

EVOLUTION OF GRYPHAEATE OYSTERS IN THE MID-JURASSIC OF WESTERN EUROPE

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ABSTRACT. European Callovian (and later) forms of *Gryphaea* (*Bilobissa*) arose not from earlier representatives of the subgenus but from *Catinula*, a much smaller, frequently ribbed form, here regarded as a subgenus of *Gryphaea*. Evolution was essentially gradualistic. *G. (Catinula)* itself arose from an early *G. (Bilobissa)* species at the Toarcian/Aalenian boundary. In this case evolution was rapid (and apparently restricted to a small geographical area) but there is little evidence of stasis before and afterwards. The earlier *G. (Bilobissa)* lineage became extinct in the late Bajocian or early Bathonian. The morphologies of *G. (Bilobissa)* and *G. (Catinula)* may represent alternative adaptations for reclining in similar, low-energy environments, respectively favoured under conditions of high and low potential for shell growth. Such potential may have been controlled by ocean temperature and/or salinity. Most of the change between *G. (Bilobissa)* and *G. (Catinula)* probably resulted from alteration of growth rates. This almost certainly involved genetic change, although ecophenotypic variation may have been a precursor.

THE coiled oyster *Gryphaea* has been dubbed the 'Drosophila' of palaeontology (Gould 1972, p. 91). Certainly its evolution has been the subject of many more papers than most other fossil organisms (Gould 1980). However, while studies of *Drosophila* revolutionized genetics, the same cannot yet be claimed for evolutionary studies on *Gryphaea*. This is because the history of *Gryphaea* research is 'replete with biometrical errors' (Gould 1972, p. 91), and there is still far from complete agreement on the course of *Gryphaea* evolution. In his most recent publication on the subject, Hallam (1982) has claimed that *Gryphaea* is a monophyletic genus that evolved in a step-wise fashion, roughly according to the theory of punctuated equilibrium (Eldredge and Gould 1972). However other authors (e.g. Arkell 1934; Cox 1946, 1952; Sylvester-Bradley 1959, 1977) have regarded *Gryphaea* as no more than an evolutionary grade, attained polyphyletically, and Sylvester-Bradley considered that the genus provided good evidence of phyletic gradualism as well as of 'quantum' evolution. Sadly, Professor Sylvester-Bradley died before he was able to present morphometric data, assembled over an interval of nearly thirty years, which he believed supported his views. It is the principal intention of this paper to appraise Sylvester-Bradley's views in respect of European mid-Jurassic forms, the main subject of his collection and measurement. He put forward a quite explicit gradualistic evolutionary scheme for some of these forms (1959, 1977). This can be tested both as a putative example of gradualism, and, since evolution to *Gryphaea* allegedly proceeded from forms referred to a separate genus (*Catinula*), as a case serving to demonstrate the iterative evolution of *Gryphaea*. We review other phylogenetic schemes involving *Catinula* and find no evidence that it is more closely related to other oyster genera than to *Gryphaea*; Sylvester-Bradley's scheme is thus shown to be plausible at the outset as an alternative to the view of *Gryphaea* monophyly. We then identify those areas of species-level phylogeny that are critical to the question of the relationship between *Catinula* and *Gryphaea*. These are investigated in depth in order to reach ultimately a decision on the overall course of evolution.

We also investigate Sylvester-Bradley's views concerning other aspects of the phylogeny of mid-Jurassic gryphaeate oysters, partly in conjunction with a critical assessment of whether the morphological changes observed are, in fact, evolutionary. Conclusions in respect of the latter are taken into account in the formulation of a revised scheme of supraspecific classification. Extensive reference is made throughout to the work of Brannan (1983); unfortunately this remains

unpublished but as a recent and comprehensive study of Jurassic non-lophate oysters it demands the fullest attention.

Through the kindness of Mrs Joan Sylvester-Bradley we had available for study the collection of some 15,000 specimens assembled by her late husband. Our investigation of these was supplemented by studies at many of the field localities from which the specimens were derived and by limited recourse to other collections.

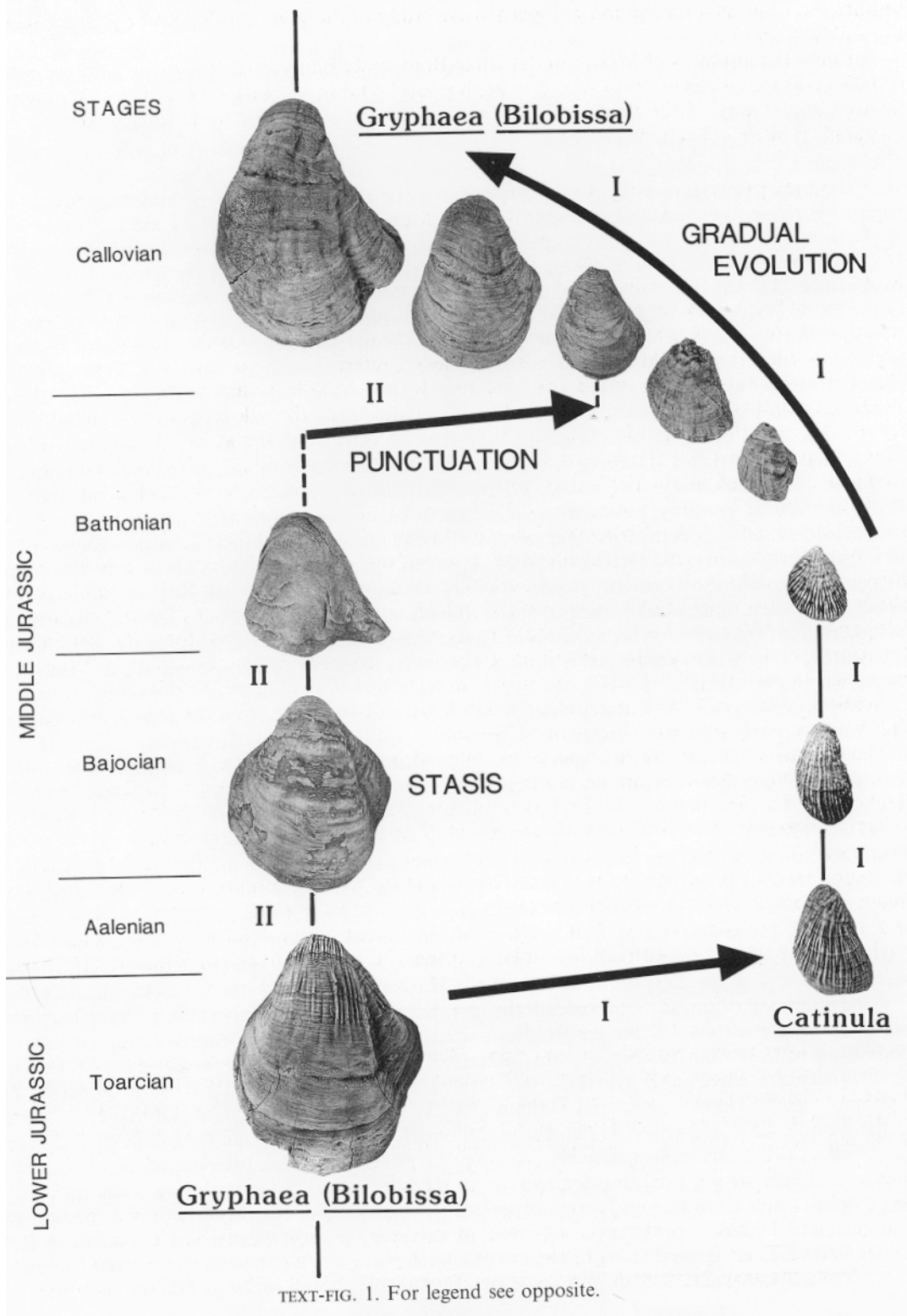
CONFLICTING HYPOTHESES FOR THE PHYLOGENY OF EUROPEAN MID-JURASSIC GRYPHAEATE OYSTERS

Principal current views

Most large, gryphaeately-coiled oysters encountered in mid-Jurassic rocks in Europe bear a marked radial posterior sulcus on the left (coiled) valve distinguishing them from representatives of the weakly-sulcate, and principally Liassic, *Gryphaea* lineage which has been the subject of so many previous studies (see Gould 1980). The latter lineage, referred by Stenzel (1971) to the subgenus *G. (Gryphaea)* Lamarck, may extend into the very lowest Middle Jurassic (Hallam 1982; Brannan 1983) but there is general agreement that at higher horizons the sulcate forms, which are known from as early as the Sinemurian (Hallam 1982), are the sole *Gryphaea* stock represented in Europe. This group of forms was referred to the subgenus *Bilobissa* by Stenzel (1971). While opinions have changed or differed about phylogeny within *Bilobissa*, most recent workers (Hallam and Gould 1975; Hallam 1978, 1982; Brannan 1983) have ruled out the involvement of any other taxon of similar or higher rank. However, Sylvester-Bradley (1959, 1977) considered that European Callovian forms of *Gryphaea* (i.e. *Bilobissa*) had evolved not from the forms of *Bilobissa* common early in the mid-Jurassic but from Bathonian forms of the oyster *Catinula* Rollier, similarly deeply-excavate but distinguished by its very much smaller size and development of radial ribbing on the left valve. This idea had been put forward in its essence by Arkell (1934); Sylvester-Bradley added the claim that the transition involved gradualistic change. Sylvester-Bradley's hypothesis is presented as part of 'phylogenetic pathway I' in text-fig. 1. Included within this latter scheme is the derivation of *Catinula* from an early *Bilobissa* species (from the uppermost Lower Jurassic) and a link between early and later forms of *Catinula*.

These latter concepts are not clearly expounded in Sylvester-Bradley's published writings but manuscript notes demonstrate he realized that uppermost Lower Jurassic '*Catinula*' *pictaviensis* (Hébert) of his 1959 paper – the supposed ancestor of Middle Jurassic *C. beaumonti* (Rivière) – is in fact a representative of *Bilobissa*, a view adopted by all other recent workers (Hallam 1982; Brannan 1983; Bayer *et al.* 1985). Manuscript notes also show that Sylvester-Bradley intended to refer such early *Catinula* species as *C. beaumonti* to a new genus. However, it is reasonable to assume that Sylvester-Bradley saw the ultimate ancestry of later forms of *Catinula* as lying within this genus, and thus to present route I in text-fig. 1 as a characterization of his views concerning the phylogenetic pathway between early and later forms of European *Bilobissa*. Brannan (1983) did not

TEXT-FIG. 1. Contrasting proposals for the origin of European Callovian *Gryphaea* (*Bilobissa*). Route I – the 'Sylvester-Bradley' model: gradual evolution from *Catinula*, itself derived from an early *G. (Bilobissa)* species. Route II – Hallam's (1982) model: direct evolution of Callovian *G. (Bilobissa)* from earlier members of the subgenus by a process involving punctuational change. The first model implies extinction of an early *G. (Bilobissa)* lineage before the Callovian; the second implies that *Catinula* died out without leaving any descendants by the early Callovian. Specimens illustrating gradual evolution are from the series depicted by Sylvester-Bradley (1977, text-fig. 11), with the largest (latest) specimen excluded. All specimens are left valves, seen from the exterior. From top, clockwise: Leicester University, Dept. of Geology (LEIUG) 104892, 104893, 104880, 104510, 104450, 104537; British Geological Survey, Keyworth, Nottingham GSM 73019; LEIUG 61452; Office national de gestion des collections paléontologiques, Villeurbanne, Lyon, France (ONCP), EM 35001; Muséum National D'Histoire Naturelle, Paris, France, B. 48576, B. 48575; all $\times 0.75$.



consider it necessary to refer early forms of *Catinula* (e.g. *C. beaumonti*) to another genus but endorsed Sylvester-Bradley's views with respect to their origin from *Bilobissa* (see also Stenzel 1971, p. N1102). He did not, however, agree with the idea that *Catinula* subsequently evolved back into *Bilobissa*. In text-figure 1 we have followed Brannan in referring both earlier and later forms of the small, ribbed oyster to *Catinula*.

Route II in text-figure 1 is a characterization of Hallam's latest views (1982) on the origin of European Callovian *Bilobissa* and of evolutionary tempo within the subgenus. Hallam considers that the uppermost Lower Jurassic forms of *Bilobissa* referred to above may not be specifically separable from Aalenian and Bajocian forms referred to *G. (B.) bilobata* J. de C. Sowerby (*recte sublobata* (Deshayes)), to which species he also assigns three early Bathonian specimens recorded by Fischer (1964) from France. These are the only examples of *Gryphaea* recognized from this stage in Europe. An extended period of stasis (> 14 Myr) is thus recognized, ended by the sudden appearance early in the Callovian of a smaller, morphologically distinct, *Bilobissa* species which persisted for a further 2 Myr. In view of the extreme rarity of Bathonian *Bilobissa* in Europe one may wish to question whether the origin of the Callovian species can be said to represent a punctuation event, but the essential fact is that Hallam rules out any involvement of Bathonian *Catinula*. (He expresses no view on the alleged evolution of *Catinula* from *Bilobissa*.) Brannan (1983) also excludes *Catinula* from the ancestry of Callovian *Bilobissa* but considers that the phylogeny of European *Bilobissa* is much more complicated than envisaged by Hallam, with as many as three coexisting species in the early mid-Jurassic, and both the Bathonian and earliest Callovian forms possibly representing a separate lineage from one (for which there is no fossil evidence) linking Bajocian and other early Callovian *Bilobissa*. While it is of no special relevance to our main concern – the relationships of supraspecific taxa – we would agree with Brannan that at least early in the mid-Jurassic, *Bilobissa* exhibits considerable morphological variation (see Bayer *et al.* 1985) such that the existence of stasis must be questioned. In-text-figure 1 forms which best evince Hallam's views have been deliberately selected; much more divergent forms could have been illustrated. Of greater significance is the position of the later forms mentioned above – these will be discussed in due course.

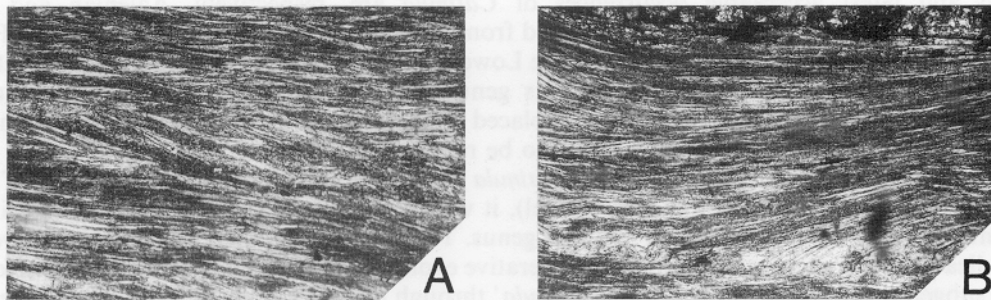
Summarizing, Sylvester-Bradley thought that '*Catinula*' evolved from *Gryphaea* (*Bilobissa*) in the Aalenian and subsequently evolved back into *Bilobissa* in the Callovian; Hallam thinks that these Callovian forms derive from a persistent (albeit in the Bathonian, exceedingly rare) *Bilobissa* lineage, and that they are unrelated to *Catinula*.

