EVOLUTIONARY MORPHOLOGY OF OBLIQUE RIBS OF BIVALVES

by ANTONIO G. CHECA *and* ANTONIO P. JIMÉNEZ-JIMÉNEZ

ABSTRACT. Fossil bivalves bearing oblique ribs first appeared in the Mid Ordovician but their diversity remained low during the Palaeozoic. The diversity soon increased after the Early Triassic, peaking in the Early Cretaceous. The Palaeozoic–Mesozoic record is dominated by burrowing bivalves (mainly pholadomyoids and trigonioids), which developed oblique ribs with symmetric profiles, probably adapted for shell reinforcement, although there are indications that the ribs of trigonioids also enhanced burrowing efficiency. After the Paleocene, the main groups of burrowing bivalves were veneroids (primarily tellinoideans and lucinoideans) and nuculoids, which generated oblique ribs of the shingled type, adapted to increase burrowing efficiency. The inferred change in function at the Mesozoic/Cenozoic boundary can be correlated with an increase in mean mobility of the bivalve faunas bearing oblique ribs through time. This implies a major ecological cause for the observed temporal patterns, which forced bivalve faunas to burrow more rapidly and efficiently. In particular, either the Phanerozoic increase in the diversity of durophagous predators or the accelerating rate of sediment reworking (both being a consequence of the Mesozoic Marine Revolution), or both, could have provided the necessary evolutionary force.

KEY WORDS: functional morphology, evolutionary morphology, diversity, macroevolution, Mesozoic Marine Revolution, oblique ribs, bivalves.

MOST rib patterns in bivalves are of the commarginal (often called concentric) or radial (longitudinal) type. The former are secreted periodically by extrusion of the entire mantle margin, while the latter are secreted continuously by specialized areas distributed intermittently along the mantle margin. A third, less common pattern is the oblique (Seilacher 1972) or discordant (Stanley 1969) type, in which ribs migrate along the margin with growth. Several varieties can be differentiated according to whether there are one (single) or more (divaricate) branches, whether ribs maintain a constant angle to the growth lines, and whether they are composed of discrete elements (Text-fig. 1). A total of 176 living species displaying such patterns has been recognized, with tellinoideans, unionoideans and veneroideans being the most speciose (Checa 2002). Antimarginal ribs of the Ostreoidea and Plicatuloidea remain perpendicular to the shell margin during growth and can be classified as oblique. They are produced because the bivalve mantle margin grows allometrically, and the extra length adjusts by producing folds (Checa and Jiménez-Jiménez 1999; pers. obs. 2002). Therefore, they are morphogenetically unrelated to other types of ribs, including oblique ribs. Accordingly, they are excluded from the present paper.

From the standpoint of their function, oblique ribs in bivalves are usually assumed to perform a burrowing-related function (Stanley 1969, 1970; Seilacher 1972, 1973). Seilacher (1972), in applying the paradigmatic method (Rudwick 1964), found three essential requirements for this function: (1) orientation transverse to the burrowing direction (cross orientation); (2) asymmetric cross section, such that they show a gentle slope in the burrowing direction and a steep, sometimes inverted slope in the opposite direction (frictional asymmetry); and (3) constant size, so as to maintain a certain correspondence to grain size, which is usually achieved by allometric densing (i.e. introduction of new ribs). A fourth feature is perimeter smoothing, by which ribs are subdued at the zone of maximum cross-sectional area. As pointed out by Seilacher (1972) these highly functional patterns display little variability among specimens. Terrace-shaped sculptures closely approaching the functional paradigm for burrowing have also been found in other invertebrate groups (Seilacher 1961, 1972; Schmalfuss 1978*a*, *b*; Savazzi 1981, 1989; Signor 1983; Stanley 1988).

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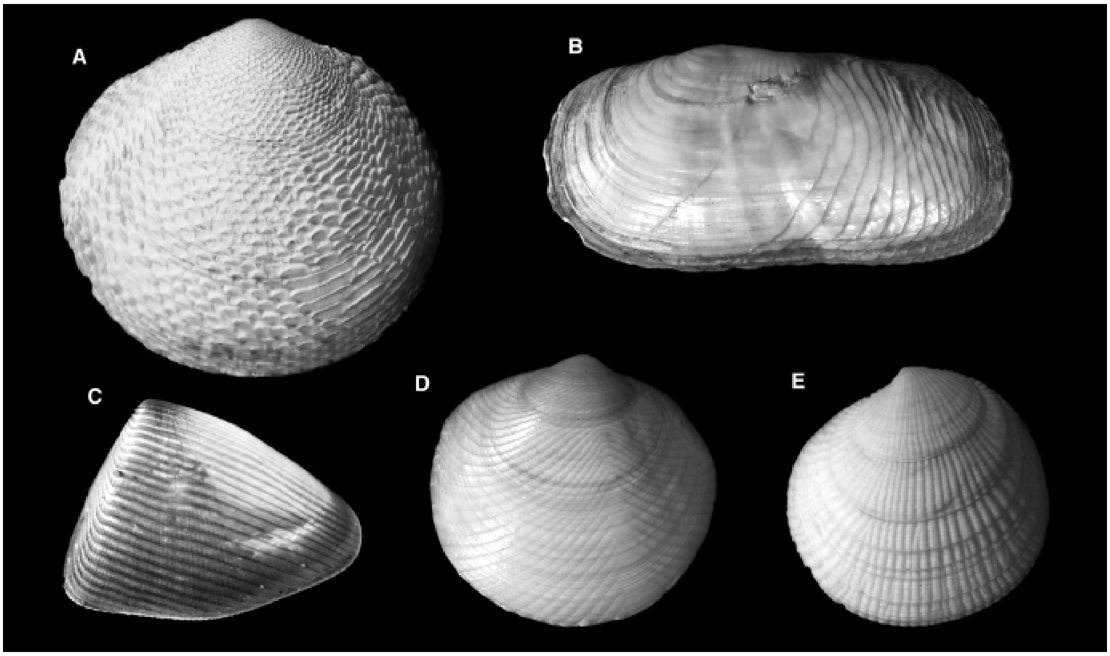


TEXT-FIG. 1. Varieties of oblique ribs in Recent bivalves. A, *Tellina scobinata*, MNHN (unreg.), loc. unknown, right valve; oblique ribs are composed of scaly elements which alternate among growth episodes; ×1. B, *Solecurtus philippinensis*, MNCN 15.07/4768, Philippines (loc. unknown), left valve; ribs are divaricate, with an axis of divergence subtended from the umbo to the posterior margin; ×1. C, *Donax madagascariensis*, EPUGR.BV.207, Durban, South Africa, left valve; straight ribs initiate as commarginal and acquire increasing angles to the margin with growth; ×2. D, *Divalucina cumingi*, MNHN (unreg.), south coast of Natal, South Africa, right valve; the axis of divergence of divaricate ribs runs from the umbo to the anterior ventral margin; ×1·5. E, *Ctena bella*, EPUGR.BV.200, western Australia (loc. unknown), left valve; ribs are radial in the posterior and central shell areas, but approximately transverse to the margin in the anterior area; ×1·7. Ribs are shingled in B and D, scaly in A, and with rounded profiles in C and E.

