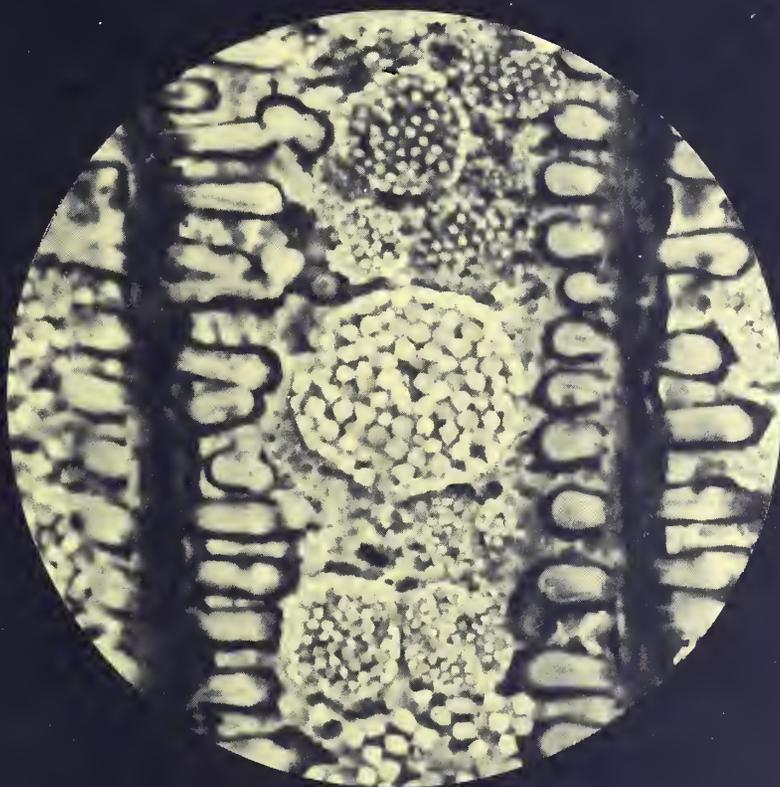


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PRESERVATION OF SOFT-BODIED AND OTHER ORGANISMS BY BIOIMMURATION – A REVIEW

by P. D. TAYLOR

ABSTRACT. Bioimmuration is a poorly-known mode of preservation which results from organic overgrowth of sessile organisms. Soft-bodied organisms (and organisms with lightly mineralized skeletons) can be preserved if overgrown by other organisms possessing mineralized skeletons. These bioimmured fossils are visible on the attachment areas of the overgrowing organisms as natural moulds which sometimes become filled by diagenetic mineral growth to give a natural cast. Three types of bioimmuration are distinguished: substratum bioimmuration, epibiont bioimmuration and bioclaustration. Common bioimmuring organisms include oysters and oyster-like cemented bivalves, serpulid worms and cyclostome bryozoans. Among organisms found preserved by bioimmuration are algae, marine angiosperms, hydroids and ctenostome bryozoans. Most documented finds of bioimmured fossils are from the post-Palaeozoic, especially the late Cretaceous, reflecting both the stratigraphical distribution of potential bioimmuring organisms and concentration of research effort. Future finds of bioimmured fossils offer considerable scope for adding to our knowledge of the fossil history and ecological contributions of soft-bodied organisms living on firm or hard substrata.

SEDIMENTS containing fossils of soft-bodied marine organisms (i.e. organisms lacking mineralized skeletons) provide invaluable windows into parts of the biosphere which are normally unavailable to the palaeontologist. Several such deposits, described as fossil Lägerstätten, have been intensively studied, notably the Burgess Shale, Hünshuck Shale and Solnhofen Limestone (e.g. see papers in Whittington and Conway Morris 1985). Instrumental in the preservation of these soft-bodied biotas were rather special taphonomic factors generally involving rapid burial in fine-grained sediments and inhibition of organic decay. Because these circumstances have occurred rather infrequently during the Phanerozoic, soft-bodied Lägerstätten are comparatively rare in the marine record.

In contrast, bioimmuration is a process of organic overgrowth which routinely results in the preservation of sessile soft-bodied organisms in unexceptional palaeoenvironments. Very few studies have been undertaken of bioimmuration, and even the existence of this important mode of preservation is poorly known among palaeontologists. Vialov (1961) first recognized immuration as a mode of fossilization. He distinguished two types of immuration: lithoimmuration (e.g. envelopment of snakes by calcareous tufa during hibernation) and bioimmuration (e.g. overgrowth of balanid barnacles by oysters). Only Voigt (1956, 1966, 1968*a, b*, 1972, 1973*a, b*, 1977, 1979, 1980, 1981, 1983; Voigt and Harmelin 1986) has published extensively on bioimmured fossils in a series of mostly German language papers, mainly dealing with bioimmured fossils from the late Cretaceous Chalk-Tuff of Maastricht. The present paper sets out to review the process of bioimmuration and the variety of soft-bodied organisms which have been found as bioimmured fossils.

Specimen repositories: figured specimens are in the collections of the British Museum (Natural History) (abbreviated BMNH) and the Voigt Collection, Universität Hamburg (VH).

TYPES AND PROCESSES OF BIOIMMURATION

To 'immure' means to imprison. Sessile organisms are routinely bioimmured when partially or completely overgrown by other organisms. If the overgrowing organism possesses a mineralized skeleton, then the basal surface of this skeleton may carry a preservable replicate in negative relief

of the upper surface of the overgrown organism. Such natural moulds are bioimmurations of soft-bodied organisms. For example, many species of present-day animals and plants live as epiphytes on the fronds or stipes of marine plants. The attached undersides of these epiphytes are often adpressed very closely to their plant substrata, thereby creating a natural mould which is revealed when the epiphyte is detached from its substratum. Similarly, epiphytes sharing the same plant substratum are often found to overgrow one another. This too may result in a natural mould of the overgrown (or bioimmured) epiphyte on the base of the overgrowing (or bioimmuring) epiphyte.

It is useful to distinguish three principal types of bioimmuration: (1) *substratum bioimmuration* in which the organism being overgrown is the substratum for the bioimmuring organism (text-fig. 1A); (2) *epibiont bioimmuration* in which the overgrowing and overgrown organism share the same substratum (text-fig. 1B); (3) *bioclaustration* in which the substratum is a living organism and is itself responsible for overgrowing the bioimmured organism (text-fig. 1C).

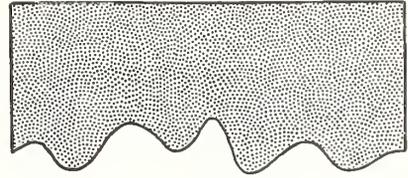
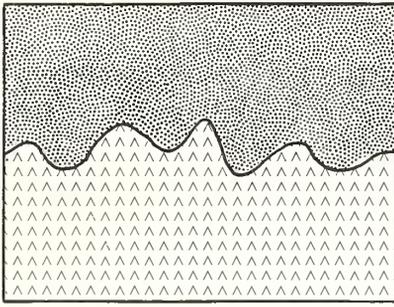
Substratum bioimmurations are two component systems (substratum organism + bioimmuring organism). For example, an impression of an algal frond on the attachment area of an oyster which lived as an algal epiphyte is a substratum bioimmuration. Epibiont bioimmurations are three component systems (substratum + bioimmuring encruster + bioimmured encruster). If two bryozoans encrust the same bivalve shell and one overgrows the other, then the mould of the overgrown bryozoan on the base of the overgrowing bryozoan is an epibiont bioimmuration (note that the term epibiont is here used in accordance with the recommendation of West 1977 for an organism living on rather than within a substratum; there is no implication regarding the nature of the substratum). Bioclaustrations are a special type of bioimmuration with two components (combined substratum/bioimmuring organism + bioimmured organism). An example of bioclaustration is the embedment of a sponge growing on the surface of a coral by continued growth of the coral.

Substratum bioimmurations

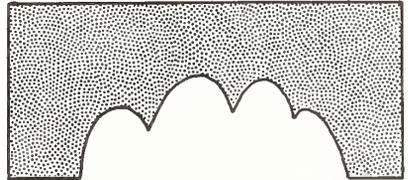
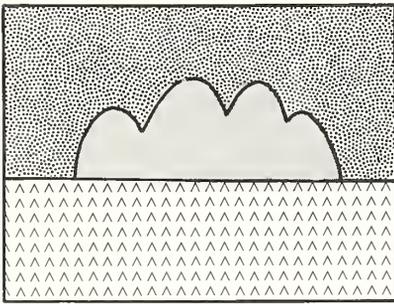
These are a consequence of fouling of a biotic substratum, i.e. the settlement of a larva directly onto the surface of the substratum. Such substrata include organisms alive at the time of fouling and also dead, especially skeletal, remains. Although fouling of the shell can be advantageous in some bivalves which are less likely to be victims of predators when fouled (e.g. Pitcher and Butler 1987), fouling is very often disadvantageous to living organisms, e.g. the photosynthetic output of seaweeds may drop as a result of fouling (Cancino *et al.* 1987), and organisms fouling mussels can increase drag and therefore the probability of dislodgement (Witman and Suchanek 1984). Marine organisms frequently possess defences (e.g. antibiotic surface secretions, see Dyrinda 1986) which enable them to resist being fouled. Nevertheless, fouling is of widespread occurrence, especially on the older parts of marine plants, and away from the actively feeding regions of marine animals. Marine plants, colonial coelenterates, crinoids and other organisms with arborescent morphologies may be particularly favoured substrata because they elevate the fouling organism above the sea-bed where mortality caused by sedimentation, predation and competition may be more severe (Jackson 1979).