Other phylogenetic hypotheses and the definition of genera

Brief mention must also be made of other phylogenetic schemes involving the above forms. Perhaps the most obvious possibility is that European Callovian *Bilobissa* might have evolved from some lineage of *Bilobissa* which existed outside Europe during the Bathonian. This would go some way to explaining the embarrassing lack of *Gryphaea* in Europe stratigraphically intermediate between the abundant Bajocian and Callovian forms (Fischer's three specimens excluded). Marine clays, seemingly suitable for *Gryphaea* (although see Hallam and Gould 1975), accumulated widely in Europe in the Bathonian, and indeed the presence of *Catinula* rather than *Gryphaea* in these probably gave impetus to Sylvester-Bradley's investigation of Arkell's original claim concerning the derivation of Callovian *Bilobissa* from *Catinula*. Two species, *G. impressimarginata* McLearn and *G. nebraskensis* Meek and Hayden, are known from Bathonian rocks in N. America (J. H. Callomon, pers. comm. 1985), and Hallam (1982) recognizes *G. costellata* (Douvillé) in this stage in the Middle East. However, Hallam was sufficiently impressed by the morphological differences exhibited by these species (respectively, absence of a posterior sulcus, presence of an anterior sulcus, presence of very strong ribs) to rule them out as members of a lineage with Bajocian and Callovian representatives in Europe. Our limited experience of extra-European forms supports Hallam's view and, given the latter's preference for what might seem a rather contrived explanation (that a *Bilobissa* lineage emigrated from Europe in the Bathonian leaving, however, no trace elsewhere of its continued existence and despite possibly favourable facies in Europe), we feel justified in

excluding from further consideration the possibility that 'European' *Bilobissa* persisted during the Bathonian in N. America or the Middle East. Brannan (1983) tacitly adopted the same view.

Several other phylogenetic schemes have been proposed. Siewert (1972) considered *Gryphaea* to be monophyletic by virtue of a unique, dominantly prismatic, shell structure; similarities in shell structure were taken to indicate that *Catinula* had evolved from generally flat oysters referred to *Liostrea* Douvillé, and the allegedly invariant position of the attachment area posterior of the umbo was regarded as an indication that *Catinula* constituted part of the ancestry of the transversely-coiled genus *Exogyra* Say. The existence of prismatic structure in the innermost parts of the left valve of *Gryphaea* is not clearly demonstrated by Siewert; his pl. 2, fig. 4 shows only 'pigment prisms'. Our own investigations, and those of other recent workers (e.g. Stenzel 1971; Brannan 1983), show that where no diagenetic recrystallization has occurred, the shell structure is dominantly foliated calcite. The 'subrhomboidal' structure reported by Pugaczewska (1971, p. 276; after Čelcova 1969) may well be a variant of the latter (cf. Carter 1980, p. 81). We were unable to detect any difference in shell structure between *Gryphaea* (*Bilobissa*) and *Catinula* (text-fig. 2). Similarly, no difference exists in the mean position of the attachment area (see text-figs. 8–10; Pls. 1–3): contrary to Siewert's opinion, the attachment area usually truncates the umbo dorsally in *Catinula*, and the transverse element of coiling is very much weaker than in *Exogyra*.



TEXT-FIG. 2. Photomicrographs of acetate peels showing the foliated shell structure forming the bulk of the shell in *Gryphaea* (*Bilobissa*) and *Catinula*. A: *Gryphaea* (*Bilobissa*) – population CRC (horizon and locality, p. 472); LEIUG 106801; $\times 18$. B: *Catinula* – specimen collected from same horizon and locality as PBA population (p. 461); LEIUG 96891; $\times 42$ (almost full shell thickness shown).

Both Rollier (1911) and Charles and Maubeuge (1953) considered plicate oysters belonging to the genus *Lopha* Röding (including *Rastellum* Faujas-Saint-Fond) to be near relatives of *Catinula*. However, as pointed out by Brannan (1983), this was because of their inclusion of forms referable to the former genus within the latter. Brannan has listed a number of characters which separate the genera, bearing out an obvious distinction based on the form of the ribbing (produced by local thickening of the shell in *Catinula*, rather than plication).

Pugaczewska (1971) and Arkell (1934) considered, like Siewert (1972), that *Catinula* had evolved from flat oysters referred to *Liostrea*. The former offered no particular basis for this claim but amongst more general assertions Arkell claimed specifically that Bathonian '*Liostrea*' *hebridica* (Forbes) could be traced into a '*Catinula* stage'. While ribbed morphs are undoubtedly developed in '*L.*' *hebridica*, Hudson and Palmer (1976) have clearly indicated that the species can be distinguished from both *Catinula* and *Liostrea* (with the possible exception of early Jurassic *L. hisingeri* (Nilsson)) by the existence of prismatic structure in the outer layer of the left valve, lensoid cavities elsewhere in the shell, and other features. '*L.*' *hebridica* is referable to *Praeexogyra* Charles and Maubeuge. True *Liostrea* is distinguished from *Catinula* by the lack of any appreciable dorso-ventral incurvature in the left valve (Brannan 1983). Brannan has argued convincingly that the earliest *Praeexogyra* species evolved from *Gryphaea* (*Bilobissa*) so the idea that *Praeexogyra* descended from *Catinula*, put forward by Charles and Maubeuge (1953), can be discounted. Most

forms referred to *Praexogyra* are flat but two small, excavate species (commonest in the Bajocian) were included in the genus by Brannan (1983). They can be distinguished from *Catinula* by a complete absence of ribbing.

Cox (1946, 1952) held the tentative view that *Catinula* was polyphyletic but, unlike Arkell, who claimed that *Catinula* had evolved repeatedly from '*Lioostrea*', he doubted whether all *Catinula* had arisen in this way, and was also sceptical of Arkell's view (see above) that Callovian *Gryphaea* had evolved from *Catinula*. As indicated by Brannan (1983), Cox's acceptance of *Catinula* as a possibly polyphyletic genus can be explained by his inclusion of forms which in fact belong in quite separate genera. Exclusion of these renders *Catinula* a probable monophyletic taxon.

Definition of Catinula. It is evident that much of the speculation over the phylogenetic position of *Catinula* has resulted from failure to define the taxon adequately at the outset. *Catinula* can be differentiated from other supraspecific taxa in the following way. From *Gryphaea* (*Bilobissa*) it can be distinguished by the ribbing and small size previously mentioned. The development of ribs (i.e. local thickenings of the shell) and strong dorso-ventral incurvature, and the absence of plicae, external prismatic shell structure and cavities in the shell, variously distinguish *Catinula* from other superficially similar oysters. Thus defined there is no reason for supposing that any other Jurassic oyster is more closely related to *Catinula* than *Gryphaea* (*Bilobissa*) (cf. above discussion). The earliest and latest acceptable occurrences of *Catinula* are, respectively, Aalenian and early Callovian. Pugaczewska's (1971, p. 216) record from the Lower Jurassic is unsubstantiated. Forms described by Arkell (1934, pp. 60, 64) from the Lower Cretaceous of Texas have since been referred to *Texigryphaea* Stenzel (Stenzel 1971). This genus exhibits a vesicular shell structure, unlike *Catinula* and *Gryphaea* (*Bilobissa*), and is placed in a separate subfamily (Pycnodonteinae as opposed to Gryphaeinae). *Catinula* appears to be restricted to Europe.

It is worth noting at this juncture that if *Catinula* gave rise to forms of *Gryphaea*, but itself arose from *Gryphaea* (the 'Sylvester-Bradley' model), it would seem most appropriate to regard it as a subgenus of the latter, rather than a separate genus. Thus if the 'Sylvester-Bradley' model were to be vindicated one could not strictly have the iterative evolution of *Gryphaea*, only of forms referable to the subgenus *Bilobissa*. Reference to '*Catinula*' through the analytical sections of this paper is in accordance with recent custom (i.e. treatment of the taxon as a genus) and carries no implication of our ultimate conclusion concerning the status of the taxon or the course of gryphaeate oyster evolution.

A RATIONALE FOR TESTING PHYLOGENETIC MODELS

Thus far we have restricted our discussion of phylogenetic hypotheses mainly to the supraspecific level. Two schemes, the 'Sylvester-Bradley' and 'Hallam' models, which differ in the role accorded to *Catinula* in the ancestry of European Callovian *Bilobissa*, remain as viable hypotheses at this level. As partly indicated already, in addition to this dichotomy there exists a variety of views about species-level phylogeny within European *Bilobissa* and *Catinula*: in respect of the number of coexisting species, the evolutionary relationships of species, and the tempo of change. Thus whilst agreeing with Hallam over monophyly, Brannan's (1983) view of species-level evolution in *Bilobissa* was quite different. In particular, the three Bathonian specimens previously mentioned, considered by Hallam to represent a direct link between European Bajocian and Callovian species, were regarded by Brannan as of uncertain ancestry, providing in themselves no particular support for *Bilobissa* monophyly. It should be added that they are derived from a highly atypical coral-rich facies (Fischer 1964). The evidence of these forms, notwithstanding the stratigraphic gaps which would still remain, is clearly tenuous. Consequently, the evidence concerning gradual transition from *Catinula* to *Bilobissa*, which Hallam has only given very brief consideration (Hallam and Gould 1975, p. 536), assumes prime importance. Other than Sylvester-Bradley, only Brannan has seriously considered this evidence. His analysis led him to a conclusion opposite to Sylvester-Bradley's: that a morphological discontinuity exists between European Callovian *Bilobissa* and the latest representatives of *Catinula*.

There is a surprising measure of agreement between Brannan (1983) and Sylvester-Bradley (1958, 1959, 1977, MS notes) over specific divisions and phylogeny within *Catinula*. Differences exist over phylogeny in the early Bathonian – Sylvester-Bradley claiming the existence of a semi-discrete lineage confined to the eastern parts of W. Europe, Brannan denying it – but both authors agree that only one *Catinula* lineage existed in the later Bathonian, persisting into the early Callovian. Species and subspecies constituting this lineage formed the basis of Sylvester-Bradley's case for gradual transition (a few early Bathonian forms were included), and of Brannan's for discontinuity, so there are no grounds for suspecting that their contrasting views might result from analysis of material belonging to different lineages. Correspondingly, a reanalysis of Bathonian–Callovian forms, whatever the actual material used, should constitute a valid test of both hypotheses.

Sylvester-Bradley (1977, pp. 59–60) considered that the Bathonian–early Callovian lineage identified above was made up of 'a succession of forms in which four [gradual] trends are developed:

- (1) they increase in size;
- (2) the ribbing gets coarser and less distinct, and in later forms is restricted to early growth stages, or is absent altogether;
- (3) the left valve deepens so that there is an increase in the angle between the first growth line and the last;
- (4) a minor but increasing proportion of specimens develop a posterior radial sulcus'.

The trends were said to effect a link with Callovian *Gryphaea* (i.e. *Bilobissa*). By contrast, Brannan (1983, p. 292) concluded that 'no strong trends either towards or away from gryphaeate or any other type of morphologies exist in the phylogeny of *Catinula*'. His investigation was based on a much smaller sample than Sylvester-Bradley's and, notwithstanding the merits of the multivariate approaches used, cannot be said to constitute an adequate test of the assertions relating to single character evolution. We have therefore undertaken an evaluation of the alleged traits, adopting as rationales:

- (1) that any demonstration of gradual transitions would place the iterative interpretation of *Bilobissa* evolution on at least as credible a footing as hypotheses of monophyly involving unaccountable stratigraphic gaps;
- (2) that Sylvester-Bradley's criterion for recognizing gradual evolution (occurrence in single characters) is as valid as Brannan's (trends in values for canonical discriminant functions).

Both points could be argued: the cladistic and stratophenetic schools have debated the first and Cheetham (1987) has recently made observations relating to the second. However, we feel our approach is currently justified and hope that the presentation of more data may help towards a resolution of these philosophical questions.

We shall also investigate alleged morphological discontinuities which Brannan uses as supporting evidence to conclusions derived from his analysis of supposed transitional links between *Catinula* and Callovian *Bilobissa*.

MATERIALS AND METHODS

The Sylvester-Bradley oyster collection, which formed the basis of our study, included a large quantity of material loaned from institutions in Britain and abroad. This is now in process of being returned but most of the material, personally collected, remains available for study at the Department of Geology, University of Leicester (abbreviated LEIUG). Also available are notebooks detailing location and stratigraphic horizon of samples, unpublished manuscripts, photographs (largely the work of Derek J. Siveter), and a vast compendium of biometric data relating to all the material originally present in the main collection. Further details are given below.

Almost all the material originally assembled was from the mid-Jurassic (Toarcian to Oxfordian) interval and consisted of left (or conjoined) valves of oysters referable to *Bilobissa* or *Catinula*. Loose right valves were either not collected or separated out at an early stage and stored unprepared. Some two hundred localities, principally in Britain, France, Spain, Switzerland and W. Germany, are represented amongst the personally collected material alone. Sampling covered almost all horizons yielding significant numbers of gryphaeate

oysters in the mid-Jurassic of western Europe. Left valves were grouped according to a morphotype scheme (based on a standard series of measurements) and not according to sample or to species (as diagnosed by Sylvester-Bradley), although this information was preserved with the specimens. Presumably this was some reflection of the intended use of a morphotype-based system of analysis (Sylvester-Bradley 1958). We found it did not assist our research and therefore regrouped the material into the original samples. It is in this form that the material (including separately-bagged right valves and other unprepared material) has been curated at Leicester. The morphotype information can still be related to individual specimens. An explanation of Sylvester-Bradley's morphotype coding system, elucidated by David J. Siveter and C. P. Palmer, is available with the material.

The principal measurements taken by Sylvester-Bradley were as follows: shell height and length, the angle subtended by lines joining the origin of growth with the ventral edge of the attachment area ('first growth line') and the ventral margin of the shell ('last growth line'), the depth of the posterior radial sulcus, and the persistence, height and separation of radial ribs. These were recorded on an interval scale, presumably to facilitate Sylvester-Bradley's (1958) morphotypic scheme of analysis. We considered this too inaccurate for our purposes and felt that there were certain inconsistencies in the description of ornamental characters. We therefore remeasured non-ornamental characters using a continuous scale and, in view of the difficulty of obtaining precise values for the ribbing characters, adopted a simple presence/absence definition (together with a measure of persistence through ontogeny – see below) in respect of ornamentation. This slightly compromised our evaluation of the second of Sylvester-Bradley's trends (see above) but we have attempted to make up for this deficiency with illustrations of ornamental variation amongst representative sets of specimens. These latter (text-figs. 8–10; Pls. 1–3) give an indication of the definitions applied herein for ribbed and smooth morphs. The fact that the boundary is somewhat arbitrary, combined with the similar maximum sizes of ribbed and smooth morphs in a given population, provides very clear evidence that populations indeed consist of one species, rather than a mixture of taxa.

The measurements taken by us are illustrated approximately in text-figs. 4 and 6 (see below for precise operational definitions). We did not record the proportion of specimens with a posterior radial sulcus (trend 4 above) because the development of this character is clearly size-related and given an increase in size (trend 1) later populations would inevitably include a higher proportion of sulcate forms. Populations consisting only of small individuals clearly manifest a propensity for the development of a sulcus (text-fig. 9E, J). The relative confinement of ribbing to early growth stages (trend 2) is also a redundant parameter given phyletic size increase and if there is a programmed loss of ribbing at some size in ontogeny. This latter is undoubtedly the case – ribbing never extends beyond a peripheral height (P) of 50 mm – but we nevertheless measured the size at which ribbing is lost (RP) to investigate possible trends in this character. In order to increase the data base, in a few cases this character was measured on very weakly ribbed specimens, not otherwise recognized (see above) as ribbed morphs. As our means of estimating relative incurvature (the essential character implied in trend 3) we abandoned Sylvester-Bradley's angular measurement, which is again size-dependent, and substituted ratios of shell dimensions (H/I, H/P) as used by other workers (e.g. Hallam and Gould 1975; Brannan 1983; Bayer *et al.* 1985). We chose peripheral height as our measure of size (trend 1) since it is the largest dimension and, unlike height (H), independent of incurvature. P_{\max} refers to the largest single specimen in a population.