Checa (1993) noted that the margin of species living deep in the sediment usually becomes jagged during periods of intensive burrowing. This was corroborated in *Solecurtus strigilatus* obliged to burrow in experimentation tanks, with the particular characteristic that radial fissures produced at the margin of the reduced thin shell of this species are soon intercepted by oblique ribs and deflected towards the shell edge (Checa 1993, fig. 6). In this way, oblique ribs may function to minimize the damage caused to the shell during active burrowing.

Oblique ribs not conforming to the burrowing paradigm also appear in many living and fossil bivalves (the nuculoid *Acila*, many Unionoida and Trigonioida). In these cases ribs have symmetrical profiles and are oriented at oblique angles to the growth direction. Their function is not clear and may also serve as shell reinforcement (Seilacher 1972) against predators or sediment pressure, or to lock the bivalve within the sediment, thus avoiding exhumation by currents (in the way proposed for shallow burrowing species by Stanley 1981) or bioturbators.

Stanley (1981) and Savazzi (1982, 1983) showed experimentally that the longitudinal ribs of several cardiids and one arcid also act to reduce the number of burrowing sequences required to complete burrowing. Similar results were found for the concentric asymmetric ridges of the venerid *Anomalocardia brasiliana* (Stanley 1981) and for the concentric and the oblique nodose ornament of some fossil Trigoniidae (Stanley 1977, 1978). It might appear that shell-rib ornaments, regardless of their distribution and profile, assist burrowing, but this conclusion is not of general validity since Stanley (1981) also found that the concentric elevated ridges of *Chione cancellata* increase the number of required burrowing sequences.

Oblique ribbing is also found in Recent and fossil epibenthic bivalves (see below), in which functions other than burrowing assistance have to be proposed, including shell reinforcement, predation deterrence, scour reduction, fouling prevention, and camouflage.

Functional inferences concerning oblique ribbing in bivalves have been restricted to selected examples of mostly living species, but no historical review has been made on the kinds of ribs that have developed. The aim of this paper is to trace the Phanerozoic patterns of change both in diversity of oblique-ribbed bivalves and in morphology of such ribs in order to infer temporal changes, and to determine the causes of such patterns.

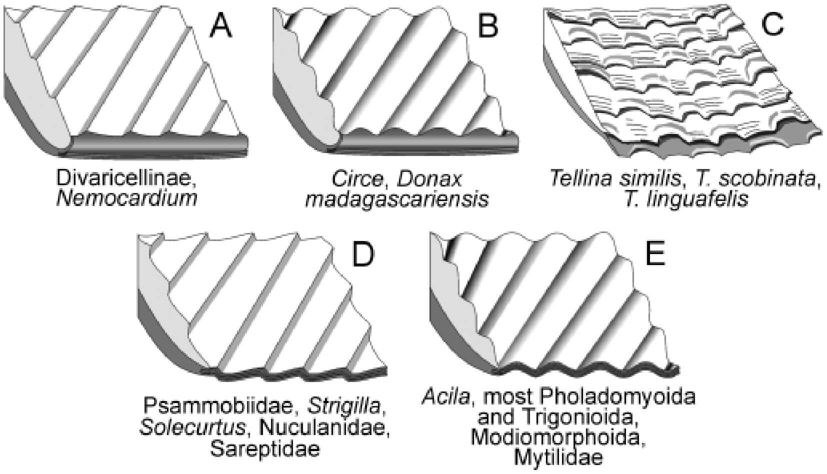
MATERIAL AND METHODS

The basis of this paper is to record, as completely as possible, the number of fossil species with oblique ribs, in order to trace their evolutionary history. Data on fossil specimens have been acquired from both the literature and fossil collections. The first task has a major disadvantage, since papers or books containing fossil bivalves cannot be searched in the corresponding databases using key words such as 'divaricate ribs' or 'oblique ribs'. We had, therefore, to bulk-scan as many journals as possible. In this way, some 35 journals and an undetermined number of reprints and monographs have been checked. Complementary data were obtained from fossil and Recent specimens housed in the collections of the following institutions: Departamento de Estratigrafía y Paleontología, Universidad de Granada (labelled EPUGR); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Geologisch-paläontologisches Institut, Philipps Universität Marburg (GPIUM); Staatliches Museum für Naturkunde Stuttgart (SMNS); and Muséum National d'Histoire Naturelle de Paris (MNHN). Recent species without a known fossil record, and figured specimens with imprecise stratigraphic reference have been excluded from the database. In this way, a set of 189 Ordovician–Holocene fossil species with oblique ribs has been assembled. We are, nonetheless, aware that our database is far from complete, particularly with regard to some groups. For example, an exhaustive review of South American trigoniids described to date (e.g. Pérez and Reyes 1991) is lacking. Also, there may be other undetected inoceramids with oblique ribs. Savazzi (1985) mentioned Eocene fossils of the cardiid subgenus *Discors* with oblique ribs, which we have not recorded. The resulting diversity diagrams have, therefore, to be regarded as merely indicative.

ASPECTS OF THE FABRICATION OF OBLIQUE RIBS

Contrary to previous theoretical models, which invoke processes of reaction-diffusion of morphogens, Checa (2002) attributed the formation of oblique ribs to elaborate behavioural patterns of the mantle (fabricational strategies). The mantle epithelium is assumed to be sensitive enough (via mechanoreceptors) to detect the position of the formerly secreted ribs, and capable of such a complex behaviour as to align the new growth increments in the appropriate directions (contact-guidance growth). Within this general model, there are two main types. In forms with *strict contact guidance* the shell margin is strongly reflected, which implies that the mantle is able to project far enough onto the outer shell surface so as to feel the already-formed relief of the outer surface of the shell. The sensitive mantle is able to record this information and to align new growth increments of the ribs in the appropriate directions (Text-fig. 2A–B). Exceptions are shells such as those of *Tellina scobinata* (Text-fig. 1A) or *T. linguafelis*, which develop a typical rasp-like ornament. The mantle can perceive scales and interscales, even though the growth front is acute (Text-fig. 2C). With few exceptions, Recent bivalves displaying such fabricational patterns construct ribs of the shingled type, adapted for higher burrowing efficiency.

Bivalves with *reduced contact guidance plus constant lateral shift* usually have an acute shell margin and the mantle cannot reach the outer shell surface (Text-fig. 2D–E). In these shells, rib undulations are impressed on the inner shell surface only towards the very margin, so that the information available to the mantle is reduced. During rib construction the mantle extrudes slightly beyond the shell-edge and then shifts laterally a certain amount. Typically, ribs accelerate their lateral displacement during periods of



TEXT-FIG. 2. Constructional patterns of oblique ribs, with examples of fossil and Recent bivalves to which they can be attributed. A–B, the mantle reflects at the margin and has updated information on the relief present on the shell surface; it is later able to align the new growth increments of the ribs in the correct direction. C, the non-reflecting mantle provides complete information, since the outer surface relief is also imprinted on the inner surface. D–E, the mantle does not reflect at the margin and the information available is reduced; at every growth increment the mantle simply moves laterally by a certain amount.

reduced shell growth. Bivalves displaying this pattern are able to construct both shingled and gorged ribs. This pattern predominates over the previous one in both Recent and fossil bivalves.