Epibiont bioimmurations

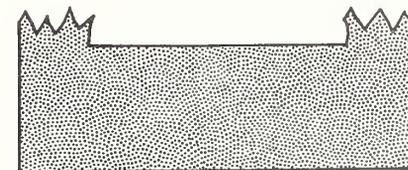
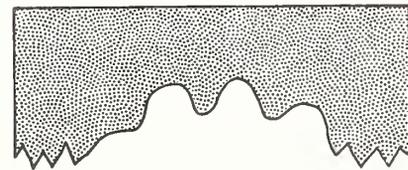
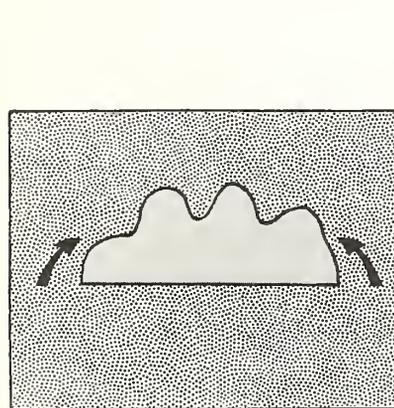
These result from lateral overgrowth in which one encruster encroaches a second encruster along the surface of their shared substratum and succeeds in overgrowing the edges of the second encruster. Overgrowth may entail a living organism growing onto the surface of a dead organism, or it may involve two living organisms in competition for substratum space. Spatial competition can be intense among encrusters colonizing firm or hard substrata, and a wide variety of physical and chemical methods are utilized by living encrusters both to assist in overgrowing competitors and to defend against being overgrown by them (see Buss 1986). Despite these, interspecific overgrowths can occur with great frequency. The effect on the overgrown organism of substantial overgrowth is usually death or, if the overgrown organism is a colonial animal, partial mortality, i.e. death of some of the zooids within the colony but not the entire colony (see Jackson and Hughes 1985). Some



A



B



C

TEXT-FIG. 1. Diagrammatic vertical sections depicting the three types of bioimmuration and their formation. A, substratum bioimmuration; bioimmuration is revealed on the underside of the overgrowing organism (coarse stipple) following loss of the substratum (chevron ornament). B, epibiont bioimmuration; bioimmuration is revealed on underside of overgrowing organism (coarse stipple) following loss of the epibiont (fine stipple) and its substratum (chevron ornament). C, bioclausturation; bioimmuration becomes visible when the embedding organism (coarse stipple), which formed both the substratum and overgrowing organism, is fractured to reveal the mould of the epibiont (fine stipple) within.

bryozoans are now known to survive in a dormant state pending removal of the covering organism (Todd and Turner 1988).

Bioclaustrations

The term bioclaustration was introduced by Palmer and Wilson (1988) to describe the process of embedment of a soft-bodied infesting organism by the skeletal growth of a host organism. The result of embedment is a pseudoboring, often mistaken for a true boring. Palmer and Wilson (1988, p. 940) regarded bioclaustration as distinct from bioimmuration because bioclaustration is 'a response to an interaction that is of one partner's seeking' whereas bioimmuration 'demonstrates chance competition for space'. However, such distinction depends upon the inference of biological processes (host selection and competition) which in most cases cannot be made with sufficient confidence, and are not always mutually exclusive. When bioclaustration is viewed in terms of the resulting pattern (text-fig. 1c), its close relationship to other types of bioimmuration becomes clear. Furthermore, to exclude from the definition of bioclaustration the embedment of organisms with hard skeletons seems inappropriate if bioclaustration is to be viewed as a category of bioimmuration; Vialov (1961) included organisms with mineralized skeletons in his original concept of bioimmuration. Rugose or tabulate corals embedded within the coenostea of stromatoporoids with which they intergrew during life (see Kershaw 1987) are, for example, here regarded as bioclaustrations.

Opportunities for bioimmuration by fouling, overgrowth and embedment are frequent on hard and firm marine substrata at the present day, and there is no evidence that they have been any less so throughout much of the Phanerozoic. 'Skeletal overgrowths' between organisms with mineralized skeletons have often been recorded among ancient hard substratum assemblages (e.g. Taylor 1979, 1984; Liddell and Brett 1982).

PRESERVATIONAL STATES

Most bioimmured fossils are preserved in negative relief as external moulds (Pl. 1, figs. 1, 5–6; Pl. 2, figs. 1 and 2, 4 and 5; text-fig. 2). These moulds become visible only after detachment of the bioimmuring organism from its substratum. If the substratum is perishable, detachment can occur before burial or shortly afterwards; if it is aragonitic, detachment often follows diagenetic shell dissolution. Oysters and many other bioimmuring organisms may remain firmly cemented to calcitic

EXPLANATION OF PLATE I

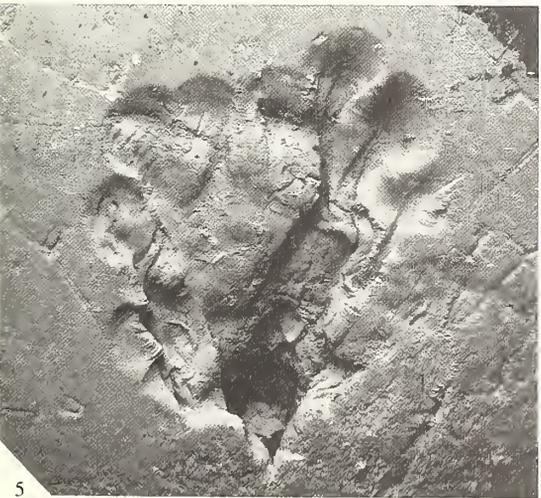
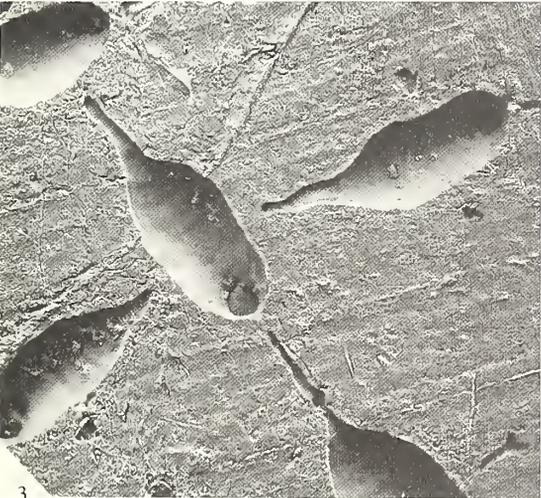
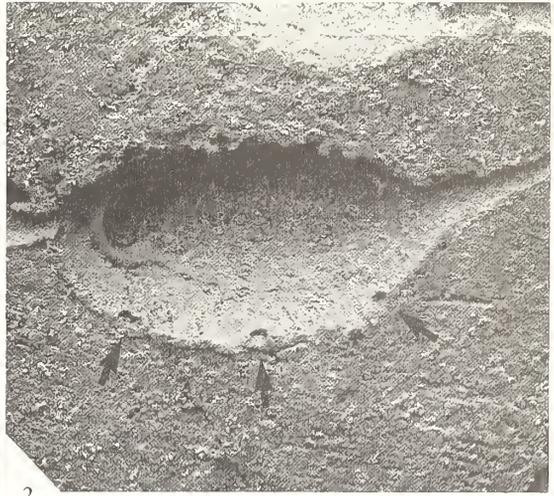
Fig. 1. *Arachnidium smithii* (Phillips), BMNH D 57495, a soft-bodied ctenostome bryozoan preserved as an epibiont mould bioimmuration on the attachment area of *Gryphaea*; note partial collapse of zooid in centre, Villers-sur-mer, Normandy, Oxfordian, $\times 45$.

Fig. 2. *Andriopora major* Larwood, BMNH D 58095, a calcified cribrimorph bryozoan showing 3 pairs of pore chambers (arrowed) which are invisible in conventionally preserved specimens but are seen in this bioimmured zooid on the attachment area of *Pycnodonte vesiculare*, Weybourne, Norfolk, Weybourne Chalk, Campanian, $\times 86$.

Figs. 3 and 4. *Hippothoa flagellum* (Manzoni), BMNH 1988.12.1.1, a calcified ascophoran bryozoan preserved on the attachment area of an overgrowing oyster which encrusted a plastic pipe, Piràn, Adriatic Sea, Recent. 3, zooid (growth direction top left to bottom right) with a distal and two lateral buds, $\times 90$. 4, detail of bud origins showing oyster shell seemingly filling the narrow gap between the slightly raised points of origin of the buds and the substratum, $\times 230$.

Figs. 5 and 6. Bioimmured soft-bodied organisms on the attachment area of the bivalve *Pycnodonte vesiculare*, BMNH H 5501, Thanet, Kent, Santonian, 5, distorted bioimmuration of organism with cusped margins which has collapsed in the direction of overgrowth (top to bottom), $\times 15$. 6, *Eisenackiella thanetensis* Taylor, the erect stem of a probable hydroid pushed flat against the substratum during overgrowth, $\times 25$.

All illustrations are back-scattered electron micrographs of uncoated specimens.



substrata (e.g. other oysters, sedimentary hardgrounds) during fossilization. Therefore, the organisms they overgrew are seldom revealed but may on occasions be visible as hummocks and irregularities on the inner side of the attached valve. Sometimes the mould is filled during diagenesis by calcite or pyrite giving an external cast of the bioimmured organism (see Taylor 1990, text-fig. 1). Cast bioimmurations may become visible through fracturing or exfoliation of the encrusting organism from its substratum. The fidelity of casting can be very high, especially when the casting material is pyrite (Taylor 1990, pl. 2, figs. 1 and 2). Whereas epibiont bioimmurations are found as both moulds and casts, substratum bioimmurations are preserved only as moulds.

Each bioimmuration is formed gradually during the period of progressive overgrowth by the bioimmuring organism. The shorter this period of time, the more likely it is that the process will be completed before significant deterioration of the overgrown organism. Therefore, bioimmurations of the highest fidelity should occur when the bioimmuring organism grows rapidly and/or when the bioimmured organism is small and is consequently overgrown quickly. Organisms which retain their shape during overgrowth should provide the most easily distinguishable bioimmurations. Conversely, flaccid organisms may become flattened and distorted during overgrowth, and can be difficult to identify when bioimmured. The ability of colonial animals such as hydrozoans and bryozoans to sustain partial mortality favours their preservation by bioimmuration because while certain zooids are being overgrown, other zooids remain alive and continue to sustain the colony. Large organisms fouled by small epibionts may be affected insignificantly by overgrowth, suffer little deterioration and therefore yield good quality substratum bioimmurations.