In addition to measurements taken to test Sylvester-Bradley's specific claims we investigated length/periphery (L/P) and height/length (H/L) ratios, the direction of the transverse component of coiling (see text-fig. 6F), and the height (AH) and length (AL) of the attachment area, in order to identify any possible morphological discontinuities or further gradual trends. In common with almost all previous work attention was confined to the left valve – in our case principally because of the availability of material.

It should be noted that the names applied to the various dimensions are not entirely concordant with any previous scheme but represent a compromise which we hope will be accepted as standard by future workers.

The various shell dimensions are defined precisely as follows (partly adapted from Stenzel 1971, p. N958). Length (L) is the maximum dimension obtained by projecting the extremities of the shell onto the hinge (anteroposterior) axis. Height (H) is the maximum dimension obtained by projecting the extremities of the shell onto a line (the dorsoventral axis) perpendicular to the hinge axis and lying within the plane of commissure. Inflation (I) is the maximum dimension obtained by projecting the extremities of the shell onto a line perpendicular to both the latter line and the hinge axis. Attachment area length (AL) is the maximum dimension obtained by projecting the extremities of the attachment area onto the hinge axis. Attachment area height (AH) is the maximum dimension obtained by projecting the extremities of the attachment area onto a line perpendicular to the hinge axis and lying within the plane of the attachment area. Peripheral height (P) is the distance between the origin of growth and the ventral margin, measured along an imaginary line running around the shell exterior, perpendicular to the hinge axis. Peripheral height of the ribbed zone (RP) is the distance along this line from the origin of growth to the ventral edge of the ribbed zone. Approximate illustrations of these dimensions are provided in text-figs. 4 and 6. Other morphological terms are explained by Stenzel (1971).

Whilst we felt unable to make use of Sylvester-Bradley's biometric data we would emphasize its availability and suggest that it might facilitate future testing of our conclusions, perhaps through a more sophisticated analysis of ornamentation. Our own raw data and statistics are deposited with the collection at Leicester and also with the British Library, Boston Spa, Wetherby, Yorkshire, LS23 7BQ, U.K. as Supplementary Publication No. SUP 14036 (23 pages). Mean sample size for individual statistics – excluding P_{\max} for which entire 'populations' (see below) were samples – averaged just under 37.

ANALYSIS OF BATHONIAN AND CALLOVIAN FORMS

In order to assess the validity of the Bathonian–Callovian section of route I for text-figure 1 we made use of the following 'populations' in the Sylvester-Bradley collection. They constitute the largest and stratigraphically best-defined samples from this interval. All are from western Europe to avoid inclusion of a possibly separate 'eastern' lineage (see above).

We would point out the existence of further material to investigate both this latter topic and the validity of the conclusions reached below. Our survey of populations allegedly representative of the eastern lineage revealed that they span a much shorter interval than supposed by Sylvester-Bradley (being of early Bathonian age rather than as stated in the 1959 and 1977 papers); thus their incorporation into the present analysis could have little affected the overall results.

PBA: Port-en-Bessin, Calvados, France; base of the Marnes de Bessin (*tenuiplicatus* zone). Notebook reference: S51 PBA3, 'Cliff section on the west side of Port-en-Bessin harbour. About 15 ft of clays ("Marnes de Port-en-Bessin") with harder bands of marlstone, overlying the "Passage Beds" (c. 1 ft)...'. ALAJ visited this section in 1984 and found abundant comparable material in a c. 3 cm shell-bed about 6 m above the base of the 'Marnes'. Less clearly *in situ* material, possibly derived from a second bed, was found at a level some 4 m below. 61 left valves (also 4 'miscellaneous' specimens): LEIUG 104604–104668.

WWA: Withy Wood Lane, W. Cranmore, Somerset; float almost certainly from Rugitela Beds (*hodsoni* zone). Notebook reference: S49 WWA, 'Ploughed fields at top of Combe Bottom', Grid reference: ST 679427. 74 left valves (also 1 'miscellaneous' specimen): LEIUG 104373–104449.

CVA: Colleville-sur-Orne, Calvados, France; Lower Cornbrash equivalent (*discus* zone, *discus* subzone). Notebook reference: S51 CVA, 'Louis Guillaume collns'. In 1984 ALAJ was unable to find any sections at this horizon around Colleville, but nearby coastal exposures between Lion and Luc yielded abundant comparable material. 36 left valves: LEIUG 104474–104509.

FA: Le Fresne d'Argences, Calvados, France; Upper Kellaways Clay equivalent (*calloviense* zone, *koenigi* subzone). Notebook reference: S57 FA, '... oysters (*O. alimena*) from base of brick pit (along drainage trench) – a thin (1 ft) layer of marly limestone and clay...'. This horizon was not exposed when ALAJ visited the now defunct brick pit at Argences in 1984. J. H. Callomon (pers. comm., 1985) has however confirmed the presence

of comparable oyster material at this level. 55 left valves (also 5 'miscellaneous' specimens): LEIUG 104669–104728.

PL1, PL2: Putton Lane, Chickerell, Dorset; Upper Kellaways Clay (PL1: *calloviense* zone, *koenigi* subzone) and Kellaways Rock (PL2: *calloviense* zone, *calloviense* subzone). Notebook reference: S57 PL, 'Putton Lane brickyard... Arkell's [1947, p. 27] Beds 1 and 2, with large cementstone concretions 1 ft 6 ins below top of section. Uncontaminated samples of Bed 1 difficult to collect, but a collection was made from clays dug out of the flooded base of the pit to form a retaining wall for a sump. Possibly slightly contaminated'. This pit has been long defunct and Bed 1 obscured. However, there are reports of a restart to working. PL1; 105 left valves (also 38 'miscellaneous' specimens): LEIUG 104729–104871. PL2; 1179 left valves (also 21 'miscellaneous' specimens): LEIUG 104872–106071.

KD1: Material collected by K. L. Duff from the London Brick pit at Stewartby, Bedfordshire; Kellaways Rock/Lower Oxford Clay (*calloviense* zone, *enodatum* subzone). Notebook reference: S76 KD1, 'Stewartby, Bed 4 [of Callomon, 1968, pp. 281–2]'. 143 left valves: LEIUG 69964, 69967, 69970, 69971, 69973–69975, 69978, 69980, 69981, 69988, 69991, 70041–70075, 70077–70085, 70090–70099, 70101–70176, 70936.

The relative stratigraphical positions of the samples are shown in text-figure 3. KD1 was only investigated at a late stage in our study and results were only derived for size and incidence of ribbing.

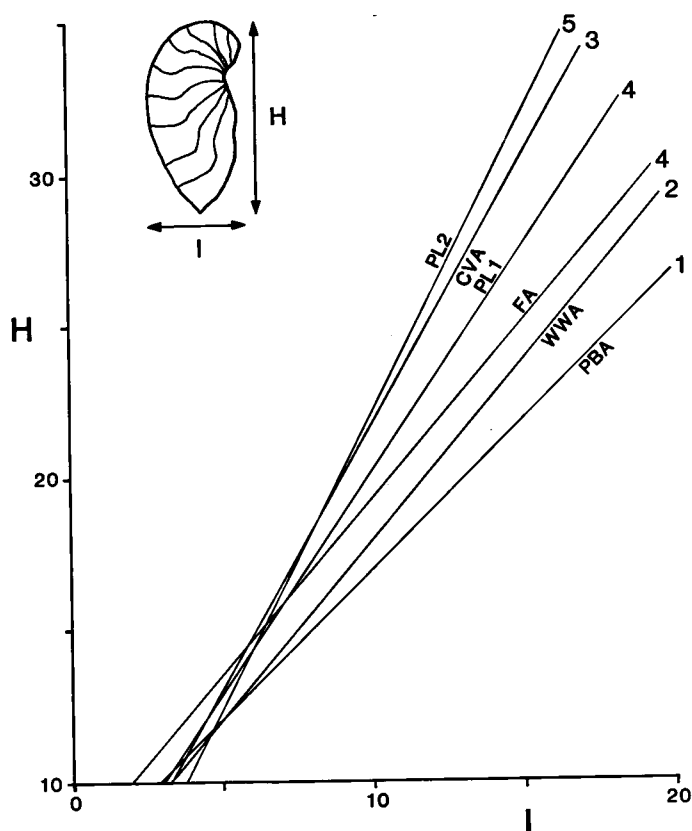
	Zones	Subzones	Populations
CALLOVIAN	Calloviense	Enodatum	KD1
		Calloviense	PL2
		Koenigi	FA PL1
	Macrocephalus	Kamptus	
		Macrocephalus	
BATHONIAN	Discus	Discus	CVA
		Hollandi	
	Aspidoides		
	Hodsoni		WWA
	Morrisi		
	Subcontractus		
	Progracilis		
	Tenuiplicatus		PBA

TEXT-FIG. 3. Stratigraphic position of Bathonian and early Callovian *Catinula* and *Gryphaea* (*Bilobissa*) populations in relation to ammonite zones and subzones. Biostratigraphic scheme is that of Cope, Duff *et al.* (1980).

Appraisal of alleged discontinuities

In addition to finding no evidence for gradualistic links between *Catinula* and Callovian *Bilobissa*, Brannan (1983) claimed the existence of important morphological discontinuities between the taxa: in degree of incurvature, and in two internal features, commissural shelf development and muscle scar shape. The latter claim had been previously advanced by Stenzel (1971). We investigated all three claims in respect of forms from the Bathonian–Callovian interval.

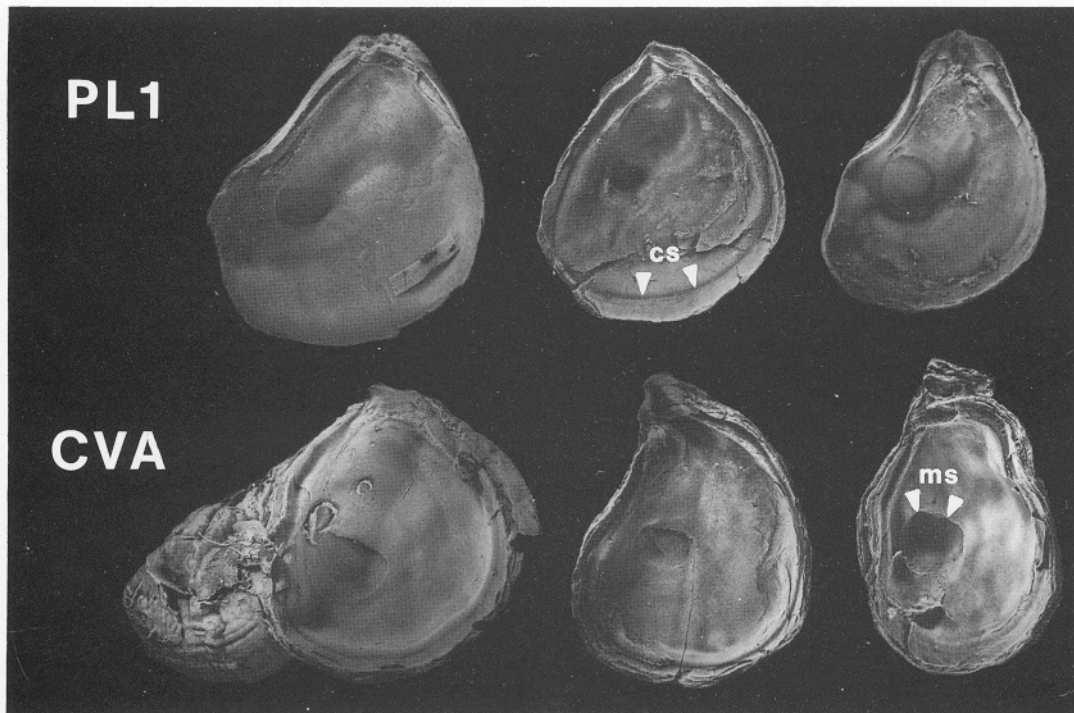
Relative incurvature. Brannan (1983, p. 291) considered that late Bathonian populations of *Catinula*, allegedly transitional to *Bilobissa*, could be distinguished from the latter on the basis of degree of incurvature (implying in this case height/inflation ratio). However, regression lines for H against I (text-fig. 4) do not suggest any fundamental discontinuity between Bathonian *Catinula* and *Bilobissa*. Rather, there is a marked trend towards higher H/I values with higher stratigraphic position amongst the studied populations. This is interrupted only by the CVA regression which, being based on the smallest statistical sample (28), may be least representative. Of particular interest is the FA population, which, judging from Brannan's taxonomic scheme and record of stratigraphic range, might well have been placed by him in *Gryphaea (Bilobissa) alimena* (see also Sylvester-Bradley's assignment above). This species was considered by Brannan to be separate from the main (unpreserved) *Bilobissa* lineage leading to later early Callovian forms. However, the intermediate position of the regression for FA in text-fig. 4 suggests that, rather than being a side-issue to a story of monophyletic *Bilobissa* evolution, such populations actually provide evidence to support a quite different hypothesis; namely, that Callovian *Bilobissa* evolved from *Catinula* (as suggested by Sylvester-Bradley from coiling considerations). This issue is considered in full below in conjunction



TEXT-FIG. 4. Least squares y -on- x regressions for height (H) versus inflation (I) of left valves from *Catinula* and *Gryphaea (Bilobissa)* populations from the Bathonian and early Callovian. Numbers indicate relative age of populations (5 = youngest). For actual stratigraphic positions of populations see text-fig. 3. Dimensions in mm.

with a more refined analysis of relative incurvature. For the purposes of diagrammatic representation and argument we henceforth regard FA as a very late *Catinula* population. Notwithstanding his views in general concerning *G. (B.) alimena*, it is only fair to add that Brannan might also have preferred to associate population FA with *Catinula* (e.g. 1983, p. 105), a taxon in his view unrelated to *Bilobissa*.

Internal features. Brannan (1983) claimed that *Catinula* and *Bilobissa* could be distinguished on the basis of two internal features: the presence of a marked commissural shelf (a ledge parallel to and just inside the margin of the left valve) in the former, and of an adductor scar with a strongly convex dorsal margin in the latter. Text-fig. 5 shows internal views of left valves from populations which Brannan would refer to *Catinula* (CVA) and *Bilobissa* (PL1). It is evident that the supposedly diagnostic features are highly variable and that a marked commissural shelf may occur in *Bilobissa* while an adductor scar with a convex dorsal margin may be developed in *Catinula*. Clearly there is no justification for considering that *Catinula* and Callovian *Bilobissa* represent entirely separate lineages on the basis of these characters. It therefore remains to assess whether there is any evidence for intergradation amongst other characters.



TEXT-FIG. 5. Internal views of left valves from populations belonging to allegedly discrete *Gryphaea* (*Bilobissa*) (PL1) and *Catinula* (CVA) lineages, showing the range of variation in muscle scar (ms) shape and commissural shelf (cs) development in each population. See text for further details. PL1, left to right: LEIUG 104753, 104737, 104742. CVA, left to right: LEIUG 104477, 104479, 104480. All $\times 2.3$.

Intergradation

Size and ribbing. In connection with the trends reported by Sylvester-Bradley (1977) in these characters, we investigated size (measured by maximum peripheral height), incidence of ribbing (measured by the proportion of ribbed to non-ribbed morphs), and coarseness and distinctness of ribbing (assessed visually).