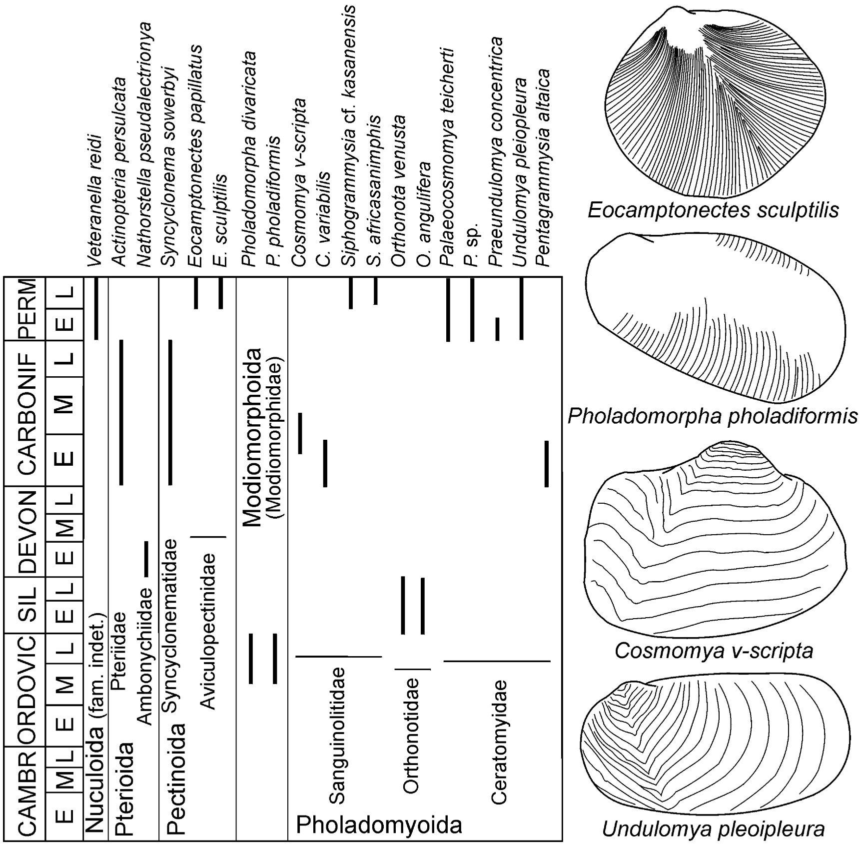
From the morphogenetic standpoint and mantle structure, oblique ribs are related to commarginal ribs and both differ from other types, such as radial or antimarginal oyster-like ribs.

THE FOSSIL RECORD OF OBLIQUE RIBS

Palaeozoic (Text-fig. 3). Divaricate ribbing in bivalves had already appeared by the Mid Ordovician with species of the epibenthic genus *Pholadomorpha*, which were replaced in the Silurian by other endobenthic and epibenthic bivalves of different families. The Palaeozoic diversity peaked in the Late Permian and, taxonomically, the order contributing the most to diversity was the Pholadomyoida. Morphological patterns became varied in the Palaeozoic, with the presence of both divergent and V-shaped ribs. A total of 19 species has been recorded, with a primacy of endobenthic forms (63 per cent).

Mesozoic (Text-fig. 4). Oblique-ribbed forms were absent from the beginning of the Mesozoic until the late Mid Triassic. The Triassic record is sparse and from then on the diversity rose progressively to attain a maximum in the Late Jurassic and Early Cretaceous, owing to the essential contribution of two groups: Trigonioida and Pholadomyoida. Pectinoids constituted a third, far smaller, group. Trigonioids clearly dominated during the Cretaceous Period and exhibited the most diverse array of oblique patterns, showing both single and divaricate ribs (sometimes highly complex, e.g. *Vaugonia literata*). Pholadomyoids, the dominant group during the Mid–Late Jurassic, generated a more restricted morphological range of divaricate ribs. The Mesozoic proportion of endobenthic forms (84·6 per cent) increased compared to the Palaeozoic, although Fisher's exact test for small samples indicates that the difference is at the limit of significance (conditional p-value = 0·0516).

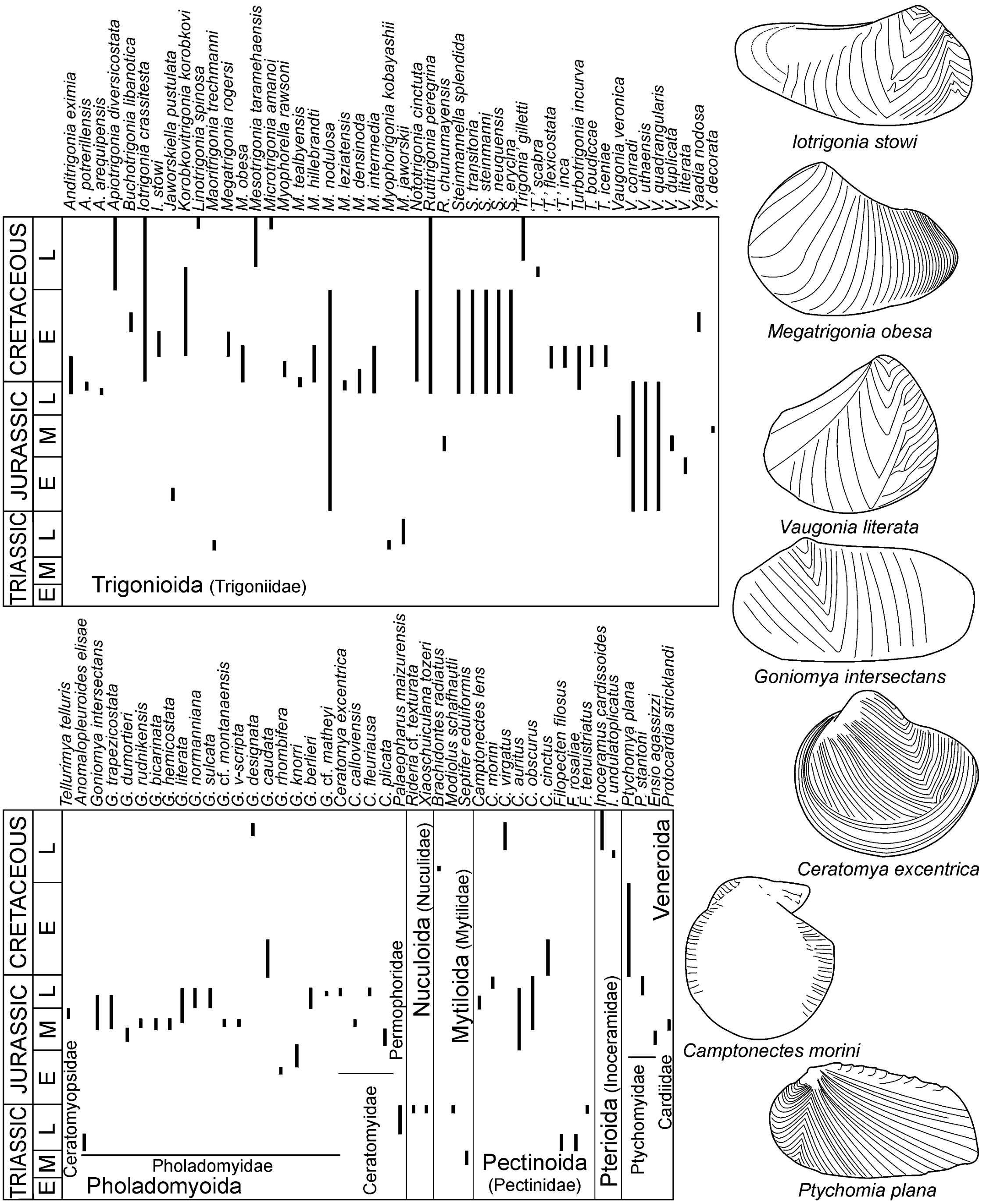
Cenozoic (Text-fig. 5). We have found no Paleocene record of bivalves with oblique ribs. From the Eocene to the Miocene the diversity rose steadily to a maximum in the Burdigalian and then dropped slightly, reaching a Phanerozoic peak in the Quaternary. The three dominant groups (Veneroida, Nuculoida and, to



