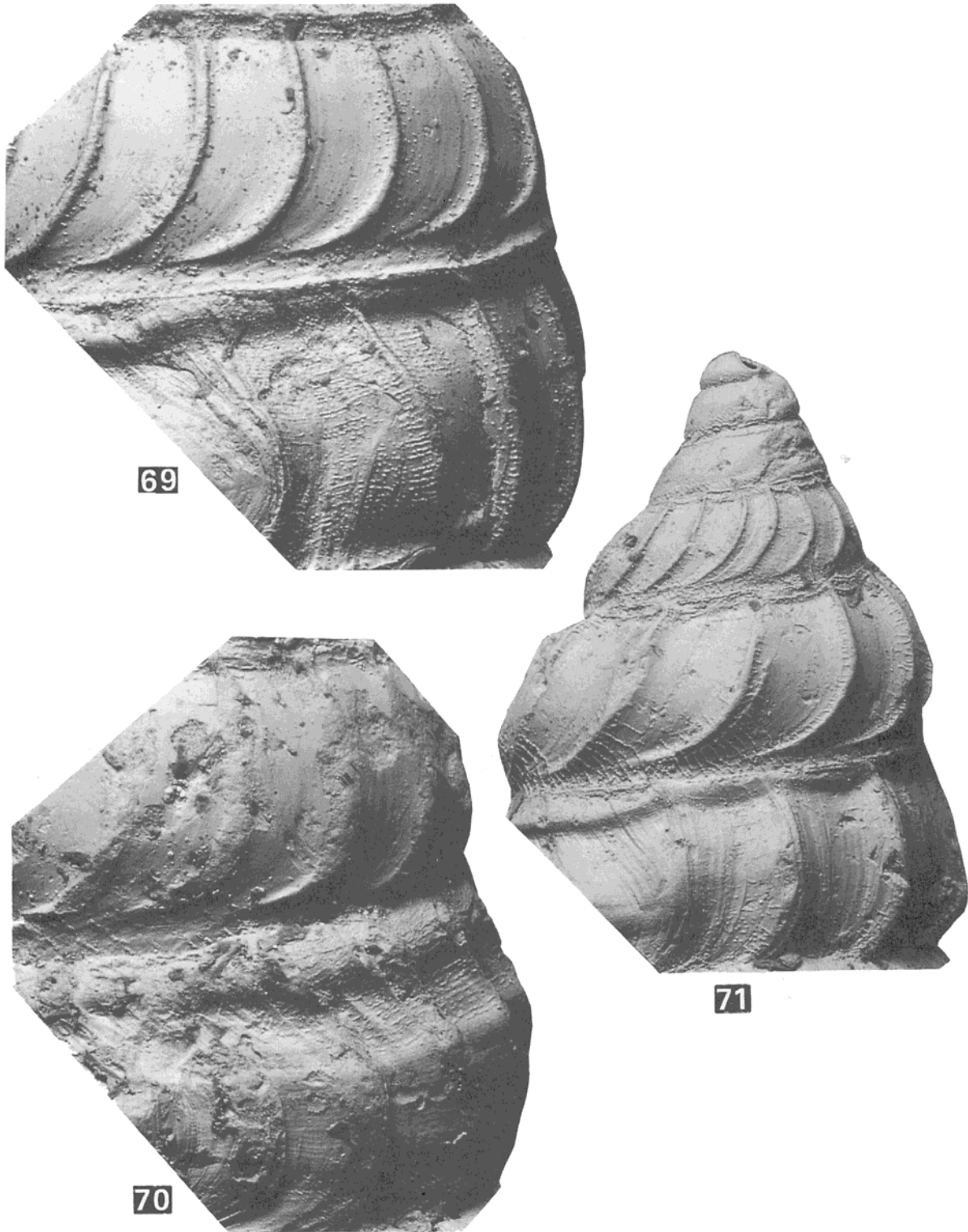
**Description** (Selsey Formation juvenile): Protoconch small, narrow, multispiral, somewhat pupoid ending in slightly more than 1 whorl of curved brephic axials. Junction with teleoconch abrupt, marked by the appearance of a beaded subsutural ridge and a peripheral band of long nodules occupying most of the whorl. Apical angle 42°. Three juvenile teleoconch whorls. Subsutural ridge prominent, becoming irregularly nodular. Ramp narrow, concave, smooth. Peripheral band wide with 18-20 bar-like nodules, truncated above and below. Sinus broadly U-shaped, as for the subgenus. Base with 5 strong spiral cords and rostrum with c.10 finer threads. Aperture ovate, smooth within.