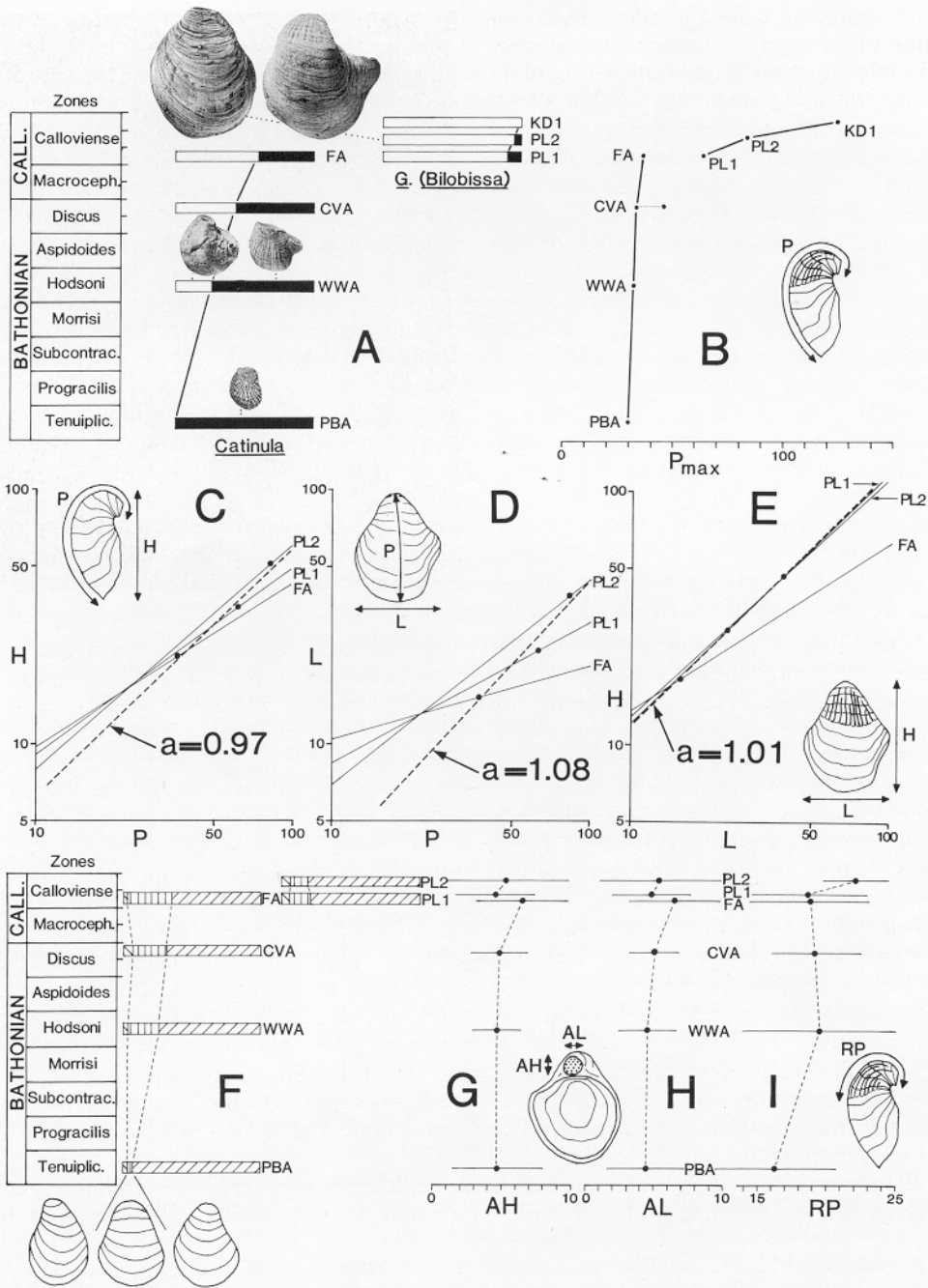
The proportion of ribbed to non-ribbed morphs shows a clear trend, a gradual decrease in the proportion of the former, through the sequence of populations (text-fig. 6A). A progressive increase in maximum peripheral height is also apparent (text-fig. 6B). However, in this case the rate of change is markedly faster amongst early Callovian *Bilobissa* populations. This fact, together with the geographical variation in both size and incidence of ribbing evinced by the FA and PL1 populations (from the same ammonite subzone), allows of the faint possibility that *Catinula* and *Bilobissa* constituted two separate lineages, the latter replacing the former following immigration into Europe in the *koenigi* subzone. This hypothesis fails, however, to account for the evolution of a more *Gryphaea*-like form in *Catinula*. Also, of course, it is not substantiated by the existence of an appropriate *Bilobissa* lineage outside Europe during the Bathonian. One could make the *ad hoc* suggestion that the gryphaeate trend in *Catinula* is the result of introgression of *Bilobissa* genes (implying the existence of two lineages, reproductively incompletely isolated). However, this would be to place yet further demands on the incompleteness of the fossil record. To be tenable, an introgression model – corresponding to some form of ‘reticulate’ evolution (Sylvester-Bradley 1977) – surely requires support from the occurrence of fairly frequent Bathonian *Bilobissa* in Europe; at least more than the paltry three specimens known. On the grounds of parsimony, the most reasonable interpretation of the above data is in terms of a single late Bathonian–early Callovian lineage.

Text-figure 7 shows that the largest representatives of the FA population (‘latest *Catinula*’; text-fig. 6A) are approaching the fully gryphaeate form of examples from the PL1 population (‘first Callovian *Bilobissa*’; text-fig. 6A). The same specimens are seen in lateral view in Plates 1 and 2 (respectively figs. 6 and 4) which also depict ornamental variation (and the general range of shape). It can be seen that there is little difference between populations FA and PL1 in respect of style of ribbing, and no other distinguishing features immediately present themselves. Plates 1 and 2 are part of a series (text-figs. 8–10; Pls. 1–3) intended to facilitate assessment of the supposed overall trends in the coarseness and distinctness of ornamentation. It is possible to perceive a gradual trend towards coarser ribbing (as defined by longer wavelength) through the sequence of populations, although the presence of individuals with relatively few ribs in CVA should be noted. No unidirectional trend in distinctness (amplitude) of ribbing can be recognized – the highest ribs are developed midway through the *Catinula* series. Nevertheless, it is important to point out that the difference between PBA and CVA (i.e. within *Catinula*) is probably as large as that between CVA and FA, and certainly larger than that between FA and PL1. Both of these latter ‘discontinuities’ might have been argued to represent displacement of *Catinula* by a separate *Bilobissa* lineage.

To summarize the results thus far: there is compelling evidence for the evolution of *Catinula* into *Bilobissa* through a gradual, unidirectional trend in the proportion of ribbed morphs. Slightly more equivocal trends exist in maximum peripheral height and wavelength of ribbing. Rib amplitude follows an oscillatory pattern but this character, and the last two, gives no suggestion of a real discontinuity between *Catinula* and European Callovian *Bilobissa*.

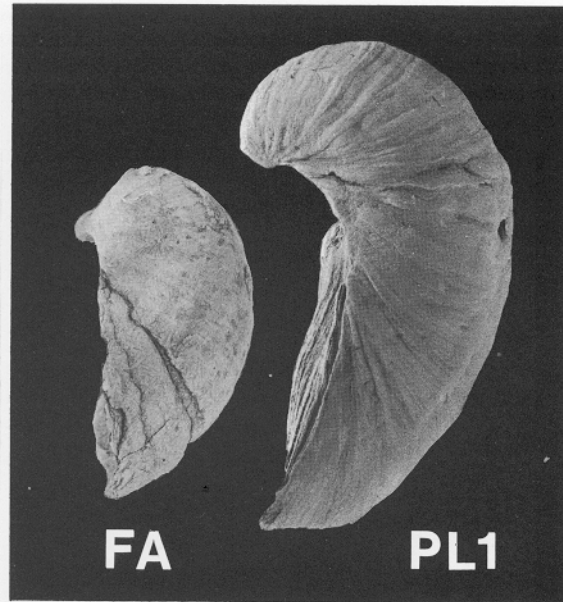
Gross shell dimensions. We pointed out above that Sylvester-Bradley’s angular measurement does not allow a true evaluation of relative incurvature (left valve ‘depth’; trend 3). Analysis of height (H) in relation to inflation (I), as carried out in connection with Brannan’s claims (see above), represents a better means of assessment but is subject to the difficulty of measuring inflation accurately in small specimens. We investigated incurvature through an analysis of height in relation to peripheral height (P), calculating log–log regressions in accordance with the allometric relationship between these characters. Similar investigations were made of length (L) against peripheral height, and height against length.

The results for the three critical earliest Callovian populations are presented in text-figure 6C–E. As expected, the H/P regressions differ but there also exist differences between the populations in respect of L/P and H/L. Points on the regressions corresponding to the largest individuals in each population have been identified. The dashed lines represent ‘secondary’ regressions calculated from the coordinates of these points. An interesting fact emerges from this analysis. In each plot the slope



TEXT-FIG. 6. Biometric data for left valves from Bathonian and early Callovian *Catinula* and *Gryphaea* (*Bilobissa*) populations. A, B. Stratigraphic variation in: A, proportion of ribbed (solid) to smooth morphs; B, maximum peripheral height (P_{max}). Larger value for P_{max} of CVA population derived from a possible contaminant (see text-fig. 10A). C-E. Least squares y -on- x regressions (form $\log y = a \log x + \log b$, axes log scale) for shell proportions of three early Callovian *Catinula* and *Bilobissa* populations (continuous lines). Dashed lines are regressions (slope $- a$ indicated) calculated from values (solid circles) corresponding to the

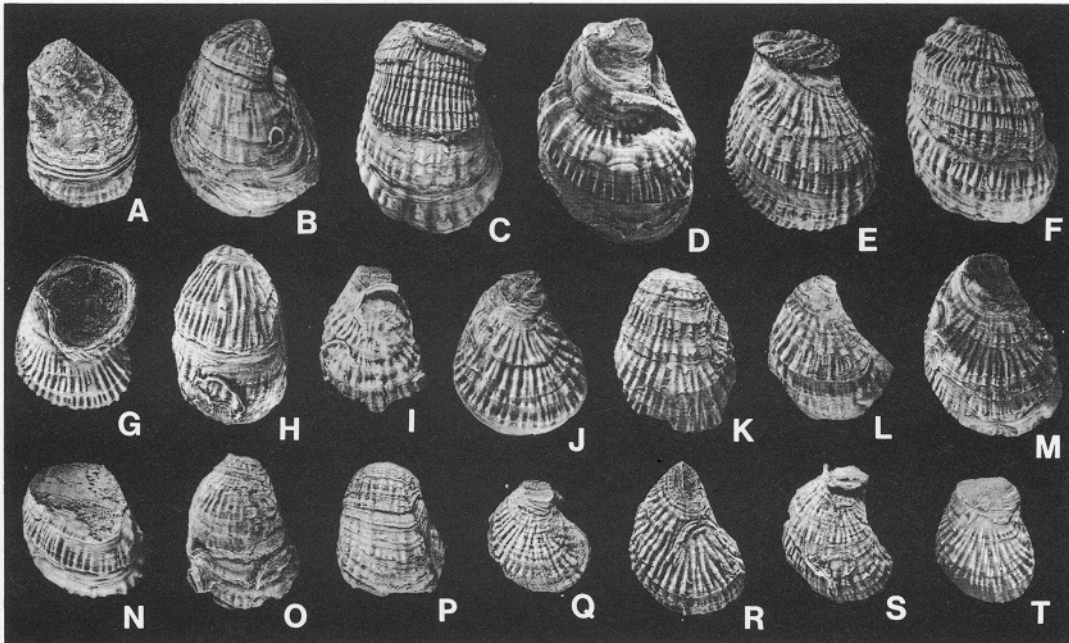
TEXT-FIG. 7. Anterior views of left valves from populations FA and PL1, showing the approach toward the fully developed gryphaeate coiling of the latter population within the former. LEIUG 104674 (FA), 104732 (PL1); $\times 1.7$.



(a) of the secondary regression is close to unity, implying that the shape of the largest ('adult') individuals in each population is extremely similar (cf. Gould 1977, p. 239). To use Gould's terms, the larger adults of the PL2 population are 'proportioned giants'. The relationship is preserved if the earlier populations are included in the analysis ($a = 0.88, 0.93, 0.98$ for secondary regressions of, respectively, H/P, L/P, H/L) but clear graphical representation of the full data set cannot be easily accomplished. This maintenance of adult geometric similarity can be readily interpreted in the context of dissociated size and shape development, and as such strengthens the case for a direct relationship between Callovian *Bilobissa* and *Catinula*. However, the observed relationship could result from either retarded shape development and greater longevity in populations reaching a larger size, or from accelerated size increase (and unaltered longevity and rate of shape development) in such 'giant' populations. The latter might in turn be no more than an aspect of ecophenotypic variation. Ignoring for the moment the seemingly conflicting evidence of differences in the *relative frequency* of ribbed morphs, this would mean that *Catinula* and *Bilobissa* were not simply directly related but, in fact, effectively genetically identical! The link between size and stratigraphic position perhaps favours an evolutionary (i.e. genetic) interpretation, whether involving retarded shape development or accelerated size development, but the apparent existence of geographical variation within the *koenigi* subzone lends support to the ecophenotypic view. We shall return to this question in discussion of earlier *Catinula* and *Bilobissa* from near the Lower-Middle Jurassic boundary.

From the analysis of H/P it is evident that *adult* shells show *no* change in incurvature, contrary to what is implied in Sylvester-Bradley's trend 3. However, as we have shown, far from refuting the

maximum size (x dimension) in each population. C, height (H) versus peripheral height (P); D, length (L) versus peripheral height; E, height versus length. F-I. Stratigraphic variation in: F, proso- (left), to ortho-, to opisthogyral (right) morphs; G, attachment area height (AH); H, attachment area length (AL); I, peripheral height of ribbed zone (RP). Bars in G-I extend one standard deviation either side of the mean. Dimensions in mm. Divisions of ammonite zones are subzones. Line diagrams illustrating characters are of exteriors of ribbed morphs in B, E, I; remaining line diagrams of smooth morphs. Halftone illustrations - PL2: LEIUG 104872 (left), 104874; WWA: LEIUG 104379 (left), 104382; PBA: LEIUG 104623; all $\times 0.55$.