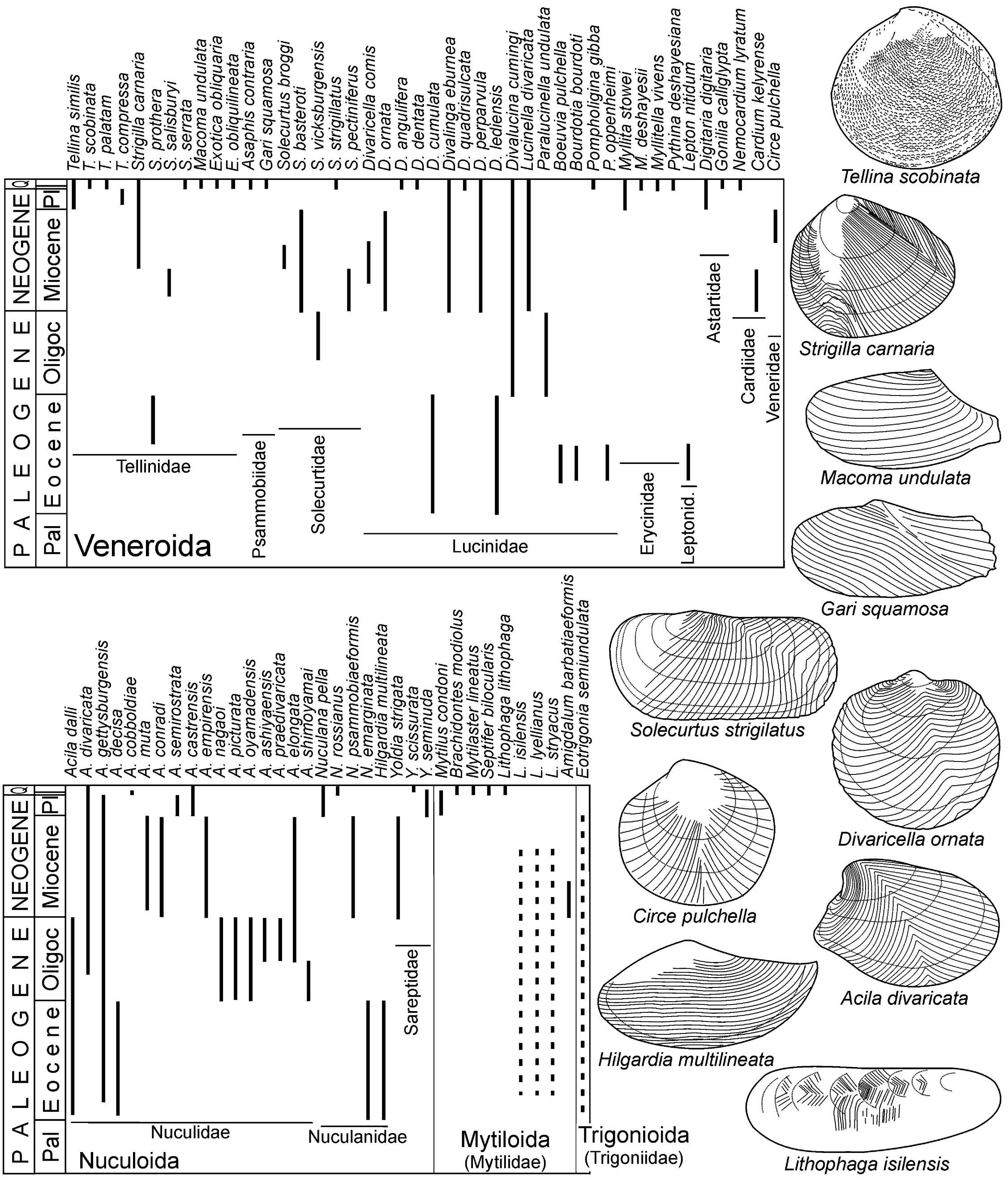
TEXT-FIG. 3. Stratigraphic distribution of Palaeozoic bivalves with oblique ribs and sketches of some representative forms. Taxonomy after Cox *et al.* (1969), with modifications after Morris *et al.* (1991), Skelton and Benton (1993), Beesley *et al.* (1998) and Amler (1999).

a lesser extent, Mytiloida) were residual during the Mesozoic. An enormous variety of oblique patterns emerged, including single, straight, divaricate, antimarginal and the strange rasp-like ornament of some species of *Tellina* (Text-fig. 1A). The proportion of endobenthic species (88·6 per cent) significantly surpassed that of the Palaeozoic (Fisher's exact p-value = 0·0133), but not that of the Mesozoic (p = 0·4939).