The time required for the formation of a bioimmuration obviously depends on the growth rate of the bioimmuring organism. Rather than being instantaneous 'snap-shots', bioimmurations are summations over time of the morphology of the substratum and its epibionts as they were progressively covered by the advancing growing edge of the bioimmuring organism. This has two implications. First, the morphology of a bioimmured organism need not necessarily correspond to its appearance at any one time during its life. This may be especially true for large and/or colonial organisms which do not suffer mortality immediately on commencement of overgrowth. For example, the single specimen of bioimmured hydroid *Eisenackiella thanetensis* described by Taylor (1988) may have been a large colony or a narrow strip-like colony which inhabited the substratum just in front of the bioimmuring bivalve *Pycnodonte vesiculare* and advanced with growth of the bivalve. Secondly, bioimmurations can document temporal successional changes in the organisms living on firm or hard substrata; the early growth stages of the bioimmuring organism overgrow epibionts recruited during early stages of ecological succession, the later formed parts overgrow epibionts recruited during later successional stages. This offers a potentially useful way of studying short-term ecological succession in fossil material.

Erect components of soft-bodied organisms are generally pushed over during overgrowth and are flattened against the substratum, resting in an orientation parallel to the growth direction of the bioimmuring organism. A good example of this is found in the weakly-calcified cheilostome bryozoan *Aetea* which has been described as a bioimmuration from the Pliocene and Recent by Voigt (1983). The zooids of *Aetea* each have an adnate proximal part and a tall erect distal 'peristome'. Adnate parts of the zooid remain in position during bioimmuration, but erect peristomes are pushed over so that they lie flat and parallel to the growth direction of the bioimmuring oysters and to one another. Similarly (Pl. 1, fig. 6), erect stems of the late Cretaceous hydroid *Eisenackiella thanetensis* were flattened against the substratum by the overgrowing bivalve *Pycnodonte vesiculare*. Interpretation of bioimmured fossils must take into account such distortions. Structures formed by pushing over can be distinguished by their orientation which is parallel to the local growth direction of the bioimmuring organism.

BIOIMMURING ORGANISMS

Potential bioimmuring organisms comprise a taxonomically diverse variety of encrusting animals with mineralized skeletons. These include attached foraminifers, sponges, corals, serpulid

polychaetes, cemented brachiopods, bryozoans, oysters and oyster-like bivalves (see Nicol 1978). However, only serpulids, cyclostome bryozoans and oysters have been described frequently as bioimmuring organisms, although bioimmuration has also been recorded involving foraminifers, sponges and trepostome bryozoans.

An obvious property required of a bioimmuring organism is that it should be capable of overgrowing fellow epibionts or of fouling organic substrata. Barnacles seem rarely to yield epibiont bioimmurations, possibly because they tend to prise competitors off the substratum rather than overgrowing them. Encrusters with sheet-like morphologies (as opposed to runner-like, ramifying organisms) are generally adept at overgrowing competitors for substratum space. These are highly likely to result in bioimmuration.

The probability of an encruster encountering an epibiont, and the likelihood of successful overgrowth occurring should each increase with the size of the overgrowing organism. Furthermore, large organisms provide larger sampling areas. Therefore, large encrusters with large attachment areas are more likely to be found with bioimmurations of epibionts than are smaller encrusters.

As noted on page 6, rapid overgrowth should produce bioimmurations of the highest quality. The fastest shell growth rate known in a present day oyster occurs in *Crassostrea cuttackensis* (Smith and Newton) living in Madras Harbour. Shells may grow 0.27–0.62 mm per day (see Stenzel 1971, p. N1014). An oyster shell growing at this rate could, for example, completely overgrow an average bryozoan zooid in a matter of one or a few days, presumably before any marked deterioration in the condition of the zooid. No data appear to be available on growth rates in cyclostome bryozoans, but some Recent sheet-like cheilostomes with a similar colony morphology grow at rates of 30–110 mm per year (Jackson and Coates 1986, p. 9), i.e. 0.08–0.30 mm per day. Although these rates would not be expected to yield such good quality bioimmurations as those of the fastest growing oysters, small organisms might still be overgrown in a matter of days.

The basal calcified skeletons of encrusting animals are not usually in direct contact with the substratum but are separated from it by an organic layer which contains the cement causing adhesion of the encruster, and onto which the calcified layers are seeded. However, because these organic layers tend to be exceedingly thin, their presence seems to have little effect on the fidelity of the bioimmuration impressed on the calcified skeleton. For example, the periostacum of oysters, secreted by glands in folds of the mantle lobes, is described as 'very thin' by Stenzel (1971, p. N977; see also Carricker, Palmer and Prezant 1980), while the initial thickness of the cuticle in some cheilostome bryozoans is only a few microns (see Ryland 1976, p. 295).

Because the organic basal layer in some encrusters is very thin, the calcified layer is able to enter and mould extremely confined recesses on the substratum and any overgrown epibionts. A Recent specimen from the Adriatic Sea provides a good illustration (Pl. 1, figs. 3 and 4). Here an oyster, once attached to a plastic pipe, has bioimmured a runner-like colony of the cheilostome bryozoan *Hippothoa flagellum* (Manzoni). In *H. flagellum*, new zooids originate as buds from the pore windows of parent zooids. The pore windows are apparently situated a little above substratum level, giving a very low 'arch' before the bud regains the substratum during distal growth. The fact that this arch has apparently been filled by calcite of the oyster shell in the illustrated specimen (leaving parent and daughter zooids apparently separated) demonstrates that extremely small-scale aspects of morphology are capable of being moulded by oysters.

BIOIMMURED SOFT-BODIED ORGANISMS

The overwhelming majority of bioimmured soft-bodied organisms have been described from the Jurassic and Cretaceous. This reflects both the focus of Professor E. Voigt's research, especially on the type Maastrichtian, as well as the undoubted abundance of good bioimmuring organisms, such as cemented bivalves, serpulids and cyclostome bryozoans, in the Jurassic and Cretaceous of north-west Europe. Furthermore, the abundance of aragonitic substrata, subsequently dissolved to reveal the attachment surfaces of their encrusters, also increases in the post-Palaeozoic. Very few bioimmurations of soft-bodied organisms have been described from the Palaeozoic and there is clearly much potential for further discoveries.

Soft-bodied or poorly-mineralized organisms belonging to the following taxonomic groups have been found as bioimmurations:

1. *Algae*. Voigt (1956, 1966, 1973a) has described many examples of bryozoans from the Maastrichtian Chalk-Tuff of Maastricht which were apparently attached to the stems and leaves of macroalgae. In a sample of 1800 bryozoans with intact colony bases, 79% of colonies were inferred to have been algal epiphytes (Voigt 1973a). The substratum bioimmurations of these algae often have smooth and glossy surfaces, and in some cases it seems possible that the epiphytic bryozoan did not make close contact with its algal substratum (Voigt 1973a described some Recent epiphytic bryozoans having strut-like outgrowths at the bases of their colonies). Putative algal stem bioimmurations are recognizable as cylindrical hollows around which the bryozoan colony was wrapped (Voigt 1956, pl. 1, figs. 1–4, text-figs. 2 and 3). Some of these colonies have tubular erect branches, a colony growth-form described as cavariiform (however, not all cavariiform bryozoans were algal epiphytes: examples in which the hollow is partitioned by skeletal walls cannot have grown around algae). Specimens of the worm *Spirorbis* with concave basal parts (Voigt 1956, text-fig. 4) were also apparently epiphytes of algal stems. Bryozoans such as the cyclostome *Actinopora disticha* (v. Hagenow) sometimes bioimmured algal fronds which are preserved as narrow tubular voids around which the colony is wrapped (Voigt 1956, pl. 2, figs. 9 and 10).

The Recent chlorophytacean *Codium bursa* (L.) from the Mediterranean is a cushion-shaped alga which often supports a fauna of epiphytic bryozoans (33 species) growing on cryptic surfaces beneath the overhanging edge of the plant (Voigt and Harmelin 1986). The mammillate surface of the alga, consisting of the ends of the utriculi, is replicated on the undersides of epiphytes such as the cyclostome *Tubulipora plumosa* Harmer (text-fig. 2D). Very similar patterns have been found by Voigt and Harmelin on the encrusting bases of the fossil cyclostomes *Osculipora tetragona* (Michelin) from the Middle Cenomanian of Le Mans (France), and *O. houzeaui* Pergens, *O. truncata* (Goldfuss) and *Reteporidae lichenoides* (Goldfuss) from the Chalk-Tuff of the Maastricht region (Voigt and Harmelin 1986, pl. 2, figs. 4 and 5, pl. 3, figs. 9, 12 and 13). These are interpreted as bioimmurations of a *Codium*-like alga.

An Upper Jurassic dasycladacean alga, *Goniolina geometrica* (Roemer), from West Germany, is preserved on the cementation areas of small oysters as bioimmured impressions of the regular hexagonal surface pattern (Voigt and Harmelin 1986, pl. 4, figs. 15 and 16).

A rare example of bioimmuration in the Palaeozoic is provided by a specimen from an Ordovician erratic boulder from Gotland. Hillmer and Schallreuter (1987, fig. 3I–J) figure the bioimmuration of a putative alga with a *Goniolina*-like surface overgrown by a cryptostome bryozoan.

2. *Marine angiosperms*. The Chalk-Tuff of Maastricht contains bioimmured seagrass leaves which were described by Voigt (1956, 1966). Bioimmuring organisms include the oyster *Exogyra*, the cyclostomes *Actinopora disticha* and *Lichenopora* sp., and the foraminifer *Planorbulinella cretae* (Marsson). On their basal surfaces are moulded the patterns of epidermal cells and veins of seagrass leaves (see Voigt 1956, pl. 4, figs. 1 and 2). It seems possible that some of these leaves are from the seagrass *Thalassocharis bosqueti* (Debey ex Miquel) which occurs commonly as silicified axes and

EXPLANATION OF PLATE 2

Figs. 1 and 2. Ventriculitid sponge preserved as a substratum mould bioimmuration on the underside of the cemented bivalve *Pycnodonte vesiculare*, BMNH S 10250, England, Chalk. 1, general view, $\times 1.4$. 2, detail of sponge surface, $\times 23$.