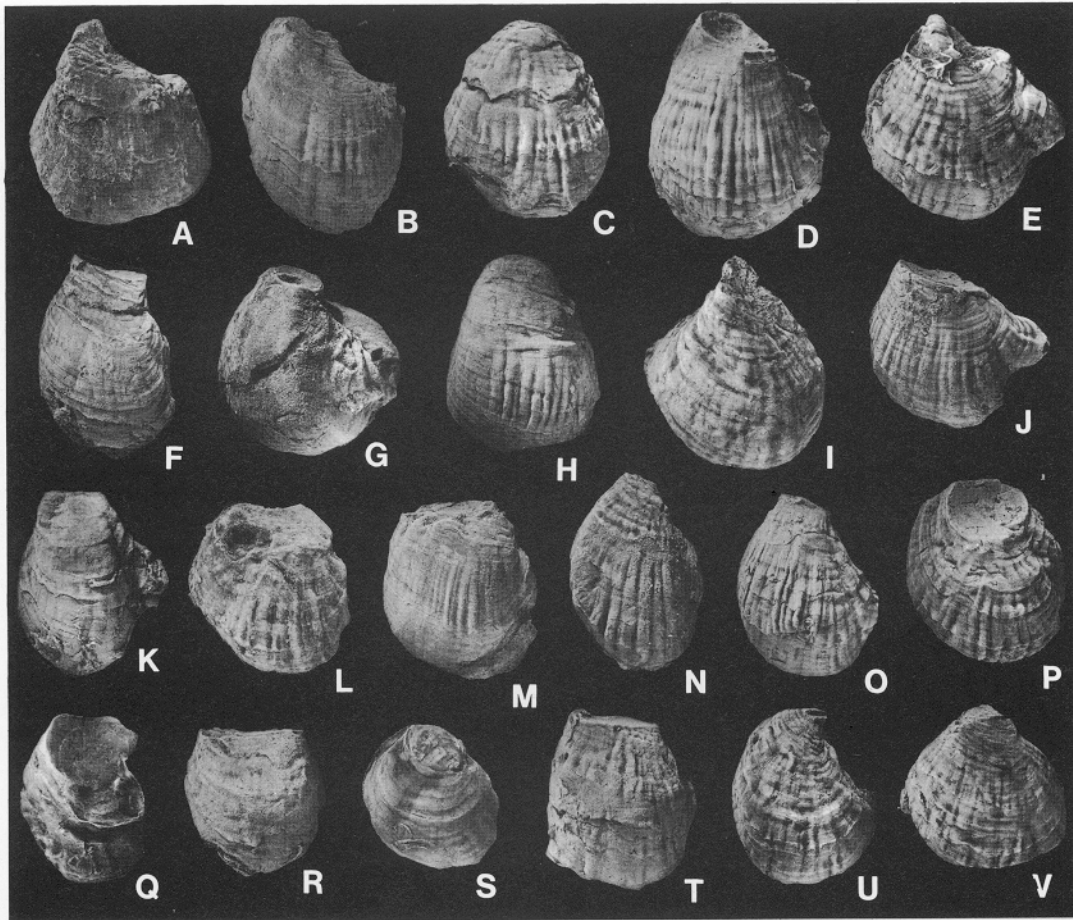
TEXT-FIG. 8. *Catinula* Rollier – population PBA (A–T: LEIUG 104604–104623 respectively): variation in external morphology of left valves. All specimens are ribbed morphs; $\times 1.7$.

possibility of a link between *Catinula* and *Bilobissa*, the very fact of maintenance of shape in the context of differing adult sizes provides compelling support for a relationship.

Additional features. Data for measures of shell obliquity, attachment area size and peripheral height of the ribbed zone are presented in text-figure 6F–I. These characters, supplementary to those considered by Sylvester-Bradley (1977), provide no grounds to support the view that *Catinula* and Callovian *Bilobissa* represent anything other than segments of a single lineage. In the case of obliquity (text-fig. 6F), some difference exists between the critical, approximately contemporaneous, FA (*Catinula*) and PL1 (*Bilobissa*) populations. However, this is comparable to the difference between successive, earlier populations – PBA and WWA – both referable to *Catinula*. Small differences also exist between FA and PL1 in respect of mean dimensions of the attachment area (text-fig. 6G and H) but here again a discontinuity cannot reasonably be inferred in view of the complete overlap of bars representing one standard deviation from the mean. In the case of peripheral height of the ribbed zone (text-fig. 6I), values for the FA and PL1 populations are almost identical, and the pattern of stratigraphic change in this character over the complete sequence of populations could be interpreted as a mildly oscillating gradual trend: positive evidence, under this view, of a link between *Catinula* and *Bilobissa*.

Summary and conclusions

There is no compelling evidence for the existence of a morphological discontinuity between L. Callovian oysters referable to *Bilobissa* and Bathonian–L. Callovian forms referable to *Catinula*. The existence of a gradual, unidirectional trend towards reduced frequency of ribbed morphs, together with somewhat less uniform trends in maximum size, coarseness of ribbing and peripheral height of the ribbed zone, provides, in contrast, positive evidence that L. Callovian *Bilobissa* evolved from *Catinula*. This conclusion is strongly supported by close similarities in gross adult shell proportions, despite differing adult sizes.

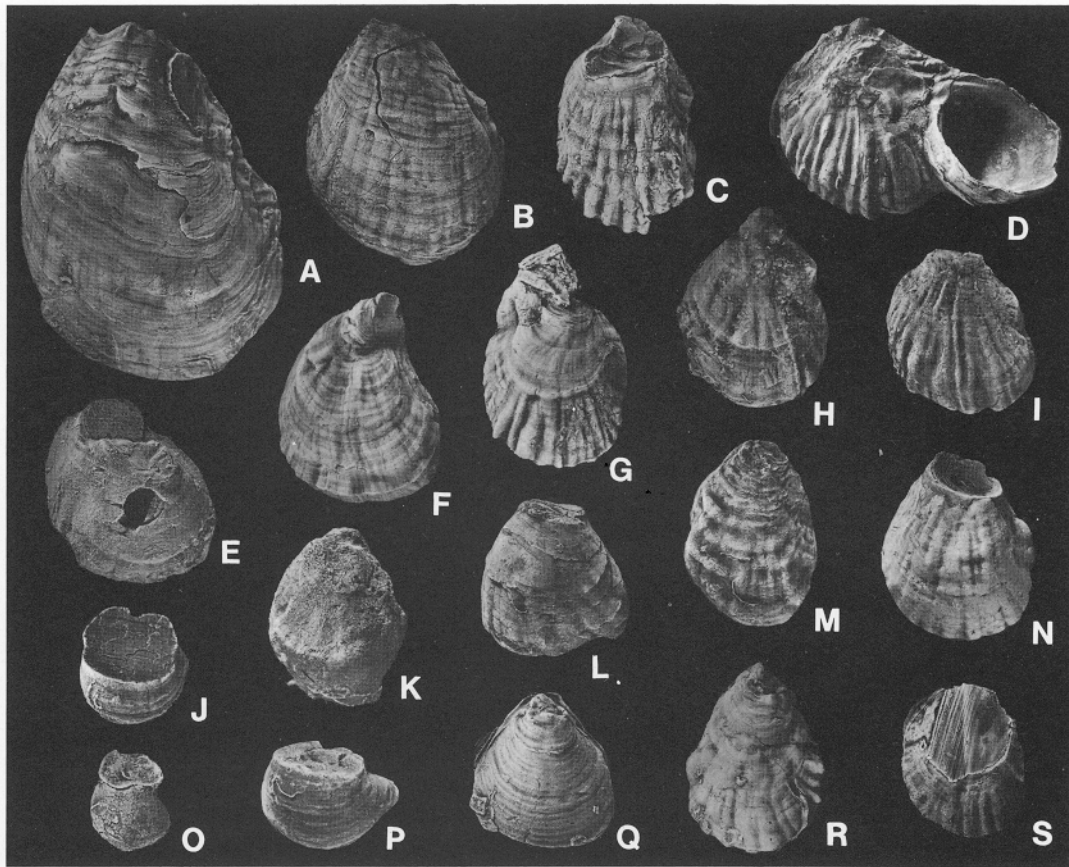


TEXT-FIG. 9. *Catinula* Rollier – population WWA (A–V: LEIUG 104373–104394 respectively): variation in external morphology of left valves. A, F, G, K, Q–S, ribbed morphs; remainder smooth; all $\times 1.7$.

ANALYSIS OF TOARCIAN AND AALENIAN FORMS

We have found in favour of the 'Sylvester-Bradley' model (route I in text-fig. 1) for the immediate (Bathonian) ancestry of Callovian *Bilobissa*. It remains to be shown whether Toarcian *G. (Bilobissa) pictaviensis* gave rise to Aalenian *Catinula beaumonti* and thus whether route I is correct in its entirety. Large amounts of material were available to us in the Sylvester-Bradley collection to test this proposition. The large number of *G. (B.) pictaviensis* samples provided, moreover, an opportunity to test whether this species, variably-ribbed like the later *Bilobissa/Catinula* group analyzed above, exhibited a pattern of within-species geographic variation in morphology analogous to that inferred in the later group of forms. The occurrence of an analogous (well-developed) pattern of variation would provide additional support for the interpretation of Callovian *Bilobissa* as a descendant of *Catinula*. We also wished further to investigate the possibility that variation might be ecophenotypic.

A similar biometric investigation was made of the following nine 'populations'; the first, following Sylvester-Bradley's MS notes, referable to *C. beaumonti*, and the last eight to *G. (B.) pictaviensis*.



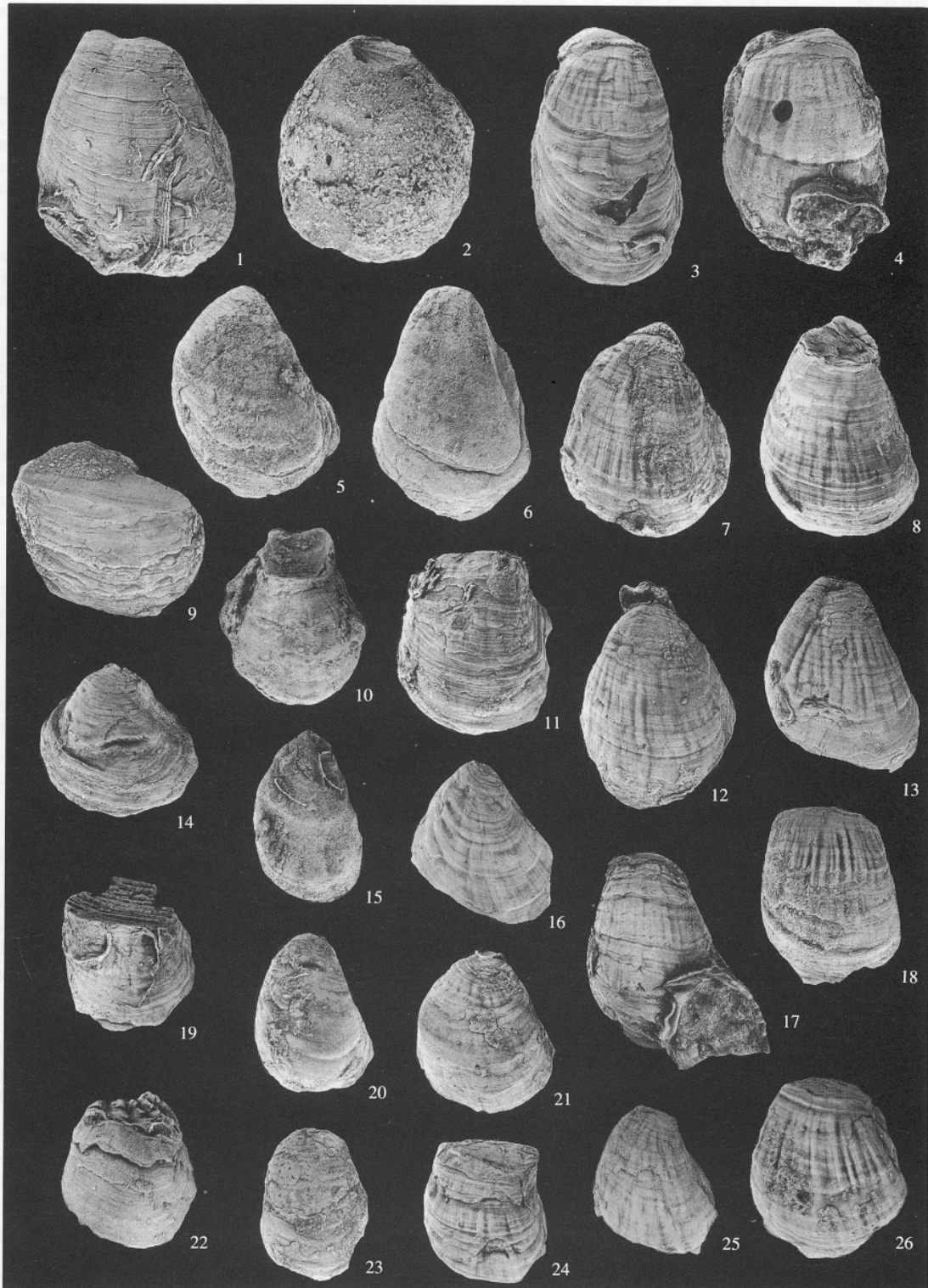
TEXT-FIG. 10. *Catinula* Rollier – population CVA (A–S: LEIUG 104474–104492 respectively): variation in external morphology of left valves. A, E, J–L, O–Q, smooth morphs; remainder ribbed; all $\times 1.7$. The exceptional size of the specimen figured as A may indicate that it is a contaminant.

AVB: Airvault, Deux Sèvres, France: Aalenian, *opalinum* zone. Notebook reference: S74 AVB, 'Old quarries in environs of new cement quarry complex. AVA: Lower beds just above unconformity with large oysters (rare) in Bed no. 13 (MS section. = Bed No. 39 of Gabilly 1973) (*maetra* horizon). AVB: Higher in section'. ALAJ visited Airvault quarry (worked by Société des Ciments Français) in 1984. Large quantities of comparable material were obtained from *c.* 1 m of limestones and marls including Bed 77 of Gabilly (1973, Annexe 1, fig. 9). There can be no doubt that these horizons were the source of sample AVB. 216 left valves (also 47 'miscellaneous' specimens): LEIUG 101333–101596.

TTB, TTC: Tartareu, Lérida, Spain. Notebook references: S75 TTB, 'Barley field about $1\frac{1}{2}$ km NE of Tartareu with *R. [Rhynchonella] cynocephala* (about 500 m N of road)'; S75 TTC, 'Hillside above fields and in maquis about 1.5 km north of TTB – especially where dam for small pond has been excavated'. TTB; 138 left valves (also 6 'miscellaneous' specimens): LEIUG 103660–103803. TTC; 175 left valves (also 3 'miscellaneous' specimens): LEIUG 70930–70933, 103482–103655.

EXPLANATION OF PLATE I

Figs. 1–26. *Catinula* Rollier – population FA (LEIUG 104669–104694 respectively): variation in external morphology of left valves. 3, 4, 7, 8, 12, 13, 16–18 and 24–26, ribbed morphs; remainder smooth; all $\times 1.7$.



JOHNSON and LENNON, *Catinula*

CRC: Camarasa, Lérída, Spain. Notebook reference: S76 CRC, 'Off trail to Ermita S. Jordi... Clutson unit D3'. No further details of Michael Clutson's stratigraphic scheme are available and it is uncertain whether it was published. 418 left valves (also 6 'miscellaneous' specimens): LEIUG 106800–107223.

NV: Néviau, Aude, France. Notebook reference: S58 NV, 'Map 1: 50000 coloured edit. (Type 1922, published 1955) – Sheet Béziers (XXV – 45). Exposure in vineyard banks on eastern slopes of small hill 1 km S by E of Néviau – [grid reference] 646.0 × 100.5. The oysters are found through vineyards extending a considerable way up the hill. It seemed that those in the higher vineyards (geographically; stratigraphical relationships not decided) were wider and less often had ribbed umbones than those from the lower vineyards; this suggests that two horizons may be implicated'. 213 left valves: LEIUG 70934, 106582–106793.

TZ: Château Tazière, Fourchambault, Nièvre, France. Notebook reference: S74 TZ, 'Mapped as a faulted inlier of Aalenian... To the east of the chateau field is apparently developed on floor of old clay pit. Fossils come from a slab of limestone weathering out of wall of pit below wall of garden of chateau'. 233 left valves: LEIUG 104012–104245.

LBB: La Bonnette valley, St Antonin, Tarn et Garonne, France. Notebook reference: S58 LLB, 'On east side of valley, natural section at foot of scars, above scree slopes. About 10' yield *Gryphaea*... LBB from scree. [Grid reference] 553.5 × 207.5 – Map 206 SE [Type 1889, 1: 50000 – Cahors]'. 56 left valves: LEIUG 106272–106327.

BZ: Bizanet, Aude, France. Notebook reference: S58 BZ, 'Oysters from outcrop off Ruisseau de la Sauzine NNE of Bizanet. [Grid reference] 643.6 × 97.4 – Map 1: 20000 Capendu No. 4 (XXIV – 46 – No. 4). A small quarry immediately above vineyard. Oysters collected from both quarry and vineyard. In quarry found at two horizons, about 6 ft apart'. 126 left valves (also 1 'miscellaneous' specimen): LEIUG 61200–61214, 106160–106271.