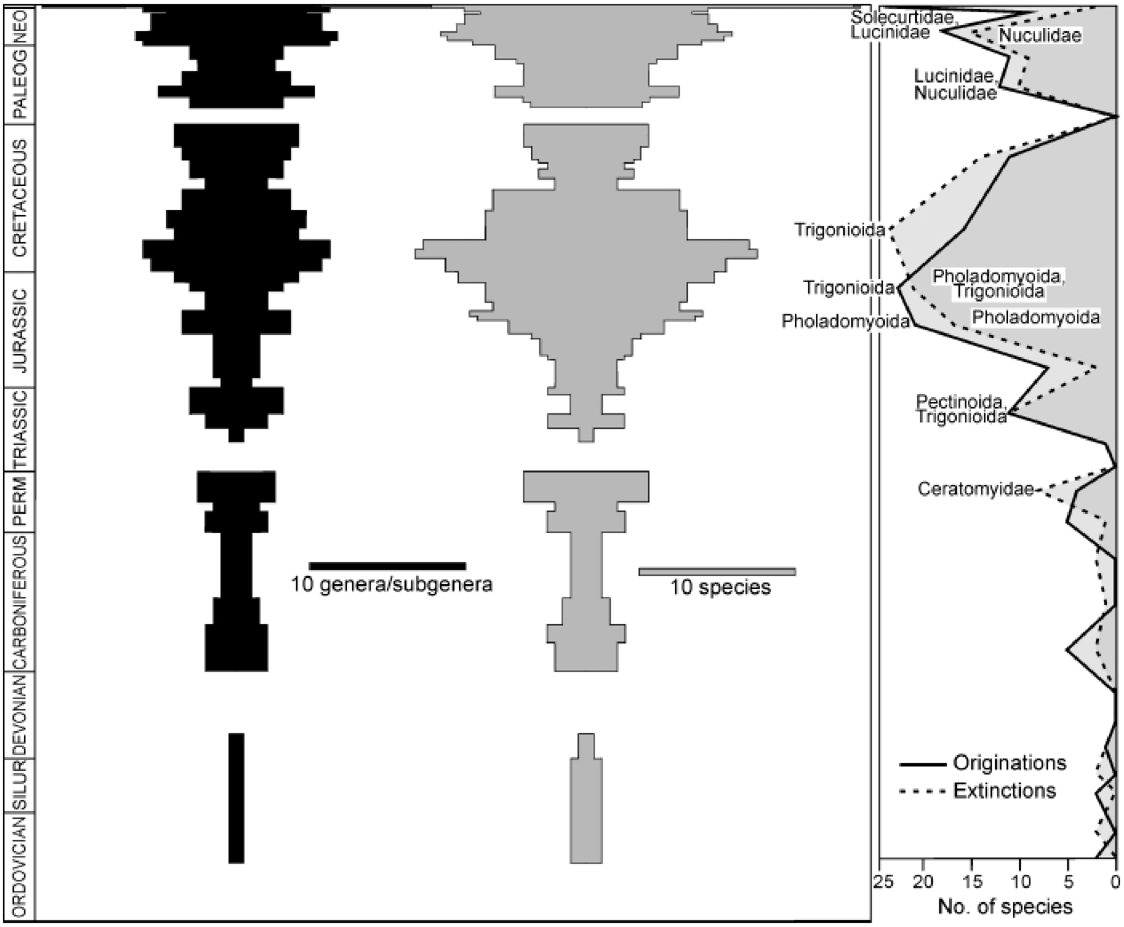
The Phanerozoic diversity curves (Text-fig. 6). Given the vagaries inherent to the survey methods, we have also drawn a genus/subgenus-diversity curve. This and the species-diversity curve show features in common. Both curves reveal gaps (already commented on) in the Mid–Late Devonian, Early–early Mid Triassic and Paleocene, and relative diversity peaks in the Late Permian, Early Cretaceous, Early Miocene and Quaternary. This last diversity value may be biased with respect to the previous record because of the existence of several well-illustrated monographic studies on fossil bivalves of this age (e.g. Moore 1983, 1988) and our own records. A similar situation applies to the Recent (176 species; Checa 2002) and fossil Quaternary (37 species) records, but also preservational reasons can be invoked here. The curve of originations/extinctions of species per epoch is also shown in Text-figure 6, with indications of the main groups involved in O/E maxima. In general it matches the species diversity curve, with higher O/E (turnover) values coinciding with diversity peaks. The pholadomyoid Ceratomyidae were involved in the only marked Palaeozoic extinction peak (Late Permian). As expected, the Trigonioida and Pholadomyoida



TEXT-FIG. 4. Stratigraphic distribution of Mesozoic bivalves with oblique ribs and sketches of some representative forms. Taxonomy after Cox *et al.* (1969), with modifications after Skelton and Benton (1993), Beesley *et al.* (1998) and Amler (1999).



TEXT-FIG. 5. Stratigraphic distribution of Cenozoic bivalves with oblique ribs and sketches of some representative forms. Taxonomy after Beesley *et al.* (1998). Broken line indicates uncertain range (species not included in the diversity diagram, Text-fig. 6).

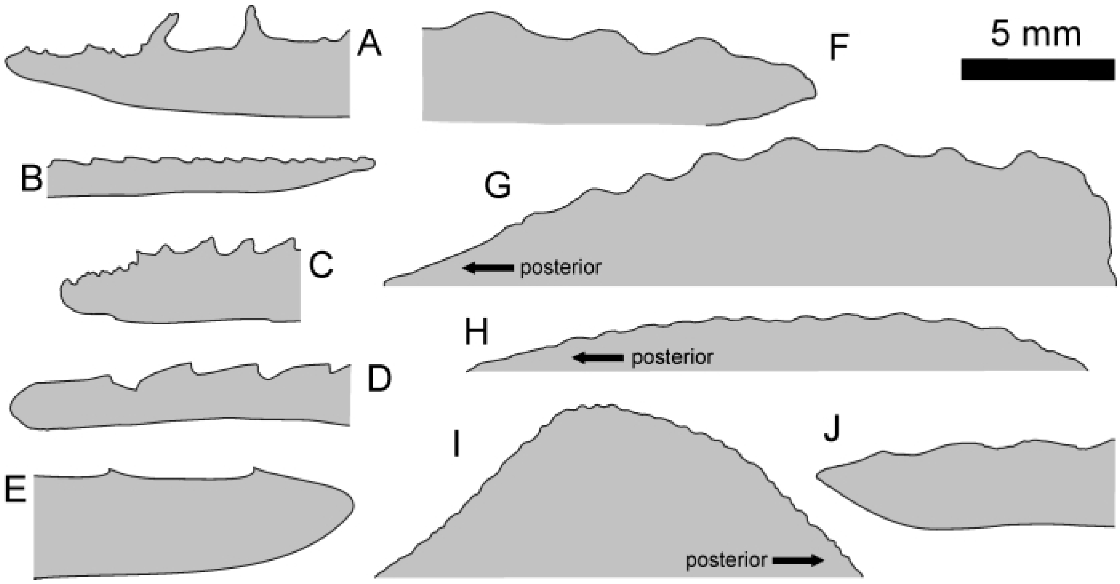


TEXT-FIG. 6. Curves for genus/subgenus and species diversity of marine bivalves having oblique ribs (left) as well as for species origination/extinction per epoch (right), with indications of the main groups involved in the major peaks.

provided most Mesozoic O/E peaks, with the exception of the Mid Triassic peak, which includes the Pectinoida. In the same way the Cenozoic O/E peaks concerned families of the Veneroida and the Nuculoida.

CHANGES IN PROFILE OF OBLIQUE RIBS AND OF THEIR ASSOCIATED FUNCTIONS OVER TIME

Except for a few cases in which illustrations do not provide evidence of rib profiles (e.g. the Palaeozoic nuculoid *Veteranella reidi*), one of the most apparent features of the record of oblique ribs is the almost complete absence of shingled ribs prior to the Cenozoic. Exceptions are the two Mesozoic species of the veneroid *Ptychomia* (see sketch in Text-fig. 4), in which the forward-directed set of ribs has an asymmetric profile (although with the steeper slope facing in the direction of burial). Stanley (1977, p. 883) reported oblique asymmetric sculptures in the anterior area of three trigoniid species; only in the case of *Psilotrigonia beesleyana* (see e.g. Stanley 1977, pl. 118, fig. 8) are anterior oblique ribs apparently of the shingled type. Out of these exceptions all recorded Trigonioida developed complex patterns of symmetric oblique ribs (Text-fig. 7F–G), sometimes consisting of aligned nodes. This does not signify