Fig. 3. Xenomorph of trioniid bivalve on the unattached, right valve of a *Gryphaea*, BMNH 24065, Weymouth, Jurassic, Oxford Clay, $\times 0.8$.

Figs. 4 and 5. Substratum bioimmurations of unknown identity visible on the attachment areas of cemented bivalves. 4, BMNH Z 1062, Le Mans, Sarthe, Cenomanian, Sables du Perche, $\times 8$. 5, BMNH D 32168, Bognor, Sussex, Eocene, London Clay, $\times 28$.

Figs. 2, 4 and 5 are back-scattered electron micrographs of uncoated specimens.



rootlets, sometimes bryozoan encrusted, at Kunrade 30 km ESE of Maastricht (Voigt and Domke 1955; Voigt 1973a).

3. *Protists*. Ernst (1985) reported the occurrence of cylindrical tubes, up to 1.5 mm long and 0.10–0.15 mm in diameter, within zooecia of the cheilostome bryozoans *Onychoella piriformis* and *O. cyclostoma* from the Maastricht Chalk-Tuff. The tubes were apparently secreted by the bryozoans in response to the presence of an infesting organism and are thus bioimmurations of the bioclaustration type. Ernst regarded the infesting organism as probably a folliculinid ciliate.

4. *Poriferans*. The spiculate surface of a putative monactinellid sponge bioimmured by a cyclostome is described by Voigt (1966, pl. 34, figs. 1 and 2).

5. *Hydrozoans*. Although very abundant members of present-day hard and firm substratum communities, hydrozoan cnidarians (excepting a few well-calcified groups such as milleporids and stylasterines) have a meagre fossil record, and many putative body fossils of hydrozoans from the Palaeozoic require confirmation (Hill and Wells 1956). Scrutton (1975) described the hydroid *Protulophila gestroi* Rovereto preserved by bioclaustration. This Middle Jurassic to Pliocene species occurs in association with serpulid worms, having become embedded in the tubes as they grew.

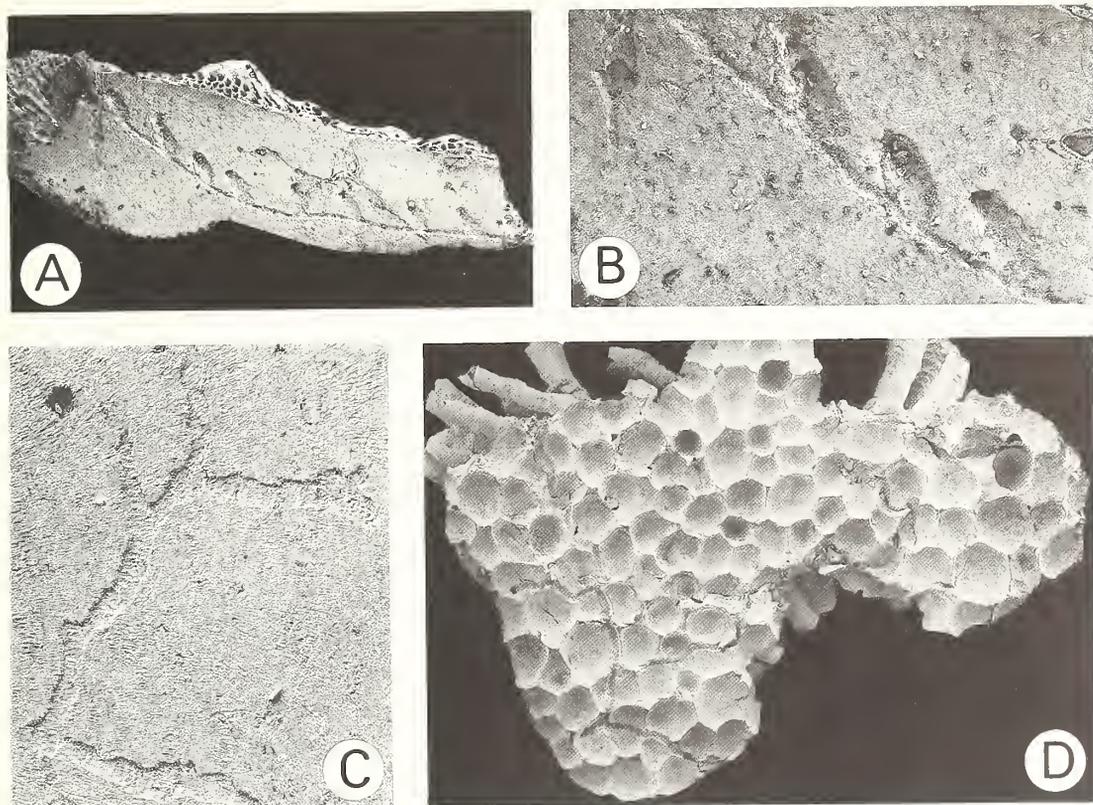
Epibiont bioimmurations of thecate hydroids have been described by Voigt (1973b) and Taylor (1988). *Hydrallmania graptolithiformis* Voigt, 1973b, preserved as a mould on the underside of the cyclostome *Actinopora disticha* from the Maastricht Chalk-Tuff, is the only known fossil of the Sertulariidae, a family of hydroids which is common at the present day. The Maastrichtian species closely resembles some Recent species of *Hydrallmania* in having an imbricate arrangement of hydrothecae along one side of the branch. Of more problematical affinity is *Eisenackiella thanetensis* Taylor, 1988, based on a single specimen bioimmured by the bivalve *Pycnodonte vesiculare* (Lamarck) from the Santonian of Kent. The colony appears to have an adnate system of hydrothecae-bearing stolons which gives rise to a series of erect stems also bearing hydrothecae (Pl. 1, fig. 6). Both the upright distal parts of the stolonial hydrothecae, and the erect stems have been flattened in the direction of growth of the bioimmuring bivalve. Stolonial morphology recalls that of certain Recent Lafoeidae, whereas stem morphology is reminiscent of the Family Sertulariidae. *E. thanetensis* is possibly a compound organism resulting from chance juxtaposition of stolon forming and an erect hydroid species. Voigt (1966, fig. 1) illustrates an unidentified bioimmured Maastrichtian hydroid which he compares with the living species *Syncoryne sarsi* Lovén.

6. *Octocoral anthozoans*. One of the few bioimmurations recognized from the Palaeozoic is of an inferred gorgonian octocoral. *Phumalina conservata* was described by Glinski (1956) from the Middle Devonian of the Eifel. It is represented by a single pinnate specimen bioimmured by a trepostome bryozoan determined as *Heterotrypa* sp.

7. *Ctenostome bryozoans*. The Ctenostomata are an exclusively soft-bodied, primitive, paraphyletic order of bryozoans. A minority of species bore into calcareous substrata and are found as trace fossils, and encrusting species preserved by bioimmuration are not uncommon in the Mesozoic (see Taylor 1990). Although ctenostome classification is somewhat contentious, it has been traditional to distinguish two groups of ctenostomes: the Stolonifera in which the autozooids are linked by a stolonial system comprising kenozooids, and the Carnosa in which stolons are wanting.

Voigt (1966, 1972, 1979) has described bioimmured stoloniferan species assigned to one extinct and two extant genera. *Stolonicella* Voigt, 1966 is a probable ctenostome known only as bioimmurations. The colony consists of a stolonial system bearing erect autozooids at intervals (text-fig. 2A and B), and resembles the living ctenostome *Avenella fusca* Dalyell. Zooids often possess a fine transverse ornament. Three species of *Stolonicella* occur in the Chalk-Tuff of Maastricht (*S. schindewolfi* Voigt, 1966; *S. filosa* Voigt, 1966; *S. hillmeri* Voigt, 1979) bioimmured by bryozoans and oysters, and one in the Turonian Greensand of Mülheim-Broich, West Germany (*S. westfalica* Voigt, 1966) bioimmured by *Ostrea (Lopha) semiplana* Sowerby and small *Exogyra*. Voigt (1979, pl. 3, figs. 1 and 2) illustrates an unusual colony of *S. filosa* which apparently encircled a colony of the cyclostome *Stellocaeva francquana* d'Orbigny before being overgrown by the cyclostome.

The extant ctenostome genus *Amathia* is characterized by erect stolons which bear biserial clusters of autozooids (see Chimonides 1987). *A. immurata* Voigt, 1972 from the Maastricht Chalk-Tuff is



TEXT-FIG. 2. Bioimmured organisms preserved as moulds on the undersides of overgrowing organisms. A and B, VH 8611, the probable ctenostome bryozoan *Stoloniceella* sp., Blom Quarry, near Maastricht, Upper Maastrichtian. A, zooids arising from a stolon, $\times 12$. B, detail of zooids and stolon $\times 33$. C, ribbon-like thallus of the alga *Fosliella inexpectata* Voigt, VH 9494, Blom Quarry, Maastricht, Upper Maastrichtian, $\times 60$. D, VH 10522, bioimmuration of the chlorophytacean alga *Codium bursa* (L.) on the underside of the cyclostome bryozoan *Tubulipora plumosa* Harmer, Mediterranean, Recent, $\times 20$. Electron micrographs kindly provided by Professor E. Voigt.

the only known fossil species, owing its preservation to bioimmuration by the cyclostome *Idmidronea macilenta* (v. Hagenow). Colonies of the Recent *A. cornuta* Lamouroux bioimmured by the foraminifer *Acervulina adhaerens* (Schultze) were shown by Voigt (1972) to have an appearance very like the Maastrichtian fossil. Another extant stoloniferan genus, *Buskia*, is represented by two fossil species preserved as bioimmurations (Voigt 1979): *B. inexpectata* Voigt from the Upper Maastrichtian of Curfs preserved on the base of the cyclostome *?Ditaxia* with which it shared an algal substratum, and *B. hachti* Voigt from the Pliocene of Puget sur l'Argens (France) bioimmured by a serpulid tube.