AG: Château d'Aguilar, Tuchan, Aude, France. Notebook reference: S58 AG, 'Oyster beds outcrop between fossiliferous Whitbian (*Hildoceras*, big pectens, belemnites, terebratulids) shales and unfossiliferous massive Bajocian limestones in col immediately north of chateau. *In situ* in vineyard banks, and ploughed up in vineyards. (Perhaps mainly upper horizon present?)'. 88 left valves: LEIUG 106072–106159.

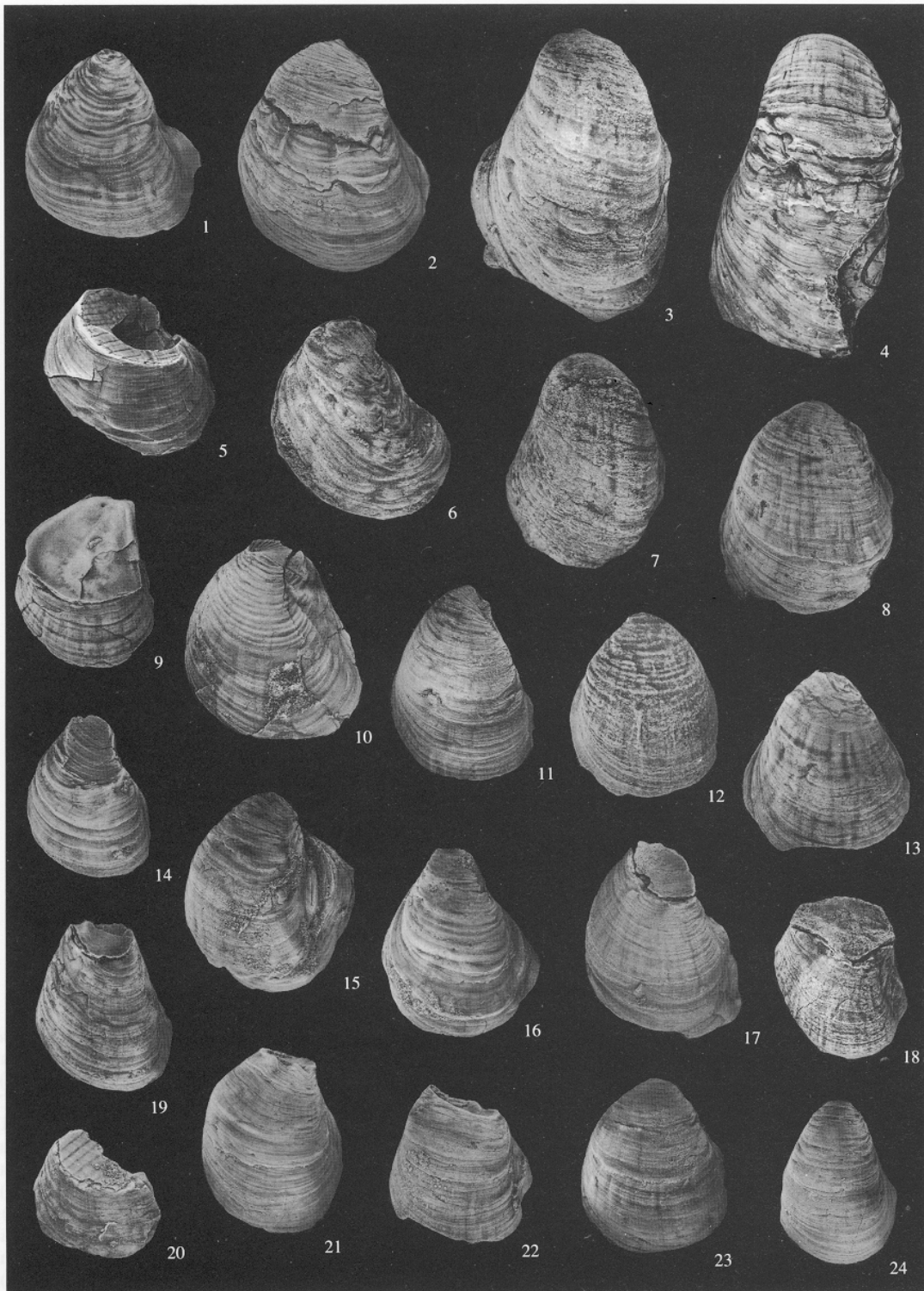
Sylvester-Bradley (MS notes) apparently considered that all the *G. (B.) pictaviensis* samples (last eight) were from the *levesquei* zone of the Toarcian. We have accepted the opinion of J. Gabilly (University of Poitiers; pers. comm., 1984), founded on detailed work in the Poitou region of France, that *G. (B.) pictaviensis* does not occur outside this zone. *C. beaumonti* (restricted to Poitou) appears in the succeeding *opalinum* zone (Gabilly 1973).

Size and ribbing. Data for these characters are presented in the form of a bivariate plot (text-fig. 11A). From this it is clear that *G. (B.) pictaviensis* exhibits considerable inter-population variation, of a magnitude rather larger than that observed in the *koenigi* subzone of the Callovian and, in that case, ascribed to geographic variation within one species. Even given that the *G. (B.) pictaviensis* samples may not all be from precisely the same horizon (see locality details), it seems highly probable that there was a good deal of geographic variation in this species. By implication therefore, variation in the *koenigi* subzone may be confidently accepted as intraspecific – developed within a single *Catinula/Bilobissa* lineage.

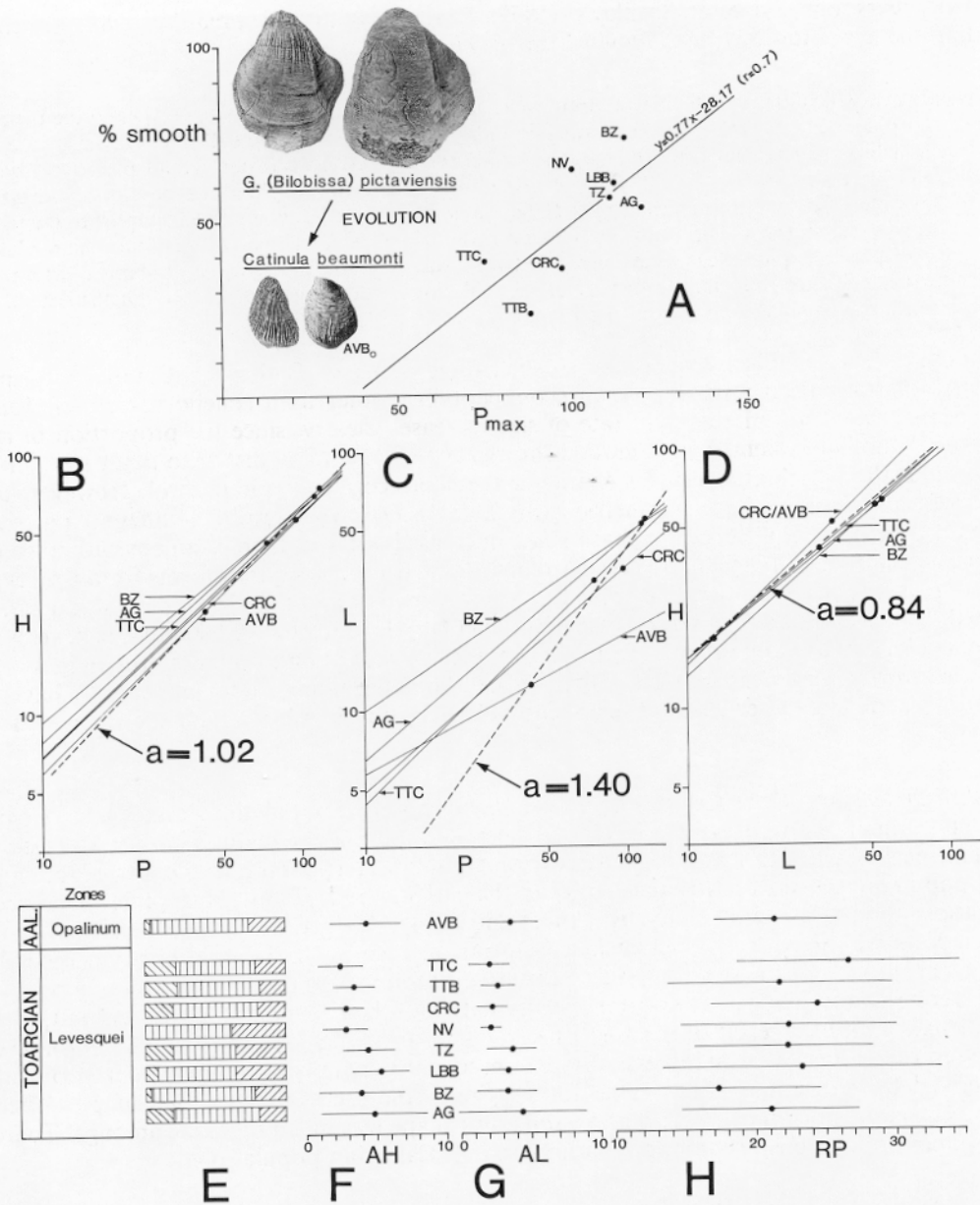
A regression calculated from the *G. (B.) pictaviensis* data passes remarkably close to the value for the *C. beaumonti* population (AVB). The whole array of data points can thus be interpreted in terms of a simple pattern of covariation. This, together with the near identity of ribbing form (see text-

EXPLANATION OF PLATE 2

Figs. 1–24. *Gryphaea (Bilobissa)* Stenzel – population PL1 (LEIUG 104729–104752 respectively): variation in external morphology of left valves. 8, 13, 17 and 18, ribbed morphs; remainder smooth; all × 1.7.



JOHNSON and LENNON, *Gryphaea (Bilobissa)*



TEXT-FIG. 11. Biometric data for left valves from Aalenian *Catinula beaumonti* and Toarcian *Gryphaea (Bilobissa) pictaviensis* populations. A. Plot of percentage smooth morphs versus maximum peripheral height (P_{max}). Regression (least squares y -on- x) calculated from data for *G. (B.) pictaviensis* populations (solid circles). B-D. Least squares y -on- x regressions (form $\log y = a \log x + \log b$, axes log scale) for shell proportions of *C. beaumonti* (AVB) and four *G. (B.) pictaviensis* populations. Dashed lines are regressions (slope- a -indicated) calculated from values (solid circles) corresponding to the maximum size (x dimension) in each population. B, height (H) versus peripheral height (P); c, length (L) versus peripheral height; D, height versus length. E-H. Stratigraphic and geographic (*G. (B.) pictaviensis*, *levesquei* zone) variation in: E, proportion of proso- (left), to ortho-, to opisthogyral (right) morphs; F, attachment area height (AH); G, attachment area length (AL); H, peripheral height of ribbed zone (RP). Populations arranged in order of decreasing maximum peripheral height upwards. Bars in F-H extend one standard deviation either side of the mean. Dimensions in mm. Characters illustrated in text-fig. 6. Halftone illustrations - *G. (B.) pictaviensis*: ONCP EM 35001 (left), LEIUG 61920; *C. beaumonti*: LEIUG 61452 (left), 101333; all $\times 0.4$.

fig. 11A), bears out Sylvester-Bradley's (1959, MS notes) and Brannan's (1983) conclusions regarding the evolution of *C. beaumonti* from *B. pictaviensis*.

In that the available data (text-fig. 6A, B) point to an inverse relation between size (P_{\max}) and the proportion of ribbed morphs, a comparable form of covariation also exists in the *koenigi* subzone. However, the details of the relationship are different (the two populations from the *koenigi* subzone would plot well above the *levesquei*-zone regression in text-fig. 11A), so in respect of the actual morphologies developed, information derived from study of geographical variation in *G. (B.) pictaviensis* lends only qualified support to the idea that but one lineage exists in the *koenigi* subzone. However, the fact that the whole array of Bathonian–Callovian populations displays a quite clear relationship between size and the incidence of ribbing (text-fig. 6A, B) provides further evidence that they form part of an evolutionary continuum, even though the details of the relationship are obviously different from those applying to *G. (B.) pictaviensis*.

We noted above in discussion of gross shell dimensions of Bathonian–Callovian forms the possibility that variation might be of an ecophenotypic rather than genetic nature (cf. Johnson 1981), being related to differences in rate of size increase. Clearly, since the proportion of ribbed morphs in Toarcian–Aalenian populations shows such a close relationship to adult size, we must also consider the possibility that this character is under ecophenotypic control. However, unlike gross shell dimensions, whose allometric growth must *inevitably* result in different patterns of size/shape development if the relative rate of size increase is altered, there is no obvious reason why a higher incidence of ribbing should result from stunting (or more smooth forms from the reverse). For this reason genetic rather than ecophenotypic explanations for ribbing variation must be preferred. However, it is worth noting that Medcof (1949) documented ecophenotypic development of ribbing (albeit of a rather different form) in conjunction with reduced rates of growth in the living oyster *Crassostrea virginica* (Gmelin). In this case the determining factor appears to have been exposure to sunlight. Other cases of ecophenotypic variation in rib strength are known (Stenzel 1971).

Gross shell dimensions. Data for four of the *G. (B.) pictaviensis* populations and for the single *C. beaumonti* population are presented in text-figure 11B–D. Secondary regressions (see discussion of Bathonian–early Callovian forms) calculated from values corresponding to the largest individuals in each population have slopes near to unity in the case of the H/P and H/L plots. In respect of these ratios, therefore, adult shape is almost identical amongst the populations and can be interpreted, as before, as a product of heterochronic change in the rates of either size or shape development. In view of the stratigraphic equivalence of four of the populations, an ecophenotypic control is conceivable. The relatively poor approximation of the L/P secondary regression to a slope of unity might well be a result of the small size range of the AVB sample (P: 14–43 mm), leading to an unrepresentative primary regression and consequently inappropriate coordinates for 'adult' L/P (derived by projection of the value for P_{\max} onto the regression) in this sample. There is therefore no special reason to doubt that overall adult shape was much the same amongst Toarcian and Aalenian populations, as amongst Bathonian and Callovian populations.

Additional features. Data for shell obliquity, attachment area dimensions and peripheral height of the ribbed zone (text-fig. 11E–H) show no significant difference between the *opalinum* zone population and the *levesquei* zone samples. There are thus no reasons to doubt that *C. beaumonti* evolved from *G. (B.) pictaviensis* on the bases of these data.

Summary and Conclusions

None of the features considered suggests a fundamental discontinuity between *G. (B.) pictaviensis* and *C. beaumonti*, and the patterns of variation in size and the incidence of ribbing, and in gross shell dimensions, provide particularly compelling evidence that these conventionally generically-separated species have an ancestor–descendant relationship. Analogies with the pattern of variation

in Bathonian–Callovian forms support the conclusion that Callovian *Bilobissa* evolved from *Catinula*.

The earlier group of *Bilobissa/Catinula* provides particularly strong grounds for suspecting that variation might be, at least partly, under ecophenotypic control. This possibility could be substantiated by demonstration of a facies correlation. ALAJ visited Poitou to examine sites yielding forms referable to *G. (B.) pictaviensis* and *C. beaumonti* but could find little significant correlation with sedimentary or biofacies. Both forms occur in marls and marly limestones with an apparently fully marine fauna including belemnites and articulate brachiopods. Ammonites are rare in association with *C. beaumonti*, and other bivalves with *G. (B.) pictaviensis*, but it is doubtful whether this has great environmental significance. A slight change in water depth may be implied (see also Gabilly 1973). It is possible that temperature differences might have little impact on sedimentation and the general composition of the fauna, and yet influence form in the *Bilobissa/Catinula* group. A salinity effect is an alternative explanation, but rather less plausible given the apparently marine fauna associated with both *G. (B.) pictaviensis* and *C. beaumonti*. Certainly mollusc growth rates are affected by both these factors (Vermeij 1980; Tevesj and Carter 1980). Isotopic analysis of shell material would be a way of evaluating these possibilities (Tann and Hudson 1974; Rye and Sommer 1980). A control by the amount and/or intensity of sunlight is worth considering (cf. above) but, other than perhaps variation in aquatic plant growth, it is difficult to conceive a cause for significant sunlight variation, given the geographical proximity and apparently similar palaeoenvironments of the populations.