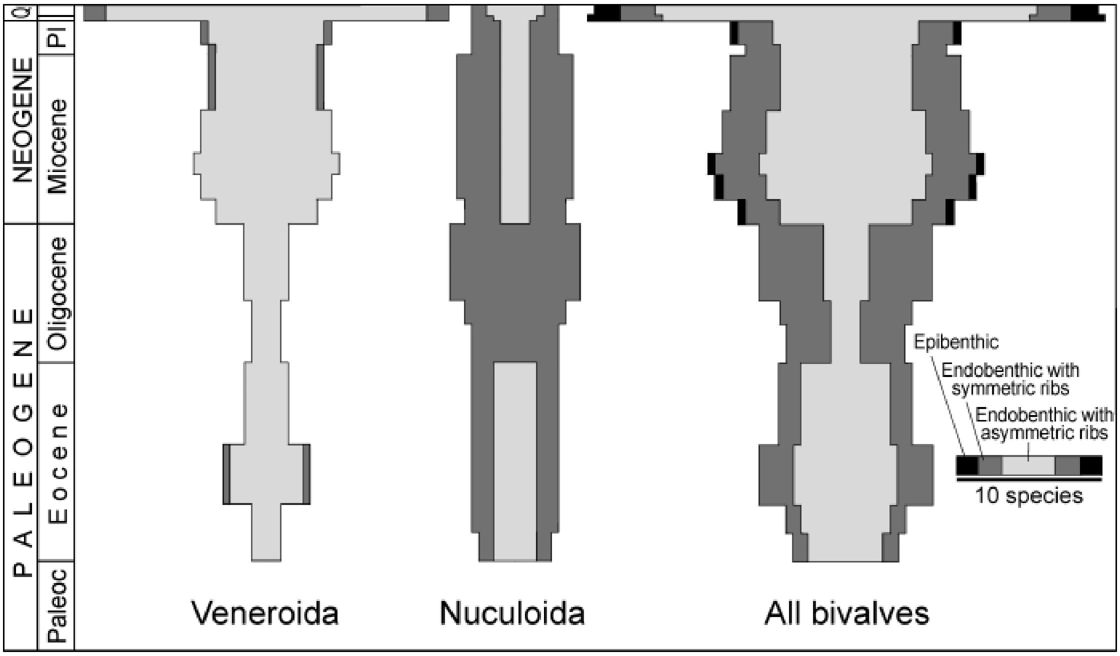


TEXT-FIG. 7. Transverse sections of fossil and Recent bivalves with shingled (A–E) and gorged (F–H, J) ribs. A, *Tellina scobinata*, EPUGR.BV.213, Recent, Bushy Island, Australia. B, *Gari* sp., GPIUM (unreg.), Recent, loc. unknown. C, *Gari maculosa*, MNCN 15.07/0005, Cebú, Philippines. D, *Divalucina quadrisulcata*, EPUGR.BV.95, Isla Mujeres, México. E, *Nemocardium lyratum*, EPUGR.BV.206, Laminusa Island, Philippines. F, *Trigonia subtriangularis*, GPIUM B70, Upper Bajocian–Bathonian?, Bielefeld, Germany. G, *Myophorella navis*, GPIUM B68, Lower Aalenian, Elsass, Germany, left valve, anteroposterior section through the left valve. H, *Goniomya v-scripta*, SMNS (unreg.), Lower Aalenian, Teufelsloch bei Boll, Germany, antero-posterior section through the right valve. I, *Ceratomya plicata*, EPUGR (unreg.), Lower Aalenian, Campillo de Arenas, Jaén, Spain, anteroposterior section through the left valve. J, *Acila* sp., MNHN (unreg.), Recent, Philippines (loc. unknown).

that these ornaments were non-functional in burrowing, given that Stanley (1977) demonstrated experimentally that they increased burrowing depth (for a given number of digging cycles) in two species of Trigoniidae, one of them (*Yaadia nodosa*) with oblique nodose ribs. Nevertheless, the prominent ornamentation and thick valves of trigoniids suggest that their oblique ribs could have resulted from a functional compromise with a shell-reinforcement function. From our data, the second most important Mesozoic group, the Pholadomyoida, had invariably symmetric ribs (Text-fig. 7H–I).

The shingled ribs first appeared in the Eocene with some members of the lucinid Divaricellinae (see examples in Text-fig. 7A–E). A record of the Cenozoic diversity of forms with asymmetric (shingled) and symmetric ribs is shown in Text-figure 8. With the exception of the Oligocene, species with shingled ribs dominated the Cenozoic record, this being particularly true for the Quaternary. The scenario varies clearly for the two main orders of burrowing bivalves. Most Veneroida had shingled ribs, the only exceptions being *Lepton nitidum, Digitaria digitaria, Gonilia calliglypta* and *Circe pulchella*. Within Nuculoida, symmetrically ribbed forms were dominant, but with a sharp distinction at the family level, as all nuculids had symmetric ribs (Text-fig. 7J), whereas nuculanids and sareptids bore shingled ribs.

During the Palaeozoic and Mesozoic, many divaricate ribs of burrowing bivalves had a dorsoventral divergence axis and formed acute angles (Text-figs 3–4). Additionally, the branch running anteriorly is the least developed. Cenozoic forms developing shingled ribs adapted for burrowing, such as many tellinoideans and lucinoideans, have obtuse divergence angles (Text-figs 1, 5). When the divergence axis has an anterior trend (Divaricellinae, or the tellinid *Strigilla*; Text-fig. 5) both branches co-operate in the rocking movement used by the bivalve during burrowing (Stanley 1969). Divergence axes running posteriorwards (*Solecurtus*; Text-fig. 5) permit ribs running ventralwards to acquire a great development



TEXT-FIG. 8. Cenozoic diversity curves for oblique-ribbed bivalves, with indication of epibenthic bivalves and endobenthic bivalves with symmetric (non-shingled) and asymmetric (shingled) ribs.

and to orient transversal to the burrowing direction. In other cases (nuculanids, sareptids, psammobiids, *Nemocardium* and some tellinids) most of the shell (the central and anterior areas) is covered by anteroventrally running ribs, thus oriented at a high angle to the burrowing direction (see also Stanley 1969; Seilacher 1972).

From the above observations we conclude that many Cenozoic burrowing bivalves had oblique ribs with morphological traits adapted to burrowing. Except for rare instances in the Thigonioida, this was never clearly the case with Palaeozoic and Mesozoic bivalves. Therefore, the function of oblique ribs appears to have changed at the Mesozoic/Cenozoic boundary.

MOBILITY OF BIVALVE FAUNAS

An informative approach to the problem of the functional change at the Mesozoic/Cenozoic boundary is the examination of the characteristics of the faunas with oblique ribs in different eras. The dominant Palaeozoic group of burrowing bivalves was the Pholadomyoida. The living pholadomyid *Pholadomya candida* is a sluggish burrower (Morton 1980). According to Prezant (1998), all living Pholadomyoidea are sedentary and probably unable to burrow if disinterred. Sluggish burrowing to sedentarism has been reported for other thin-shelled anomalodesmatans (e.g. Laternulidae: Morton 1976; Savazzi 1990), although there is evidence that *Laternula* and *Myadora* can burrow efficiently (E. Harper, pers. comm. 2000). Many of these anomalodesmatans have valves that usually gape posteriorly and sometimes also anteriorly, being therefore comparable to Palaeozoic and Mesozoic Pholadomyoida. Ovate-shaped Palaeozoic pholadomyoids (e.g. sanguinolitids) also developed posterior shell gapes, which indicate a similar sedentary endobenthic mode of life (e.g. Morris *et al.* 1991). Little is known about the life habits of these Palaeozoic forms but, judging from their modern counterparts and from morphological features, we deduce that most must have been medium to deep endobenthic forms (see Runnegar 1974). The only detected nuculoid species with oblique ribs was probably similar in life habits to Recent nuculoids: shallow endobenthic and relatively mobile (e.g. Stanley 1970; Reid 1998).