Several Jurassic and Cretaceous bioimmured carnosan ctenostome species have been described, all referred to the extant family Arachnidiidae (see Taylor 1990). Their encrusting colonies are composed of uniserial chains of zooids which ramify across the substratum (Pl. 1, fig. 1). The zooids have a pyriform outline shape and sometimes possess a long and narrow proximal portion (cauda). *Arachnidium brandesi* Voigt, 1968a is founded on a single specimen from the Lower Cretaceous (Barremian) of Hoheneggelsen (West Germany). The colony is preserved as a cast bioimmuration which was revealed when the bioimmuring serpulid, *Proliserpula* (*Proliserpula*) *bucculenta* Regenhardt, was stripped away from the substratum, a guard of the belemnite *Oxyteuthis*

brunsvicensis v. Stromb. A similar species, *Arachnidium jurassicum* Voigt, but with smaller zooids, was subsequently described by Voigt (1977) from the Middle Jurassic (Aalenian) of Goslar (West Germany). As in *A. brandesi*, the ctenostome is preserved as a cast bioimmuration on the guard of a belemnite (*Megateuthis*). In this case, however, the bioimmuring organism is an oyster. Taylor (1978) recognized that the type specimens of two nineteenth-century species of Jurassic bryozoans previously regarded as belonging to the cyclostome genus *Stomatopora* Bronn were in fact cast bioimmurations of *Arachnidium*. The first of these had been described by Phillips (1829) as *Cellaria smithii* and originated from the Middle Jurassic ('Cornbrash'; probably Callovian) of Scarborough (Yorkshire). The holotype of *Arachnidium smithii* (Phillips) is a cast bioimmuration attached to the bivalve *Cardium citrinoideum* Phillips, and was possibly bioimmured by an oyster though little remains of the bioimmuring organism. The second species, *Stomatopora phillipsii* Vine, 1892, placed in synonymy with *A. smithii*, is represented by a cast bioimmuration, overgrown by an oyster, attached to the brachiopod *Obovothyris* from the Middle Jurassic (Bathonian, Cornbrash) of Thrapston (Northamptonshire). Three new species of arachnidiids from the Jurassic are described by Taylor (1990) who emphasizes the relative abundance of these bioimmured ctenostomes in late Jurassic deposits. Finally, Voigt (1980) described *Arachnidium longicauda* from the Chalk-Tuff of Maastricht. This species is represented by a mould bioimmuration of a colony originally attached to an algal leaf and overgrown by the cyclostome *Truncatulipora*. Many of the zooids have extremely long caudae which serve to distinguish *A. longicauda* from previously described species of *Arachnidium*.

8. *Incertae sedis*. Very many bioimmurations are taxonomically indeterminate. This may be a consequence of distortion of the bioimmured organism during overgrowth, insufficient morphological characters for identification, lack of knowledge of the appearance when bioimmured of comparative living organisms, or a combination of these factors. Two particular morphotypes of *incertae sedis* occur commonly among epibiont bioimmurations: threads and mounds.

Bioimmurations of narrow thread-like structures are often encountered on the attachment areas of Mesozoic to Recent oysters and bryozoans. The threads may ramify and cover substantial areas of substratum. Several different groups of organisms are potentially responsible, including stoloniferan ctenostome bryozoans (zooids of Recent stoloniferans are sometimes deciduous, their loss leaving an undiagnostic stolonial system), hydroids, filamentous fungi and algae.

Mound-shaped bioimmurations are commonly distorted as a result of overgrowth of a semiflaccid organism. Only the basal outline shape of the organism may be preserved as a potential distinguishing character. For example, an Upper Cretaceous mound bioimmuration (Pl. 1, fig. 5) occurring with the holotype specimen of *Eisenackiella thanetensis*, was evidently a soft-bodied organism with a scalloped edge which was pushed over and severely distorted during overgrowth by *Pycnodonte vesiculare*. This and similar mound bioimmurations may possibly be zoanthid or actiniid cnidarians, ascidiaceans or sponges.

Two substratum bioimmurations of unknown identity are shown in Pl. 2, figs. 4 and 5. Both occur on the attachment areas of cemented bivalves. The Cretaceous example (Pl. 2, fig. 4) overgrew a substratum of matted fibres, and the Eocene example (Pl. 2, fig. 5) a substratum with a pattern of conjugate ridges.

Rohr and Boucot (1989) have recently described a substratum bioimmuration preserved by individuals of the oyster *Lopha ramicola* Beurlen from the Upper Cretaceous of Brazil. These oysters bioimmured stem-like structures, about 1 cm in diameter, which were covered with closely-spaced circular nodules arranged in a spiral pattern. The bioimmuration is replicated in positive relief on the unattached valves by xenomorphism. Rohr and Boucot regard the bioimmured organism as of unknown affinity, but make comparisons with gorgonacean octocorals and axes of plants (e.g. gymnosperm stems bearing the traces of leaf scars).

The bioclaustrated ichnotaxon *Catellocaula vallata* Palmer and Wilson, 1988, embedded in trepostome bryozoan colonies from the Upper Ordovician of the Cincinnati area of the USA, is another organism of unknown affinity. The fossil consists of a series of 2 mm wide radiating tunnels connecting pits in the surface of the host bryozoan colony. Palmer and Wilson interpret the

organism as a stoloniferous colony, possibly a hydroid but more probably a colonial ascidiacian tunicate.

Circular-parabolic pits are commonly found in fossil echinoderms, particularly Palaeozoic crinoids (see Brett 1985 and references therein). They were apparently produced by a combination of boring and embedment (i.e. bioclaustration). Brett introduced the ichnogenus *Tremichnus* for such structures and regarded them as the work of a sessile, host-selective, probably filter-feeding epibiont.

BIOIMMURED SKELETAL ORGANISMS

Although the most interesting bioimmured fossils are undoubtedly those of soft-bodied organisms, bioimmurations of organisms with mineralized skeletons may also be valuable in certain circumstances. This is true if the skeletons are normally disarticulated, suffer from diagenetic dissolution, or cover only part of the external surface of the organism.

Aragonitic shells

Many fossil assemblages lack molluscs with diagenetically unstable shells of aragonite. For example, aragonitic molluscs are generally absent from the Aptian Faringdon Sponge Gravel of Oxfordshire. However, some aragonitic gastropods at Faringdon are preserved as substratum bioimmurations formed on the undersurfaces of cyclostome bryozoans and neuroporid sponges which fouled the gastropod shells. These natural moulds accurately replicate details of shell ornamentation and permit taxonomic identification of the gastropods (R. J. Cleavelly, in prep.). Similar moulds of mollusc shells occur in the Bathonian of Normandy (T. J. Palmer, pers. comm. 1988).

Celleporid bryozoans from the Neogene occasionally bioclaustrate small solitary corals (Pouyet 1978). Whereas the bryozoans are calcitic, the corals are aragonitic and their skeletons tend to be lost during diagenesis. However, their past presence can be indicated by horn-shaped cavities remaining in the surface of the host bryozoan colony (e.g. in material from the Pliocene Coralline Crag of Suffolk).

Numerous examples have been described of oysters bioimmuring lost substrata such as ammonites and other aragonitic molluscs (see Stenzel 1971 and references therein). Most accounts focus on the positive relief replica of the aragonitic mollusc carried by the free valve of the oyster (Pl. 2, fig. 3) as a result of the two valves maintaining a constant separation during growth across the mollusc shell, a process termed xenomorphism by Stenzel. However, it is the cemented valve which plays the primary role in the preservation of these substratum bioimmurations. To use a photographic analogy, the cemented valve captures the image as a negative, while the free valve makes a positive print from the negative. Xenomorphic impressions on the free right valves of oysters are rarely as sharp as bioimmurations on the attached left valves. Therefore, they are of less value in identifying the overgrown organism.

Exposed soft tissues

Not all organisms with mineralized skeletons have their entire external surface covered by hard material. Sponges have a spicular skeleton enveloped during life by soft parts. Hexactinellid sponges of the Family *Ventriculitidae* (see Reid 1962) are sometimes bioimmured by cemented bivalves (notably *Pycnodonte vesiculare*) in the late Cretaceous Chalk of England. These bioimmurations reveal the original surface morphology of the sponge including the ostia (Pl. 2, figs. 1 and 2). As early as 1847, Toulmin Smith (p. 89) observed bioimmurations made by oysters which had grown on the surface of ventriculitids. He used their structure to testify to 'the firmness of the texture of the body and to its noncontractility, as well as to its durability'. This enabled him to assert that structures visible in conventionally preserved ventriculitids were not artefacts resulting from post-mortem distortion.

Frontal membrane morphology in bioimmured cheilostomes has been described by Voigt (1968,

1979a) and Voigt and Ernst (1985). In *Taeniopora arachnoidea* (Goldfuss), the cuticle is ornamented by numerous small projections and pores (Voigt 1968b, pl. 4, figs. 3 and 4). The Maastrichtian onychocellid cheilostome *Nudonychocella nuda* Voigt and Ernst, 1985, has greatly reduced cryptocystal frontal wall calcification in post-ancestrular zooids giving it a resemblance to a membraniporimorph. A serpulid bioimmured colony (Voigt and Ernst 1985, pl. 2, fig. 5) confirms the onychocellid affinities of the species, and shows clearly the position of operculum and orifice.

Lightly mineralized skeletons

The coralline alga *Fosliella* Howe has weakly calcified thalli which are unknown as body fossils. However, Voigt (1981) has described a new species of this genus from the Maastrichtian of Maastricht and Kunrade which is preserved only by bioimmuration. *F. inexpectata* Voigt has narrow, ribbon-like thalli with files of cells arranged in transverse bands (text-fig. 2C). Cover cells, germination discs and conceptacles are preserved. The alga was an epiphyte of macroalgae and was overgrown by the cyclostome *Truncatulipora*. Previous notions of *Fosliella* being a primitive member of the Corallinaceae are substantiated by this early occurrence of the genus.