**Size:** 7.2 x 3.1mm.

**Range:** Middle Eocene of the Hampshire Basin, England.

**Distribution:** Selsey Formation: Studley Wood unit SW1 (rare); Barton Clay Formation: Studley Wood units SW2-3 (apex not preserved); Afton brickyard *Rimella canalis* bed (common); Highcliffe bed A3 (type; very common).

**Notes:** The early teleoconch ornament is rather constant between populations from different horizons, but juveniles of the typical form from bed A3 at Highcliffe usually have a much wider apical angle than the Studley



**Plate 7. Protoconch microsculpture of *Gemmula***

All figures are scanning electron micrographs (see Pl. 5). Magnifications are approximate.

69. *Gemmula (G.) acutangularis* (Deshayes), Middle Lutetian, wood at Villiers-St.-Frédéric (Yvelines), France. NHM PI TG 2081 (S. Tracey coll.), (x 100). Detail of last protoconch whorls showing crowded spiral microstriae below periphery.
70. *Gemmula (G.) veteratoris* sp. nov., Detail of protoconch ornament. Coalmeer Gutter, bed B. NHM PI TG 2083 (S. Tracey coll.), (x 100). Detail of last protoconch whorls showing both oblique and spiral microstriae.
71. *Gemmula (G.) pastoralis* sp. nov., Bracklesham Bay, units S8-9 (*ex situ*), NHM PI TG 2085 (S. Tracey coll.), (x 80): Protoconch showing oblique microstriae on all whorls.

Wood example, and a slightly broader protoconch. On the intermediate horizon at Afton brickyard the apical angles of individuals are more variable and include forms that are comparable to that from Studley Wood. In view of this transition, and of the great variety in adult shell morphology, the Studley Wood juvenile cannot be considered clearly distinct from the typical form.

#### EXCLUDED SPECIES

##### *Gemmula (G.) jefferyi* nom. nov.

(Pl. 4, fig. 40)

*Pleurotoma callifera* Edwards, 1861: 291, pl.30, fig.9; Tucker & Le Renard, 1993: 9 [non Conrad, 1835]

**Lectotype:** (herein designated) NHM 71322b (F. E. Edwards coll.) Highcliffe, the original of Edwards' (1861) pl. 30, figs. 9a, 9b of *Pleurotoma callifera*.

**Notes:** *P. callifera*, typically from the Barton Clay Formation bed A3 at Highcliffe, was also recorded from Brook in the original description. The characteristic combination of cyrtoconoid shape in young shells, wide condensed whorls, nodulosely granulated basal cords and the strongly bifid nature of the gemmulate keel is not found on any *Gemmula* (s.s.) from the Selsey Formation, however. As the name *callifera* is a junior homonym of a different North American species, the opportunity is here taken to rename it after Paul Jeffery of the Natural History Museum, London, who has a particular interest in the Barton turrids.

##### *Gemmula (G.) moniligera* (Edwards, 1861)

(Pl. 4, fig. 39)

*Pleurotoma callifera* var. *moniligera* Edwards, 1861: 291 [in part]

*Pleurotoma callifera* var. *monilifera* Edwards, 1861: pl.30, fig.10a-b [laps.cal., non *P. monilifera* Lea, 1833]

**Lectotype:** (herein designated) NHM PI TG 2055 (F. E. Edwards coll.), from Barton, the original of Edwards (1861) pl. 30, fig. 10.

**Distribution:** Barton Clay Formation, Barton.

**Notes:** Edwards (1861: 292) included Brook as a locality for his species *callifera* and Newton (1891) specified var. *moniligera* as occurring at that locality. However, the lectotype of *moniligera* from an unspecified horizon at Barton does not agree closely with the much smaller shells from Brook, which have been described above as *G. veteratoris* sp. nov. The seemingly transitional attenuated form of some later examples of *veteratoris* suggests that this and *moniligera* are part of the same lineage. Both *callifera* (i.e. *jefferyi*) and *moniligera* are part of a species-complex at Barton sharing the characters of a bilirate apertural process and a basal ornament of spiral cords divided into small undulating flanges by rugose collabral ridges. This nodular or granular ornament contrasts with the smoother basal cords of related *Gemmula* in the Selsey Formation.

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Nomenclature herein has been greatly aided by two catalogues which give comprehensive documentation of published turrid species-group names: those of the north-west European Palaeogene (Tucker & Le Renard, 1993) and of the world, fossil and Recent (Tucker, in press).

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