The two dominant Mesozoic groups were the trigonioids and the pholadomyoids. The life habits of most Mesozoic pholadomyoids were probably very similar to those of their Recent counterparts, that is, deep endobenthic and very slow burrowers (see above). According to Runnegar (1974) the Ceratomyidae, in having rounded, non-gaping shells and shallow pallial sinuses, were probably shallow to medium burrowers. This author also interpreted the shift of umbones in the posterior direction during the evolution of anomalodesmatans (e.g. compare *Undulomya pleiopleura* in Text-fig. 3 with *Goniomya intersectans* in Text-fig. 4) as an increase in the size of the foot and a change in the position of the pedal gape from ventral to anterior; this implies that post-Palaeozoic pholadomyoids were better burrowers than their Palaeozoic relatives. Regarding Trigonioida, the only extant genus (*Neotrigonia*) is an active burrower, with a large foot (Macpherson and Gabriel 1962; Gould 1969; Stanley 1977, 1978). This was probably not the case of many Mesozoic trigonioids, which had thick to very thick shells and were heavily ornamented. The Mesozoic Trigonioida were shallow burrowing forms and are assumed to have had levels of burrowing activity similar to those of Recent cardiids (‘the cockles of the Mesozoic’; Stanley 1977). Mesozoic nuculoids were probably also active and shallow deposit feeders. Little is known about the life habits of Mesozoic veneroids. *Ptychomya* is a compressed, elongated and thick-shelled form, probably also an active burrower. Finally, the only cardiid should be compared to Recent members of the family, which are active and shallow burrowers.

The two dominant groups of Cenozoic bivalves with oblique ribs were veneroids and nuculoids. In general, both are highly active burrowers. Both tellinids and psammobiids are deposit feeders (but see Pohlo 1972), which lie on their left valve deep within the substratum. Given their dietary habits, they are, in general, very active burrowers and, together with nuculoideans, important sediment remobilizers (Thayer 1983). Burrowing rate data provided by Stanley (1970) indicate that, despite the great range of values within the tellinaceans, some species are among the most active bivalves. The only three species with oblique ribs reported by Stanley (*Tellina similis*, *Strigilla carnaria* and *S. mirabilis*) are among the four fastest-burrowing tellinoideans. The Solecurtidae are filter-feeding tellinoideans, which are capable of very rapid deep burrowing (Bromley and Asgaard 1990; A. Checa, pers. obs. 1992). Lucinoideans are slow to very slow deep burrowers. Notably, the only Divaricellinae measured by Stanley (1970) also happened to be the fastest burrower among lucinoideans. Other veneroidean families listed in Text-figure 5 (erycinids, leptonids, astartids, venerids and cardiids) have a well-developed foot, which indicates an ability to burrow. Stanley (1970) provided numerical data only for cardiids. Nuculoids are the second most important Cenozoic group bearing oblique ribs. Two families developed oblique (shingled) ribs in the Cenozoic for the first time: Nuculanidae and Sareptidae. At least for the latter, Stanley’s measurements and comments indicate much higher burrowing rates than for the Nuculidae.

A summary of the mobility of faunas with oblique ribs at the ordinal level is provided in Table 1. The main conclusion which can be derived is that the average burrowing rate increased throughout the successive eras. The very slow Pholadomyoida constituted 58 per cent of the total number of species and 92 per cent of the endobenthic species during the Palaeozoic. The highest proportion of Mesozoic species corresponds to Trigonioida (62 per cent of endobenthic species), followed by the Pholadomyoida (30 per cent). Among the Cenozoic faunas, there was a great range of burrowing rates, from the very fast tellinoideans or sareptids to the slow lucinoideans. The group of very fast burrowers (tellinoideans + nuculanids + sareptids) amounted to 37 per cent of endobenthic species. In conclusion, oblique ribs adapted for burrowing evolved in coordination with an increasing mobility of bivalve faunas.

CAUSES

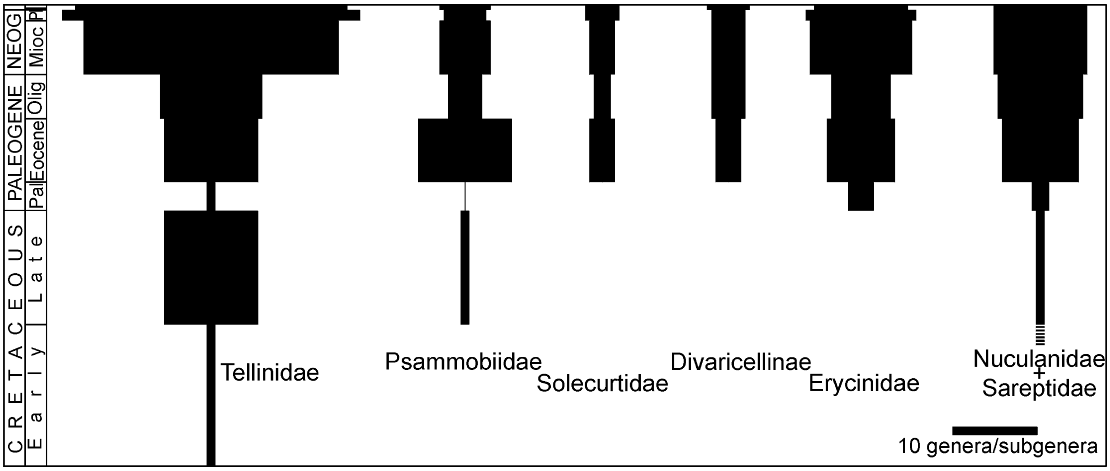
The Cenozoic increase in mobility resulted clearly from the expansion of detritus feeders: nuculoideans (although nuculanids and sareptids can also filter-feed; e.g. Reid 1998) and tellinoideans (excluding the Solecurtidae). This cannot have been the only cause for the Eocene expansion of bivalves with shingled oblique ribs, since most groups of detritus feeders had origins well before then (e.g. Skelton and Benton 1993). Nuculoids constituted an essential component of benthic faunas since the Late

TABLE 1. Ordinal composition of bivalve faunas with oblique ribs in the Phanerozoic eras, with an indication of the number of species per order, their general mode of life and mean inferred burrowing rates; see text for details. Descriptive terms for burrowing rates adopted from Stanley (1970, table 4).