We have attempted to investigate further the possibility of ecophenotypic variation by an analysis of size in relation to age (as determined by ligamental growth bands; cf. Hallam 1982). Thus far the investigation has shown only the difficulty of reliable age determination in relatively small shells. However, this method provides, at least in principle, a means for establishing that differences exist in the rate of size (rather than shape) development: a reasonable basis in our view for considering allometry-related 'static' variation to be ecophenotypic. In the absence of such information it is best to assume that all the variation described herein is genetic (see also above).

Brannan (1983) considered that the evolution of *C. beaumonti* from *G. (B.) pictaviensis* represented an example of progenesis (cf. Gould 1977). However, we have shown that the transition involves something more than a simple truncation of development because of the increased frequency of ribbed morphs. Moreover, in the case of gross shell dimensions, the relative rates of size and shape development are altered. We would nevertheless agree with Brannan that the origin of *Catinula* in a small area (Poitou) at the margins of the ancestral species' range represents a classic case of allopatric speciation. Insofar as the evolution occurs between adjacent ammonite zones and in the time taken for the deposition of only 2–3 m of sediment it also appears to represent a case of punctuational speciation (Eldredge and Gould 1972). However, morphological stasis either side of the evolutionary burst remains to be demonstrated, and in our view does not exist (see also Brannan 1983).

EVIDENCE FROM OTHER MIDDLE JURASSIC *CATINULA* AND *BILOBISSA*

Brannan (1983) has reviewed the morphology and taxonomy of the Aalenian–Bathonian group of *Bilobissa* and *Catinula* stratigraphically intermediate between the two groups considered in detail above. He found no difficulty in differentiating *Bilobissa* and *Catinula*, a point which we can endorse in the case of this group of forms. There exist populations of medium to large-sized forms which never develop umbonal ribbing on the left valve and populations of small to medium-sized forms

EXPLANATION OF PLATE 3

Figs. 1–20. *Gryphaea (Bilobissa)* Stenzel – population PL2 (LEIUG 104872–104891 respectively): variation in external morphology of left valves. 2, 3 and 11, ribbed morphs; remainder smooth; all $\times 1.7$.



JOHNSON and LENNON, *Gryphaea (Bilobissa)*

Stages	Zones	<i>G. (Bilobissa)</i>	<i>Catinula</i>
CALLOVIAN	Jason		
	Caloviense		
	Macrocephalus		
BATHONIAN	Discus		
	Aspidoides		
	Hodsoni		
	Morrisi		
	Subcontractus		
	Progracilis		
	Tenuiplicatus		
	Zigzag		
	Parkinsoni		
BAJOCIAN	Garantiana		
	Subfurcatum		
	Humphriesianum		
	Sauzei		
	Laeviuscula		
AALENIAN	Discites		
	Concavum		
	Murchisonae		
	Opalinum		
TOARCIAN	Levesquei		
	Thouarsense		
	Variabilis		

TEXT-FIG. 12. Zonal occurrence of *Gryphaea (Bilobissa)* and *Catinula* in the European mid-Jurassic. Based on material in the Sylvester-Bradley oyster collection and records in Bayer *et al.* (1985). *Gryphaea (Bilobissa)* occurrence in the early Bathonian (*G. (B.) gallica* Fischer, 1964) arbitrarily assigned to the *tenuiplicatus* zone. Zonal scheme is that of Cope, Duff *et al.* (1980) and Cope, Getty *et al.* (1980).

which include smooth and ribbed individuals. The first set can be assigned unequivocally to *Bilobissa* and the second, in view of the lack of any tendency for populations of relatively large individuals to show a reduced incidence of ribbing, to *Catinula*. It seems therefore that two lineages existed side by side during the Aalenian to early Bathonian interval. The implied genetic distinction supports our conclusion that the transitions from *Bilobissa* into *Catinula*, and subsequently of *Catinula* into *Bilobissa*, represent genuine evolutionary changes. Nevertheless, in plotting the zone-by-zone occurrences of *Catinula* and *Bilobissa* through the mid-Jurassic interval (text-fig. 12) we have noted the interesting fact that distributions are largely mutually exclusive. This again gives pause for thought that the two forms might be ecophenotypes (the products of secular environmental change), although oscillatory evolution is perhaps equally plausible. In the absence of intergradation in Aalenian to early Bathonian forms the most appropriate interpretation remains, however, that two separate lineages existed during this interval. The 'Sylvester-Bradley' model for the ancestry of Callovian *Bilobissa* (route I in text-fig. 1) can therefore be accepted in its entirety.

The absence of intergradation in Aalenian to early Bathonian forms also renders implausible any explanation for the morphological trends subsequently occurring in *Catinula* in terms of the introgression of *Bilobissa* genes (cf. above). A 'reticulate evolution' model (Sylvester-Bradley 1977), involving gene transfer between coexistent *Catinula* and *Bilobissa*, cannot therefore be sustained. It remains to be seen whether the reticulate evolution model is applicable in the more restricted sense in which it was actually proposed by Sylvester-Bradley for mid-Jurassic gryphaeate oysters. It was implied that gradual evolution in *Catinula* was the result of geographical differentiation *within* the taxon, followed (necessarily, for the applicability of the model) by introgression between demes. In fact, as noted above, those populations allegedly evincing geographical differentiation (supposedly forming a semi-discrete 'eastern' lineage) are all of early Bathonian age. Thus only for this interval does it seem possible that evolution in 'western' populations (analyzed above) was influenced by introgression. The evolution of the highly variable species *Gryphaea (Bilobissa) pictaviensis*

into relatively invariant *Gryphaea* (*Bilobissa*) and *Catinula* lineages could be interpreted as representing the first ('eruptive') and last ('stabilized') phases of a reticulate evolution cycle. However, it is not possible to say whether there was an intervening ('reticulate') phase involving introgression between demes.

Following our rejection of Hallam's model for the origin of European Callovian *Bilobissa* (route II in text-fig. 1) we must conclude that European Toarcian-early Bathonian *Bilobissa* represent a lineage that became extinct sometime in the Bathonian. If we follow Brannan's (1983) proposition that the three early Bathonian *Bilobissa* specimens (referred to *Gryphaea* (*B.*) *gallica* Fischer) are unrelated to earlier forms, then the last representatives of the lineage may be late Bajocian.

A MODEL FOR THE DEVELOPMENT OF RIBBING IN GRYPHAEATE OYSTERS

We have noted that in both the Toarcian-Aalenian and Bathonian-early Callovian groups of *Catinula* and *Bilobissa* considered above, geometrical similarity is maintained in adult forms despite differences in size. This might result from changes in the rate of shape development proportionate to length of life (and hence time available for size increase). However, a simpler alternative is that it results from a variable rate of size increase and a fixed longevity and rate of shape development. If we assume that *Catinula* and *Bilobissa* were characterized by different rates of size development we can develop a conceptual model which accounts for the relationship between ribbing incidence and size.

The growth rate model is set out in text-figure 13 and requires the existence of a 'zone of ribbing' in size/age space. Its shape is defined by the need to account for:

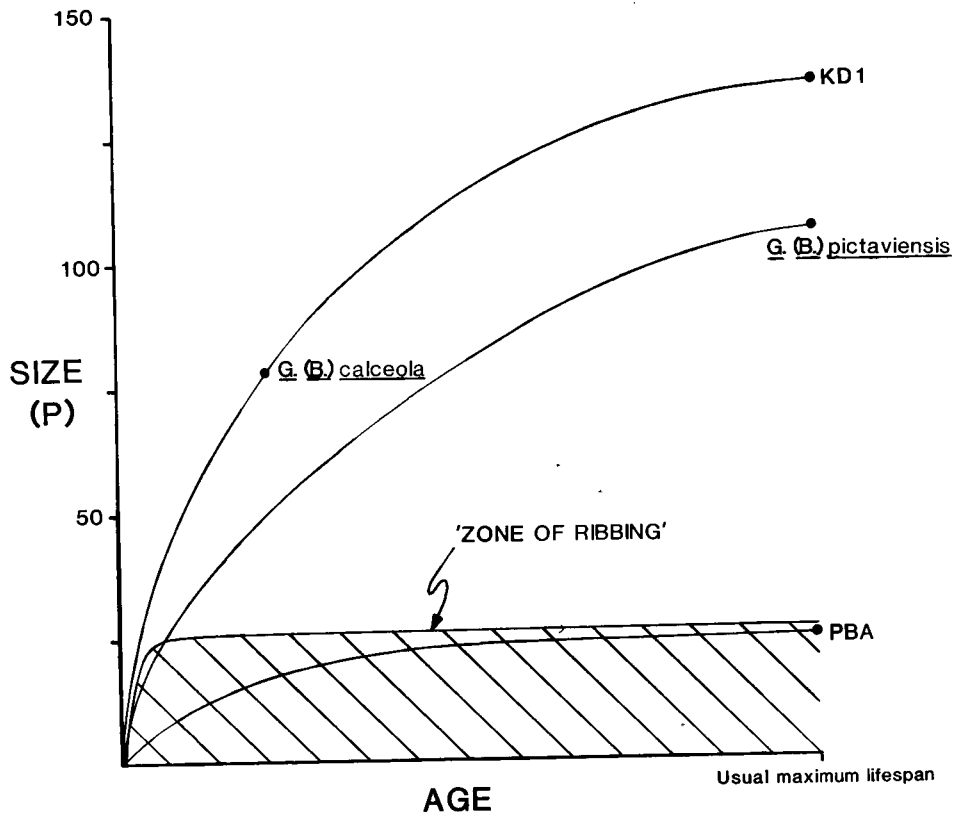
(1) ubiquitous ribbing in PBA (the most 'catinulate' population; smallest and with inferred slowest growth), combined with the late ontogenetic development of a smooth shell in the largest individuals in this population (text-fig. 8F);

(2) a complete absence of ribbing in KD1, the *Bilobissa* population attaining the largest size (inferred fastest growth).

A form such as *Gryphaea* (*B.*) *pictaviensis* fits satisfactorily into this model because, with its smaller average maximum size, it may be predicted to have had a lower growth rate and would thus pass through the 'zone of ribbing' in early ontogeny. That *G.* (*B.*) *pictaviensis* has an intermediate rate of growth could, in theory, be tested by determinations of age in relation to size through analysis of growth-bands (see above). Analysis of other mid-Jurassic forms would provide a further test of the model's applicability. The Aalenian and Bajocian species *G.* (*B.*) *calceola* Quenstedt and *G.* (*B.*) *sublobata* (Deshayes) both completely lack umbonal ribbing. A specimen (LL 35353) of the latter in the British Museum (Natural History) has a peripheral height of 260 mm, far in excess of the unribbed early Callovian population KD1, so the lack of ribbed morphs in *G.* (*B.*) *sublobata*, which presumably grew very rapidly, accords with expectation. By contrast the maximum peripheral height of *G.* (*B.*) *calceola* is about 75 mm, equivalent to that of the smallest (frequently ribbed) *G.* (*B.*) *pictaviensis* population. This anomaly might be explained by growth at a rate similar to KD1 but death at a relatively young age (text-fig. 13), a proposition which could be tested by growth-line analysis.

There appears to be no difference in the size attained by smooth and ribbed morphs in populations including both. This probably implies within-population variation in the shape of the zone of ribbing since a variety of age/size curves, all terminating at the same size, seems a less plausible explanation. This, in turn, is most easily interpreted as an aspect of genetic, rather than ecophenotypic, variation. The existence of genetic variation of this type also helps to explain the non-monotonic relationship between maximum size and proportion of ribbed morphs in Bathonian-early Callovian *Catinula* and *Bilobissa*. Therefore, we again reach the conclusion that evolutionary change is involved in this sequence of forms.

We may be able to show that there are differences in growth rate amongst the forms under consideration but this does not prove that they cause differences in the development of ribbing - i.e. that a 'zone of ribbing' of the shape indicated exists in size/age space. We can however put



TEXT-FIG. 13. Model to explain the occurrence of ribbing in *Catinula* and *Gryphaea* (*Bilobissa*) as a function of growth rate. Curves represent predicted typical growth rates for PBA (a *Catinula* population entirely composed of ribbed morphs), KD1 (a *G. (Bilobissa)* population entirely lacking ribbed morphs), and an average *G. (B.) pictaviensis* population (with an admixture of smooth and ribbed morphs). Solid circles represent maximum size (peripheral height: P) in each of these populations, and for the unribbed species *G. (B.) calceola* which is predicted to have grown rapidly but to have had a short lifespan. See text for further explanation. P in mm.

forward functional arguments, relating to habitat and mode of life, for the existence of such a zone.

Contrary to the opinion of Brannan (1983), it is our experience that *Catinula* and *Bilobissa* occur in remarkably similar sedimentological settings. Both occur most commonly in relatively isolated shell beds within clay-grade sequences. These probably represent winnowed horizons (a slightly coarser grain size and reworked shell material are common associates) which afforded a slightly firmer substrate for colonization (see also Bayer *et al.* 1985). There is an approximately equal (low) incidence of overturning in *Bilobissa* shell beds and those containing *Catinula*, so the energy of the environment cannot have been very different. Occasional occurrences of *Catinula* in very high-energy oolite deposits (e.g. Brannan 1983, p. 293) may represent transported assemblages.

Reclining bivalves, such as gryphaeate oysters, typically display some adaptation towards maintaining stability on the sea floor (Stanley 1970). Two such adaptations, large size and a thick shell, are exhibited by *Gryphaea* itself; more particularly the former in the case of *Bilobissa*. Neither condition can, however, exist without significant growth so these adaptive strategies require rapid growth for maximum efficiency. Given an inability (genetic or otherwise) to grow fast, other strategies for obtaining stability might prove superior. Brannan (1983) has suggested that the ribs of *Catinula* might function to provide stability by gripping the sediment. While secretion of ribs

entails a diversion of shell material from pure size increase, it might, at generally small sizes (and under the same hydrodynamic regime), confer a stability greater than that obtained by a slight increase in size. As such it would be a better adaptive strategy in situations where rapid growth to large size is not possible. Obviously, flume tank experiments (cf. Hallam 1968) afford a means of testing this proposition.

In conclusion, our suggestion is that the transition from *Bilobissa* to *Catinula* and then back to *Bilobissa* (as manifested in size, ribbing incidence and gross shell dimensions) may represent a response to environmental conditions which favoured, respectively, rapid, then slow, then rapid growth. Of what seem the two most plausible controlling factors, temperature and salinity (see above), the former is more likely to be implicated in view of the occurrence of *Catinula* in apparently fully marine Aalenian assemblages. However, the notion of salinity control should not be abandoned completely. Bathonian reduced-salinity faunas have been widely documented in northern Europe (Hudson 1980; Hudson and Palmer 1976; Palmer 1979). At this time *Catinula* was present in huge numbers, to the almost total exclusion of *Bilobissa*. However, it has to be said that the particular assemblages containing *Catinula* are south of the main areas of freshwater influence and do not provide any clear indications of abnormal salinity. It is worth noting here that European Bathonian scallops attain only modest dimensions (Johnson 1984), and other bivalves seem to be generally small.