Although all cheilostome bryozoans have mineralized skeletons, mineralization can be very slight and certain living groups are unknown as body fossils. Hence bioimmuration provides a valuable opportunity for fossilization of lightly calcified cheilostomes.

A new cheilostome from the Maastricht Chalk-Tuff was described by Voigt (1966) as *Taeniocellaria setifera*. The delicate erect colony, with long setose vibraculae, was flattened during overgrowth by an individual of *Exogyra* and is preserved as a mould bioimmuration on the attachment area of the oyster along with *Stoloniceella schindewolfi*, and small cyclostomes, bivalves and *Vermetus*. Such excellent preservation of this fragile colony suggested to Voigt (1979a) that overgrowth occurred rapidly, possibly during the life-time of the colony. The affinities of *T. setifera* within the Cheilostomata are obscure, but the orifice with sinus (see reconstruction in Voigt 1966, fig. 3) suggests that the species is an ascophoran.

Laterotecatia pseudamatthia Voigt, 1979a is a hippothoid ascophoran from the Maastrichtian which is known only from bioimmurations. Zooids of *L. pseudamatthia*, named because of its resemblance to bioimmured *Amatthia immurata*, are arranged in characteristic transverse rows. Colonies were algal epiphytes bioimmured by organisms such as the cyclostome *Stellocavea francquana*.

Despite frequent citation as a fossil, the extant cheilostome genus *Aetea* Lamouroux had no certain fossil record until Voigt (1983) described bioimmured specimens from the Pliocene. This weakly calcified anascan possesses zooids with an adnate proximal part from which there arises an erect tubular part containing the frontal membrane and orifice. Fossil examples (identified as *Aetea* sp., *A. truncata* (Landsborough) and *A. truncata pygmaea* Hincks) from Crete and southern France are preserved as a result of bioimmuration by oysters. Their appearance is very similar to that of Recent Mediterranean specimens of *Aetea* bioimmured by oysters, the foraminifer *Miniacina miniacea* Pallas, and the cheilostome *Watersipora cucullata* Busk.

Chitinous exoskeletons of crustaceans commonly disintegrate before burial and fail to fossilize. A bioimmured example of the lobster *Limuparus* preserved has been described by Bishop (1981) from the late Cretaceous Ripley Formation of Mississippi. The carapace of *Limuparus* was overgrown by the oyster *Exogyra costata* Say probably after the death of the lobster because living lobsters groom themselves to remove epizoans. Using growth lines on the oyster shell, Bishop estimated that complete overgrowth of the carapace took almost a year, and therefore that the carapace remained intact for at least this length of time. This period far exceeds the four weeks quoted by Schäfer (1972) for decapod cuticle to lose its strength in the North Sea at the present day.

Exposure of hidden undersides

Bioimmuration in conjunction with substratum loss, especially dissolution of aragonitic substrata, can also be useful in revealing the undersides of encrusters with mineralized skeletons which are normally juxtaposed with the substratum and hidden from view. For example, adnate cheilostome

bryozoans are usually very firmly cemented to their substrata when found as fossils, and the colony underside is not accessible for study. However, the undersides of colonies overgrown by bivalves and other bioimmuring organisms may become visible after detachment from their substratum. These include species with colonies which are too fragile to survive intact unless held together by the bioimmuring organism. Bioimmurations of zooids of *Andriopora major* reveal the existence of pore chambers (Pl. 1, fig. 2), not recorded from conventionally preserved material (Larwood 1962).

DISCUSSION

Bioimmuration is a preservational process which can preserve soft-bodied organisms, as well as lightly mineralized or unmineralized components of organisms possessing hard skeletons. Clearly, therefore, it offers considerable potential for adding to our knowledge of biotas of the past. This potential has been little explored. In particular, very few bioimmured fossils have been reported from the Palaeozoic. Potential bioimmuring organisms in the Palaeozoic include cemented articulate and inarticulate brachiopods, sheet-like trepostome and cystoporate bryozoans, cornulitids, corals and stromatoporoids.

Future research directions should include:

1. A concerted and systematic search for bioimmurations. Many examples of bioimmured fossils doubtless remain unrecognized in existing collections. Oysters with large attachment areas are a particularly fruitful source of bioimmurations in the Mesozoic and Cenozoic. The development of techniques to separate oysters and other encrusters from their substrata, thereby exposing bioimmured organisms, would surely increase the probability of making such finds.

2. Study of the details of overgrowth processes in present-day hard substratum communities, and the taphonomy of the organisms being overgrown. Nothing is currently known regarding the relative preservation potentials during bioimmuration of different organisms. Fossil finds suggest that runner-like encrusters provide the most easily preservable (and readily recognizable) subjects for bioimmuration, but this supposition requires testing by reference to modern bioimmurations.

Organisms preserved by bioimmuration are usually sessile inhabitants of firm or hard substrata. Fossil assemblages of firm or hard substrata are especially good subjects for palaeoecological studies because their constituent fossils are demonstrably *in situ*, thereby retaining their original spatial relationships to one another and to the substratum. Fouling and overgrowth interactions between organisms, and interactions between organisms and their substratum (e.g. patterns of spatial recruitment, see Bishop 1988) can be recorded with minimal interpretive assumptions. This additional information on biotic interactions, taken in conjunction with evidence of soft-bodied organisms preserved by bioimmuration, should permit inferences to be made for hard substrate which are beyond those normally possible in palaeoecological studies.

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BIOIMMURED CTENOSTOMES FROM THE JURASSIC AND THE ORIGIN OF THE CHEILOSTOME BRYOZOA

by P. D. TAYLOR

ABSTRACT. Soft-bodied ctenostome bryozoans, preserved as bioimmurations following overgrowth by encrusting organisms with hard skeletons, are described from the Middle and Upper Jurassic of England and Normandy. They include one new genus, *Cardoarachnidium*, and three new species, *C. bantai*, *C. voighti* and *Arachnoidella abusensis*. These and new bioimmured specimens of *Arachnidium smithii* (Phillips) show fine-scale details of original morphology as well as artefacts caused by partial collapse of zooids during overgrowth. The D-shaped zooidal orifices present in *Cardoarachnidium* probably indicate that the zooids were operculate. Opercula are one of the two apomorphies of the closely-related cheilostomes, and therefore the Oxfordian *Cardoarachnidium* is placed in the stem-group of the Cheilostomata, which first appear in the Tithonian.

CTENOSTOMES are unique among marine bryozoan orders in lacking a calcified skeleton. Accordingly, they are less well-represented in the fossil record than groups such as trepostomes, fenestrates, cyclostomes and cheilostomes, more familiar to palaeontologists. Fossil ctenostomes, however, can be preserved as borings (see Pohowsky 1978) and as bioimmurations, i.e. natural moulds and casts formed as a result of overgrowth by organisms with mineralized skeletons (see Taylor 1990). Boring ctenostomes, first known from the Upper Ordovician, are generally regarded as a specialized group or groups. In contrast, bioimmured fossil ctenostomes include several uniserial encrusting species which have many features apparently primitive among marine Bryozoa.

During recent years, bioimmured ctenostomes have been discovered with increasing frequency in the Jurassic and Cretaceous, mainly through the work of Voigt (1966, 1968, 1972, 1977, 1979, 1980). The present paper utilizes an uncoated SEM technique (Taylor 1986) to describe some finds and redescribe earlier finds from the Jurassic. The quality of preservation of some of the new specimens exceeds that previously known and has revealed hitherto unknown morphological features. Artefacts formed during the process of bioimmuration process are also illustrated.

Jurassic bioimmured ctenostomes have special significance because they almost certainly include representatives of the stem-group of the order Cheilostomata. Cheilostomes, the dominant bryozoans of present-day faunas, first appear in deposits of latest Jurassic age. Comparative anatomical studies have led to the belief that the ancestor of the cheilostomes was a ctenostome or, more strictly, that living ctenostomes are the primitive sister-group of living cheilostomes. The description here of a new bioimmured Upper Jurassic ctenostome which apparently possesses one of the two apomorphic features characteristic of the Cheilostomata supports this hypothesis of cheilostome origins and gives the sequence of appearance of the two apomorphies.

SYSTEMATIC PALAEOLOGY

Material. Specimen repositories are abbreviated as follows: BMNH, British Museum (Natural History); YM, Yorkshire Museum, York; VH, Voigt Collection, Universität Hamburg.

Order CTENOSTOMATA Busk, 1852
Suborder CARNOSA Gray, 1841
Family ARACHNIDIIDAE Hincks, 1877
Genus ARACHNIDIUM Hincks, 1859

Type species. Arachnidium hippothooides Hincks, 1859.

Discussion. *Arachnidium* Hincks is founded on a comparatively rare present-day type species which has been redescribed recently by Hayward (1985, p. 78). D'Hondt (1983) included five living species in the genus, all possessing uniserial branching colonies with zooids pyriform or ovoidal in outline shape. In common with many ctenostomes, the surface morphology of species of *Arachnidium* is comparatively simple, and descriptions of living species generally include only a small number of external morphological characters (notably size, shape and ornamentation of the zooids). These characters are equally available in bioimmured fossil *Arachnidium*. Not available in fossil *Arachnidium* are aspects of polypide morphology (e.g. tentacle number) which have been used in species descriptions.

The difference between *Arachnidium* and *Arachnoidella* d'Hondt, 1983 (see p. 26) is rather slight, the latter possessing rather longer peristomes and sometimes developing lateral crenulations close to the substratum. However, pending further study of living species, the two genera are retained.

Range. Jurassic (Aalenian) to Recent.

Arachnidium smithii (Phillips, 1829)

Plate 1, figs. 1–6; Plate 2, figs. 1 and 2; text-figs. 1, 2A, B, 3A, B.