Order (number of species with oblique ribs)	Mode of life	Burrowing rate
PALAEOZOIC		
Pholadomyoida (11)	Medium to deep endobenthic	Very slow
Pectinoida (3)	Epibenthic	
Modiomorphoida (2)	Epibenthic	
Pterioida (2)	Epibenthic	
Nuculoida (1)	Shallow endobenthic	Moderately rapid
MESOZOIC		
Trigonioida (47)	Shallow endobenthic	Slow to rapid
Pholadomyoida (24)	Shallow to deep endobenthic	Very slow
Pectinoida (9)	Epibenthic	
Veneroida (4)	Shallow to medium endobenthic	Slow to rapid
Mytiloida (3)	Epibenthic	
Nuculoida (2)	Shallow endobenthic	Moderately rapid
Pterioida (2)	Epibenthic	
CENOZOIC		
Veneroida (44)	Shallow to deep endobenthic	Slow to very rapid
Nuculoida (25)	Shallow endobenthic	Moderately to very rapid
Mytiloida (9)	Epibenthic	
Trigonioida (1)	Shallow endobenthic	Rapid

Cambrian, but, with the exception of Permian (*Veteranella reidi*) and Mesozoic (E. Savazzi, pers. comm. 2002) occurrences, it was not until the Eocene that they formed oblique ribs abundantly (of both the symmetric and shingled type). Something similar occurred at family level, since nuculids, nuculanids and sareptids appeared much earlier than the first corresponding oblique-ribbed form (Givetian, Late Cretaceous? and Maastrichtian, respectively; Carter 1990; Skelton and Benton 1993). The same applies to tellinoidean families, with tellinids, psammobiids and solecurtids appearing in the Hauterivian, Danian and Campanian, respectively. The case of the chemosymbiontic Lucinidae, which originated in the Wenlock, is also notable. With the exception of erycinids, the rest of the families of suspension-feeding Cenozoic bivalves mentioned in Text-figure 5 also had pre-Cenozoic origins (see data in Skelton and Benton 1993).

The fact that different bivalve families concomitantly developed oblique ribs of the shingled type argues for a cause that should have affected the bivalve faunas as a whole. Two main macroevolutionary hypotheses with an ecological basis are relevant in this context. The notion that predation pressure in marine benthic communities was not constant throughout the Phanerozoic is now widely accepted. Predation pressure upon the shelly benthos was abruptly augmented at the beginning of the Mesozoic when new groups of durivore predators appeared (Mesozoic Marine Revolution), and, from then to the present, it has been continuously increasing (Papp *et al.* 1947; Vermeij 1977, 1978, 1987). Since bivalves are frequent prey organisms, they have developed adaptive traits to cope with the mounting predation pressure (Vermeij 1983, 1987; Harper and Skelton 1993). Given their generally poor capacity for rapid repair and survivorship, epi- and endobenthic bivalves have relied essentially on enemy escape or avoidance (Vermeij 1983). Stanley (1970, 1975, 1977, 1978, 1981) noted that features enhancing burrowing, including ratchet sculpture, were rare in the Palaeozoic, but common in the post-Palaeozoic. Our study has confirmed and refined his observations in addition to being consistent with the slightly expanding diversity (except for the Oligocene restriction) of taxa with shingled oblique ribs shown in Text-figure 8. In conclusion, in line with the escalation hypothesis, the Mesozoic increase in the diversity of taxa with



TEXT-FIG. 9. Total genus/subgenus diversity in families containing species with shingled oblique ribs. Data from Cox *et al.* (1969).

symmetric oblique ribs may well reflect a mixed shell reinforcement-escape strategy, while the Cenozoic diversification of ratchet oblique ribs implies a purer escape strategy.

Thayer's (1983) extensive study has shown how the physical disturbance of the marine sediments (the rate and depth of reworking) increased over the Phanerozoic, and accelerated noticeably from the early Mesozoic. Sediment mean turnover time has decreased accordingly. Consequently, 'immune' groups of bivalves, either by mobility (free-burrowing suspension feeders) or by inhabiting hard substrates, have diversified (see also Stanley 1968). Mobile deposit feeders (including nuculoids and tellinoideans) are among the bioturbators (see Thayer 1983, figs 15–16). Therefore, features enhancing burrowing could be adaptations to the increasing sediment-reworking rate. In the case of suspension feeders, and, particularly, shallow burrowers, adaptations would be to avoid being exhumed and exposed to the action of epifaunal predators. Deposit feeders would have evolved adaptations to improve their feeding efficiency.

It is not possible to discard with certainty either of the above two possibilities, and it is also likely that both predation pressure and sediment reworking induced the increasing diversity and morphological changes of oblique ribs. In fact, both effects are partly interrelated since increased bioturbation also resulted from increased predation (see Thayer 1983, fig. 5B) and are associated with the Mesozoic Marine Revolution (Vermeij 1977).

A notable feature is the functional break at the Mesozoic/Cenozoic boundary, which is not consistent with the progressive nature of the increasing predation pressure or sediment reworking. Perhaps the notion of evolutionary constraints could be invoked here. The construction of shingled oblique ribs demands complex behavioural patterns based on mantle sensitivity and movement ability (unpublished data), and it is likely that only some groups with particularly structured mantles were preadapted for this kind of pattern formation. Only members of six veneroid and two nuculoid families developed shingled ribs and in most cases the corresponding species were closely related: *Scutarcopagia* and *Strigilla* (Tellinidae), *Gari* (Psammobiidae), *Solecurtus* (Solecurtidae), Divaricellinae (Lucinidae), *Myllita* (Erycinidae), *Nuculana* (Nuculanidae) and *Yoldia* (Sareptidae); hence, this ability apparently emerged only a few times. All of these groups appeared during the Cretaceous or later, that is, not much later than the first development of their oblique ribs. Additionally, a brief survey shows that they diversified during the Eocene–Miocene (Text-fig. 9).

Other groups were not apparently suited for the construction of shingled ribs. Within the Nuculidae (and the Nuculoida), only *Acila* developed the ability to construct oblique ribs, which were invariably of the symmetric type. Although this is a negative argument, we wonder whether the group was not preadapted for shingled rib formation. The same may apply to trigonioids, which probably compensated for the deficiency with a large foot and size. In particular, both groups already had a long evolutionary tradition and might have lacked the required genotypic plasticity.

In conclusion, during the Cenozoic radiation of veneroids and nuculanoideans, new evolutionary opportunities (the construction of shingled ribs among these) were provided for emerging groups of mobile endobenthic bivalves that invaded sandy/silty clastic substrata (abundantly provided during the intensive Cenozoic mountain-building processes).

CONCLUSIONS

Our paper demonstrates that oblique ribs of bivalves changed their function from shell protection against predators to burrowing enhancement at about the Mesozoic/Cenozoic boundary. Very few Palaeozoic bivalves secreted oblique ribs and these had primarily a shell-reinforcement function. Most endobenthic bivalves were deep burrowers. After the Early Triassic gap, the diversity of oblique-ribbed bivalves increased sharply throughout the Mesozoic to reach a peak in the Early Cretaceous. Most bivalves belonged to the Trigonioida in which ribs continued to have symmetric profiles and served a mixed function for shell reinforcement and excavation enhancement. Little is known about the function of ribs in the Mesozoic Pholadomyoida, but shell protection is most likely. Cenozoic bivalves developed oblique ribs of the ratchet type, particularly adapted for an efficient excavation. Only a few veneroids and the nuculids continued to have symmetric oblique ribs, which served entirely or partially for shell protection.

These morphological and functional changes correlate with the mobility of the faunas, which were generally augmented throughout the Phanerozoic. This and the fact that bivalves did not develop oblique ratchet sculpture until at least the Eocene (even though the corresponding families arose earlier) argues for a general ecological cause. Proposed hypotheses that may be relevant in this context are increasing predation pressure (Vermeij 1977) and sediment destabilization (Thayer 1983). The possible morphogenetic restrictions among bivalve groups must also be taken into account.

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ANTONIO G. CHECA

ANTONIO P. JIMÉNEZ-JIMENÉZ

Departamento de Estratigrafía y Paleontología
Universidad de Granada
Avenida Fuentenueva s/n
18071 Granada, Spain
e-mail acheca@ugr.es
apablojj@ugr.es

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