TAXONOMY

Having shown that *Gryphaea* (*Bilobissa*) is diphyletic it would be our preference to separate the earlier and later lineages taxonomically. This would involve creation of a new subgeneric name for the later group of European forms since *Bilobissa*, whose type species is Bajocian (Duff 1978), is clearly best reserved for the earlier group. In the present state of knowledge we could only offer a 'stratigraphic' diagnosis for the new subgenus. This would not appear to satisfy the provisions of Article 13 (a) (i) of the 'International code of zoological nomenclature' (Ride *et al.* 1985, p. 35) which states that new names must be 'accompanied by a description or definition that states in words characters that are purported to differentiate the taxon'. European Callovian *Gryphaea* (and descendant forms) must therefore still be referred to *Bilobissa* until such time as an apomorphy is discovered which can be used as a basis for the erection of a new subgeneric name.

Since *Catinula* is evidently an integral part of *Gryphaea* phylogeny it seems appropriate, as indicated earlier, to demote the taxon to subgeneric rank within *Gryphaea*. The features distinguishing *G.* (*Catinula*) from the closely related subgenus *G.* (*Bilobissa*) were outlined earlier in discussion of generic differentiation. It remains to give precise definitions of *G.* (*Catinula*) and *G.* (*Bilobissa*). The following diagnoses are therefore provided, constructed so that the boundaries of the taxa correspond most nearly with previous conceptions of *Catinula* and *Bilobissa*:

G. (*Bilobissa*) Stenzel 1971, p. N1099. Medium-sized *Gryphaea*; adult peripheral height greater than 45 mm. Usually deep radial posterior sulcus in adults with posterior flange well detached. Radial ribbing on umbonal region of left valve present in 0–80% of individuals in populations. Lower–Upper Jurassic; Europe, Asia, N. Africa, N. and S. America. *Type species*: *Gryphaea bilobata* J. de C. Sowerby, 1835, p. 244 (= 1840, Alphabetic index, p. 4; = *G. dilatata* var. β . J. Sowerby, 1816, p. 113, pl. 149, fig. 2), Inferior Oolite (Bajocian), England; original designation by Stenzel (1971, p. N1099). See Duff (1978, pp. 76, 77) for further details.

G. (*Catinula*) Rollier 1911, p. 272. Small *Gryphaea*; adult peripheral height less than 45 mm. Radial ribbing present on left (and commonly right) valve of 40–100% of individuals in populations. Middle Jurassic; Europe. *Type species*: *Ostrea knorri* Voltz (= *O. knorrii* Voltz, 1828, p. 60), Bathonian, Schönmat, near Basel, Switzerland; subsequent designation by Arkell (1932, pp. 149, 180).

These diagnoses may be used in conjunction with the extensive generic diagnoses of Stenzel (1971) and Duff (1978), amended slightly to incorporate the findings of this study so that *Gryphaea*

includes: *a*, forms which are small as adults and therefore neither particularly thick-shelled nor enrolled; *b*, forms with a weakly convex dorsal margin to the adductor scar; and *c*, prosogyrous forms.

CONCLUSIONS

(1) Forms of *Gryphaea* referable to the subgenus *Bilobissa* have evolved iteratively (at least twice).

(2) European Callovian *Bilobissa* arose from the small, ribbed, gryphaeate oyster *Catinula* by evolution over an interval of about 6 Myr (the duration of the Bathonian stage according to Harland *et al.* 1982). Change in single characters followed differing patterns – varying between unidirectional and at a steady rate, and oscillatory – but was never punctuational. Evolution between *Catinula* and Callovian *Bilobissa* can therefore best be described as gradualistic (cf. Sheldon 1987).

(3) *Catinula* apparently evolved from *Bilobissa* at the Toarcian/Aalenian boundary in the Poitou region of France. Evolution occurred rapidly in a peripheral isolate population (allopatric speciation).

(4) *Catinula* is best regarded as a subgenus of *Gryphaea*.

(5) The evidence for morphological stasis in mid-Jurassic *Gryphaea* (*Bilobissa*) is suspect and, notwithstanding point 3 above, the occurrence of punctuated equilibrium must be doubted.

(6) An early *G.* (*Bilobissa*) lineage became extinct in the late Bajocian or early Bathonian, its extinction perhaps being due to the development of cooler or less fully marine conditions in which an adaptive strategy involving rapid growth became inviable.

(7) Evolution of *G.* (*Catinula*) possibly introduced an adaptive strategy for maintaining shell stability under environmental conditions (? lowered temperatures or salinities) which precluded the acquisition of stability whilst reclining by the development of a large shell.

(8) The small size of *Gryphaea* (i.e. *G.* (*Catinula*)), and of other bivalves, during the Bathonian in Europe should serve as an impetus for further geochemical studies to investigate the possibility of large-scale environmental (? climatic) changes during the stage. Investigations should also be made of the palaeoenvironments of variably-ribbed populations of Bathonian *Praeoxogyra hebridica* (see Hudson and Palmer 1976).

(9) Both factual and philosophical considerations strongly favour the view that the transitions between *G.* (*Bilobissa*) and *G.* (*Catinula*) represent evolution and not merely ecophenotypic responses. However, this should not deter further investigation of the involvement of ecophenotypic variation (e.g. by analysis of growth lines to establish the relationship between size, shape and age). The close correspondence of patterns of variation to those which might be expected under circumstances of environmental control raises the possibility that evolution may have involved the 'genetic assimilation' of ecophenotypic variation (Waddington 1957; see also Matsuda 1982).

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REFERENCES

- ARKELL, W. J. 1929–37. A monograph of British Corallian lamellibranchs. *Palaeontographical Society, (Monographs)*, (1), 1929, 1–72; (2), 1930, 73–104; (3), 1931, 105–132; (4), 1932, 133–180; (5), 1933, 181–228; (6), 1934, 229–276; (7), 1934, 277–324; (8), 1935, 325–350, i–xvi; (9), 1936, 351–376, xvii–xxii; (10), 1937, 377–392, xxiii–xxxviii.
- 1934. The oysters of the Fuller's Earth; and on the evolution and nomenclature of the Upper Jurassic *Catinulas* and *Gryphaeas*. *Proceedings of the Cotteswold Naturalists' Field Club*, **25**, 21–68.
- 1947. The geology of the country around Weymouth, Swanage, Corfe and Lulworth. *Memoirs of the Geological Survey of the United Kingdom*, 386 pp.
- BAYER, U., JOHNSON, A. L. A. and BRANNAN, J. 1985. Ecological patterns in Middle Jurassic *Gryphaea*: the relationship between form and environment. In BAYER, U. and SEILACHER, A. (eds.). *Sedimentary and evolutionary cycles* (Lecture notes in earth sciences, **1**), 436–463. Springer, Berlin and Heidelberg, 465 pp.
- BRANNAN, J. 1983. Taxonomy and evolution of Triassic and Jurassic non-lophate oysters. D. Phil. thesis (unpubl.), 2 vols., University of Oxford.
- CALLOMON, J. H. 1968. The Kellaways Beds and Oxford Clay. In SYLVESTER-BRADLEY, P. C. and FORD, T. D. (eds.). *The geology of the east Midlands*, 264–290. University Press, Leicester, 400 pp.
- CARTER, J. G. 1980. Environmental and biological controls of bivalve shell mineralogy and microstructure. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms*, 69–113. Plenum, New York and London, 750 pp.
- ČELCOVA, N. A. 1969. *Značenie mikrostruktury rakoviny melovych ustric dlja ich sistematiki*. Nauka, Moscow, 86 pp. [In Russian.]
- CHARLES, R.-P. and MAUBEUGE, P.-L. 1953. Les huîtres plissées jurassiques de l'est du Bassin Parisien (II). *Bulletin du Muséum d'Histoire Naturelle de Marseille*, **12** (for 1952), 113–123.
- CHEETHAM, A. H. 1987. Tempo of evolution in a Neogene bryozoan: are trends in single morphologic characters misleading? *Paleobiology*, **13**, 286–296.
- COPE, J. C. W., DUFF, K. L., PARSONS, C. F., TORRENS, H. S., WIMBLETON, W. A. and WRIGHT, J. K. 1980. A correlation of Jurassic rocks in the British Isles. Part 2. Middle and Upper Jurassic. *Geological Society of London. Special reports*, **15**, 109 pp.
- , GETTY, T. A., HOWARTH, M. K., MORTON, N. and TORRENS, H. S. 1980. A correlation of Jurassic rocks in the British Isles. Part 1. Introduction and Lower Jurassic. *Geological Society of London. Special reports*, **14**, 73 pp.
- COX, L. R. 1946. Undescribed lamellibranchs from the English Inferior Oolite. *Proceedings of the Malacological Society, London*, **27**, 22–32.
- 1952. The Jurassic lamellibranch fauna of Cutch (Kachh). No. 3. Families Pectinidae, Amusiidae, Plicatulidae, Limidae, Ostreidae and Trigoniidae (supplement). *Memoirs of the Geological Survey of India. Palaeontologia Indica*, series 9, **3** (4), 1–128.
- DUFF, K. L. 1978. Bivalvia from the English Lower Oxford Clay. *Palaeontographical Society (Monographs)*, 137 pp.
- ELDREDGE, N. and GOULD, S. J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In SCHOPF, T. J. M. (ed.). *Models in paleobiology*, 82–115. Freeman Cooper, San Francisco, 250 pp.
- FISCHER, J.-C. 1964. Contribution à l'étude de la faune bathonienne dans la vallée de la Creuse (Indre): brachiopodes et mollusques. *Annales de Paléontologie (Invertébrés)*, **50**, 19–101.
- GABILLY, J. 1973. Le Toarcien du Poitou. Doctoral thesis, University of Poitiers, 1 vol. and Annexe 1 (Lithologie et biostratigraphie des ammonites).
- GOULD, S. J. 1972. Allometric fallacies and the evolution of *Gryphaea*: a new interpretation based on White's criterion of geometric similarity. *Evolutionary biology*, **6**, 91–118.
- 1977. *Ontogeny and phylogeny*. Harvard University Press, Cambridge, Massachusetts, 501 pp.
- 1980. (ed.). *The evolution of Gryphaea*. Arno, New York. (Collected papers, no sequential pagination.)
- HALLAM, A. 1968. Morphology, palaeoecology and evolution of the genus *Gryphaea* in the British Lias. *Philosophical Transactions of the Royal Society of London, Series B*, **254**, 91–128.
- 1978. How rare is phyletic gradualism and what is its evolutionary significance? Evidence from Jurassic bivalves. *Paleobiology*, **4**, 16–25.
- 1982. Patterns of speciation in Jurassic *Gryphaea*. *Paleobiology*, **8**, 354–366.
- and GOULD, S. J. 1975. The evolution of British and American Middle and Upper Jurassic *Gryphaea*: a biometric study. *Proceedings of the Royal Society of London, Series B*, **189**, 511–542.

- HARLAND, W. B., COX, A. V., LLEWELLYN, P. G., PICKTON, C. A. G., SMITH, A. G. and WALTERS, R. 1982. *A geological time scale*. Cambridge University Press, Cambridge, 131 pp.
- HUDSON, J. D. 1980. Aspects of brackish-water facies and faunas from the Jurassic of north-west Scotland. *Proceedings of the Geologists' Association*, **91**, 99–105.
- and PALMER, T. J. 1976. A euryhaline oyster from the Middle Jurassic, and the origin of the true oysters. *Palaeontology*, **19**, 79–93.
- JOHNSON, A. L. A. 1981. Detection of ecophenotypic variation in fossils and its application to a Jurassic scallop. *Lethaia*, **14**, 277–285.
- 1984. The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe. *Zitteliana*, **11**, 1–235.
- MATSUDA, R. 1982. The evolutionary process in talitrid amphipods and salamanders in changing environments, with a discussion of 'genetic assimilation' and some other evolutionary concepts. *Canadian Journal of Zoology*, **60**, 733–749.
- MEDCOF, J. C. 1949. Effects of sunlight exposure in rearing young oysters. *Journal of the Fisheries Research Board of Canada*, **6**, 209–216.
- PALMER, T. J. 1979. The Hampen Marly and White Limestone formations: Florida-type carbonate lagoons in the Jurassic of Central England. *Palaeontology*, **22**, 189–228.
- PUGACZEWSKA, H. 1971. Jurassic Ostreidae of Poland. *Acta Palaeontologica Polonica*, **16**, 195–311.
- RIDE, W. D. L., SABROSKY, C. W., BERNARDI, G. and MELVILLE, R. V. 1985. *International code of zoological nomenclature*. Third edition. International Trust for Zoological Nomenclature, London, xx + 338 pp.
- ROLLIER, L. 1911. *Les faciés du Dogger ou Oolithique dans le Jura et les régions voisines*. Fondation Schnyder von Wartensee (Mémoire), Zürich, 352 pp.
- RYE, D. M. and SOMMER, M. A., II. 1980. Reconstructing paleotemperature and salinity regimes with oxygen isotopes. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms*, 169–202. Plenum, New York and London, 750 pp.
- SHELDON, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. *Nature, London*, **330**, 561–563.
- SIEWERT, W. 1972. Schalenbau und Stammesgeschichte von Austern. *Stuttgarter Beiträge zur Naturkunde, Series B*, **1**, 1–57.
- SOWERBY, J. 1815–18. *The mineral conchology of Great Britain*, **2**, (1), 1815, 1–28; (2), 1816, 29–116; (3), 1817, 117–194; (4), 1818, 195–239. Meredith, London.
- SOWERBY, J. DE C. 1826–46. *The mineral conchology of Great Britain*, **6**, (1), 1826, 1–86; (2), 1827, 87–156; (3), 1828, 157–200; (4), 1829, 201–235; Preface to the general indexes and systematic index to the six volumes, 1835, 239–250; 7, Alphabetic index to volumes 1–6, 1840, 1–11; (1), 1840?, 1–8; (2), 1841, 9–16; (3), 1843, 17–24; (4), 1844, 25–56; (5), 1846, 57–80. Meredith, London.
- STANLEY, S. M. 1970. Relation of shell form to life habits in the Bivalvia (Mollusca). *Memoirs. Geological Society of America*, **125**, 1–296.
- STENZEL, H. B. 1971. Oysters. N953–N1224. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Bivalvia 3*. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- SYLVESTER-BRADLEY, P. C. 1958. The description of fossil populations. *Journal of Paleontology*, **32**, 214–235.
- 1959. Iterative evolution of fossil oysters. *Proceedings of the XVth International Congress of Zoology, London*, section 2, 193–197.
- 1977. Biostratigraphical tests of evolutionary theory. In KAUFFMAN, E. G. and HAZEL, J. E. (eds.). *Concepts and methods of biostratigraphy*, 41–63. Dowden, Hutchinson and Ross, Stroudsburg, 658 pp.
- TANN, F. C. and HUDSON, J. D. 1974. Isotopic studies of the palaeoecology and diagenesis of the Great Estuarine Series (Jurassic) of Scotland. *Scottish Journal of Geology*, **10**, 91–128.
- TEVESJ, M. J. S. and CARTER, J. G. 1980. Environmental relationships of shell form and structure of unionacean bivalves. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms*, 295–322. Plenum, New York and London, 750 pp.
- VERMEIJ, G. J. 1980. Gastropod shell growth rate, allometry, and adult size: environmental implications. 379–394. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms*. Plenum, New York and London, 750 pp.
- VOLTZ, P. L. 1828. Uebersicht der Petrefakten der beiden Rhein-Departemente. In AUFSCHLAGER, J. F. *Das Elsass oder die Departemente des Ober- und Niederrheins* (Supp.), Heitz, Strasbourg, 64 pp.

WADDINGTON, C. H. 1957. *The strategy of the genes*. George Allen and Unwin, London, 262 pp.

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