- 1829 *Cellaria smithii* Phillips, p. 143, pl. 7, fig. 8.
 1875 *Hippothoa smithii* (Phillips); Phillips, p. 242, pl. 7, fig. 8.
 1892 *Stomatopora phillipsii* Vine, p. 250, pl. 12, figs. 1–3.
 1894 *Stomatopora smithii* (Phillips); Gregory, p. 58, fig. 1.
 1895 *Stomatopora smithii* (Phillips); Gregory, p. 226.
 1896 *Stomatopora smithii* (Phillips); Gregory, p. 56, fig. 8.
 1907 *Stomatopora phillipsii* Vine; Lang, fig. 6.
 1911 *Corynotrypa smithii* (Phillips); Bassler, p. 521, fig. 22.
 1935 *Stomatopora smithii* (Phillips); Melmore, p. 1, test-figs. 1 and 2.
 1977 *Arachnidium jurassicum* Voigt, p. 172, figs. 1–4.
 1978 *Arachnidium smithii* (Phillips); Taylor, p. 214, pl. 7, figs. 1–4.
 1980 *Arachnidium smithii* (Phillips); Voigt, fig. 4a.
 1980 *Arachnidium jurassicum* Voigt; Voigt, fig. 4b.

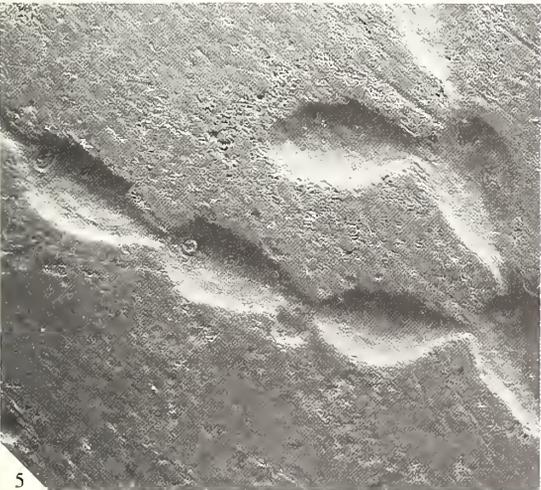
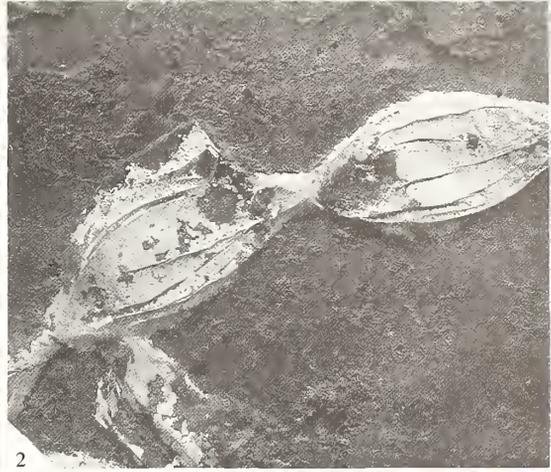
Holotype. YM 78, Cornbrash, Scarborough, Yorkshire. This specimen (Pl. 1, figs. 1 and 3; text-fig. 1), a cast bioimmuration attached to the type specimen of the bivalve *Cardium citrinoideum* Phillips, is almost certainly of Callovian age (*macrocephalus* Zone).

Other material. BMNH D 31144, Cornbrash, Thrapston, Northamptonshire; the holotype of *Stomatopora phillipsii* Vine, 1892; a cast bioimmuration attached to the brachiopod *Obovothyris* and undoubtedly originating from the Bathonian (*discus* Zone). BMNH D 53156, Bathonian, Bradford Clay (*discus* Zone), Cirencester, Gloucestershire, J. P. Woodward Collection; a mould bioimmuration on the attachment area of

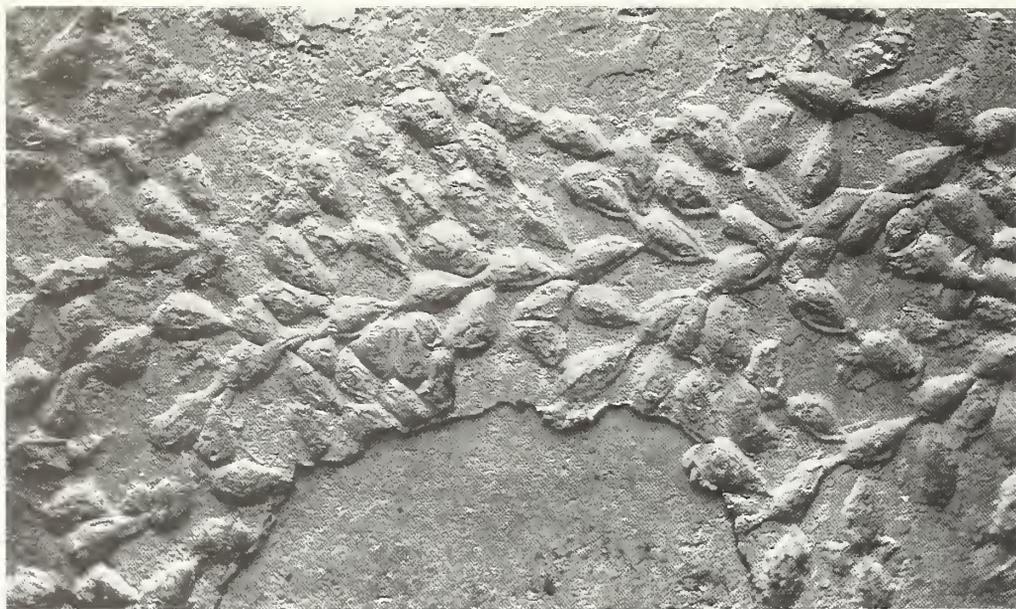
EXPLANATION OF PLATE I

Figs. 1–6. *Arachnidium smithii* (Phillips, 1829). 1, 3, holotype, YM 78, natural cast bioimmuration, Scarborough, Cornbrash (Callovian). 1, crowded zooids with overgrowing branches, $\times 28$. 3, partly collapsed zooid (with well-preserved orifice) overgrown by another zooid, $\times 100$. 2, 4, BMNH D 57497, natural cast bioimmuration, South Ferriby, Kimmeridgian. 2, collapsed zooids cast in pyrite, $\times 50$. 4, calcite cast zooids emerging from beneath the cover of the bioimmuring bivalve (bottom), $\times 16$. 5 and 6, BMNH D 57492, mould bioimmuration, Villers-sur-mer, Oxfordian. 5, uniserial chain of zooids $\times 35$. 6, orifice, $\times 240$.

All illustrations are back-scattered electron micrographs of uncoated specimens.



TAYLOR, *Arachnidium*



TEXT-FIG. 1. *Arachnidium smithii* (Phillips, 1829), holotype, YM 78, Scarborough, Cornbrash (Callovian). Extensive colony preserved as a natural cast attached to the surface of a bivalve shell. Back-scattered scanning electron micrograph of an uncoated specimen, $\times 19$.

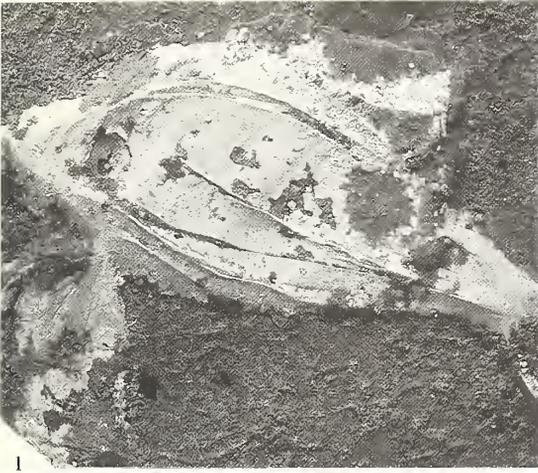
a small *Praeexogyra*. BMNH D 57492, 4–5, D 58002, Oxfordian, float probably from the 'Couches à *Myophorella ludlestoni* et *Lopha gregaria*' (*plicatilis* Zone), Vaches-Noires, Villers-sur-mer, Normandy, collected by P. D. Taylor, 1985; apart from D 58002, all are mould bioimmurations on the attachment areas of gryphaeate oysters; D 58002 is a partially exposed, partly infilled cast bioimmuration. BMNH D 57496, Kimmeridgian, Bed M8 of Birkelund *et al.* (1983) (mid *mutabilis* Zone), Westbury, Wiltshire, collected by P. Wignall, 1986; mould bioimmuration, partly infilled by pyrite, on the attachment area of a small oyster. BMNH D 57497, Kimmeridgian, Bed 9 of Birkelund and Calloman (1985) (lower *baylei* Zone), South Ferriby, Humberside, collected by M. Simms, 1986; a cast bioimmuration (Pl. 1, figs. 2 and 4; Pl. 2, figs. 1–2), partly calcitic and partly pyritic, attached to *Deltoideum delta* (Sowerby).

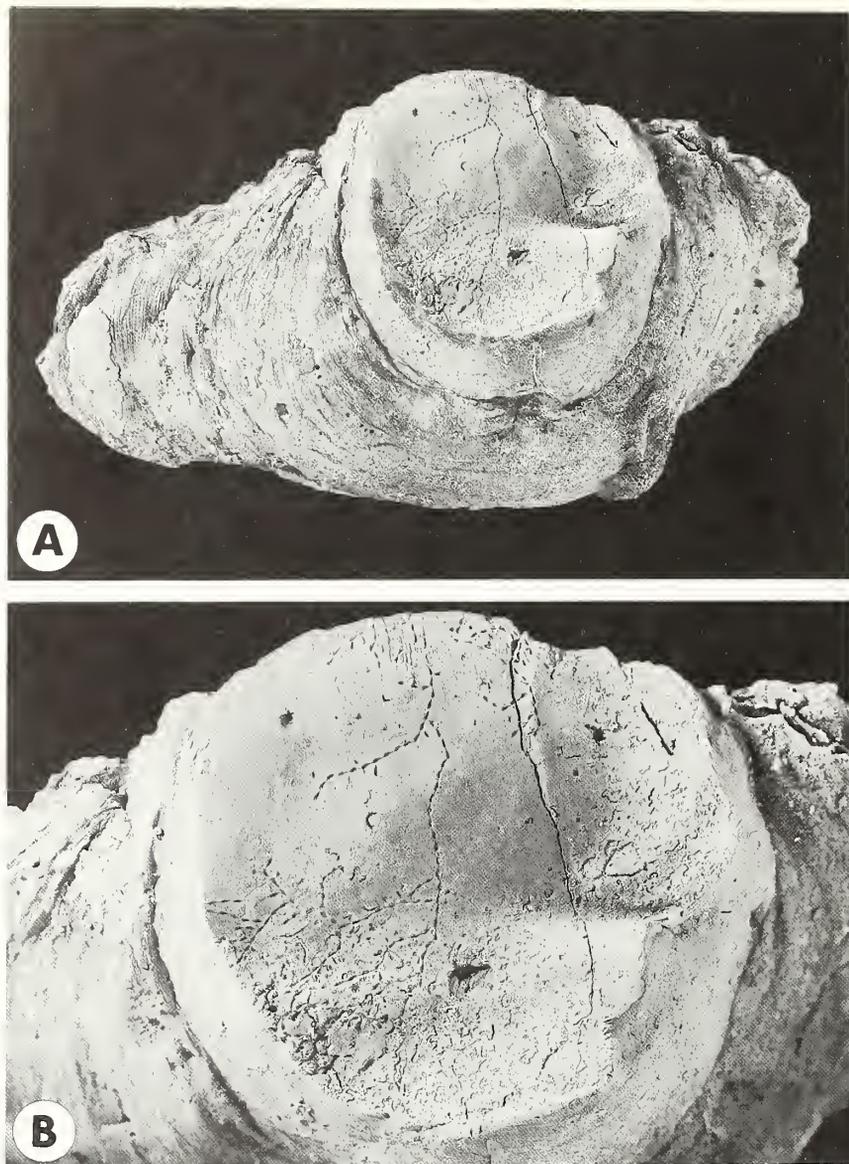
The holotype of *Arachnidium jurassicum* Voigt, 1977, unavailable for study during 1987, is VH 1899, Middle Dogger (*Polyplocus*-Schichten, Dogger γ), Goslar, West Germany; this is a cast bioimmuration attached to a guard of *Metateuthis*.

Description. Colony adnate, consisting of ramifying, uniserial branches of zooids (text-figs. 1 and 2). Branches often gently curved, new branches arising with variable frequency, sometimes in pairs but sometimes singly, by distolateral budding at an angle of between about 45° and 90° to the parent branch. Crowding of zooids

EXPLANATION OF PLATE 2

Figs. 1 and 2. *Arachnidium smithii* (Phillips, 1829), BMNH D 57497, South Ferriby, Kimmeridgian. 1, pyritic cast of collapsed zooid with wrinkled frontal membrane, $\times 100$. 2, orifice of the same zooid, $\times 270$. Figs. 3–6. *Arachnoidella abusenensis* sp. nov., holotype, BMNH D 57637, South Ferriby, Kimmeridgian. 3, crowded zooids moulded on the underside of the bioimmuring bivalve, $\times 15$. 4, astogenetic increase in zooid length along a branch originating as a lateral bud from the zooid on the left, $\times 28$. 5, mould of zooid showing marginal processes; note lack of visible orifice which is located on a distally-directed peristome hidden in the shadow at the distal end of the zooid, $\times 93$. 6, marginal processes in zooid preserved as a calcitic cast $\times 136$. All illustrations are back-scattered electron micrographs of uncoated specimens.

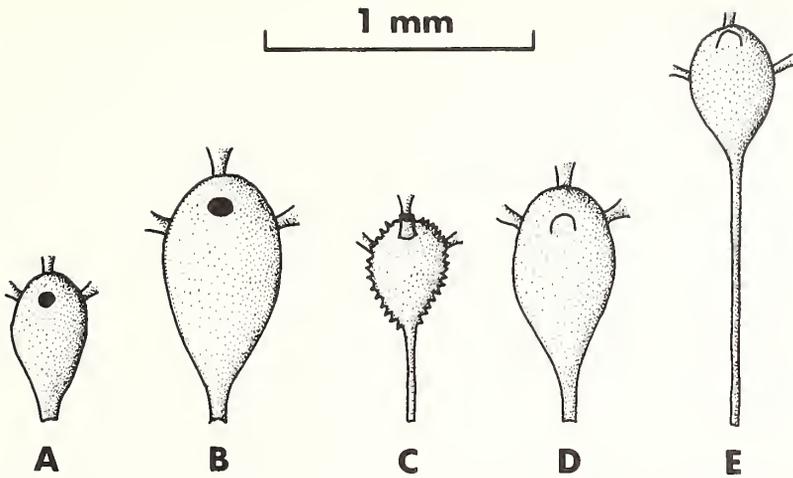




TEXT-FIG. 2. Mould bioimmuration of *Arachnidium smithii* (Phillips, 1829) visible on the large attachment area of the bivalve *Gryphaea* from the Oxfordian of Villers-sur-mer, BMNH D 57492. A, general view of the bioimmuring *Gryphaea*, $\times 1.2$ B, attachment area showing prominent branch of zooids running from top to bottom, and dense settlement of the foraminifer *Nubeculinella* on the younger, peripheral parts of the attachment area, $\times 2.1$.

may occur in colonies with a high frequency of branching, and can be accompanied by branch overgrowths (Pl. 1, fig. 3) and/or abutment of growing branches against existing branches. In early astogeny (visible only in D 57495), the ancestrula apparently buds proximal and distal periancestrular zooids which initiate two primary colony branches growing in opposite directions. A brief primary zone of astogenetic change is marked by an increase in zooid size with generation. Putative ancestrula about 0.23 mm long by 0.17 mm wide.

Autozooids moderately pyriform in frontal outline shape, narrow proximally, achieving maximum width about or a little distally of mid-length, and with rounded distal ends. Length and width of autozooids is very variable between colonies, measured length ranging from 0.47 to 1.00 mm, width from 0.25 to 0.45 mm, with



TEXT-FIG. 3. Zooid morphology in Jurassic arachnidids. A and B, *Arachnidium smithii* (Phillips, 1829) showing variation in zooid size (A is based on YM 78, B on BMNH D 57497). C, *Arachnoidella abusensis* sp. nov. D, *Cardioarachnidium bantai* sp. nov. E, *C. voighti* sp. nov.

zooids generally about twice as long as wide. Frontal wall gently convex, often preserved with flattened lateral margins flanking a raised median area which includes the orifice. Longitudinal wrinkles and folds (Pl. 1, fig. 2; Pl. 2, fig. 1) developed on frontal walls of zooids cast by pyrite in BMNH D 57497. In BMNH D 58002, the casting mineral near an autozooidal orifice contains shallow pits which may perhaps represent original pits on the frontal wall. Orifice simple, subterminal, located opposite or a little distal to origins of lateral buds, subcircular to transversely elliptical in shape (Pl. 1, fig. 6), about 0.04–0.08 mm in diameter, occasionally with a slightly raised rim. An eccentrically perforated structure partly occludes the orifice of one zooid of BMNH D 57497 (Pl. 2, fig. 2).

Kenozooids may develop in regions of crowding as small subtriangular-shaped buds (?aborted autozooids) lacking an orifice (text-fig. 1).

Dimensions (mm).

	\bar{x} autozooid length (range)	\bar{x} autozooid width (range)
YM 78 (holotype)	0.59 (0.50–0.68)	0.31 (0.26–0.36)
BMNH D 31144	0.52 (0.47–0.59)	0.30 (0.26–0.36)
VH 1899 (<i>vide</i> Voigt 1977)	0.72 (0.63–0.84)	0.33 (0.25–0.41)
BMNH D 57492	0.74 (0.63–0.90)	0.32 (0.27–0.36)
BMNH D 57494	0.66 (0.54–0.74)	0.38 (0.30–0.45)
BMNH D 57495	0.62 (0.53–0.71)	0.32 (0.30–0.38)
BMNH D 57496	0.76 (0.62–0.90)	0.38 (0.32–0.42)
BMNH D 57497	0.88 (0.80–1.00)	0.40 (0.38–0.45)

Discussion. The present concept of *Arachnidium smithii* (Phillips) encompasses colonies exhibiting a wide range of variation in autozoid length and width (compare text-figs. 3A and B). It seems possible that *A. smithii* may represent a species complex. However, the overlapping dimensions of colonies from different stratigraphical horizons prohibit convenient splitting into two or more putative species. Furthermore, there are no obvious differences in zoid shape, budding pattern etc. which might be used for this purpose. Accordingly, *Stomatopora phillipsii* Vine and *Arachnidium jurassicum* Voigt are taken into synonymy with *A. smithii*. It should be noted that the stenostome nature of *A. smithii* and *S. phillipsii* were unknown when Voigt (1977) erected *A. jurassicum*; neither species was revised until Taylor (1978) and both were presumed to be cyclostomes of the common Jurassic genus *Stomatopora* Bronn.

The Barremain species *A. brandesi* Voigt strongly resembles *A. smithii* but has considerably larger zooids; according to Voigt (1968), zoid length ranges from 1.65 to 1.75 mm.

The appearance of the zooids within colonies of *A. smithii* may vary according to the extent of their collapse during overgrowth. Uncollapsed zooids have evenly convex frontal walls (Pl. 1, fig. 5), whereas partially collapsed zooids generally have flattened lateral margins flanking a raised median area (Pl. 1, fig. 3). The pattern of collapse undoubtedly reflects some aspect of original zooidal morphology. Dried zooids of the Recent species *Arachnoidea amnosciae* figured by d'Hondt and Geraci (1976, fig. 4) show a similar collapsed structure. Banta (1975, fig. 22), in a drawing of bioimmured *A. brandesi*, labels the margins of the zooids as 'gymnocyst' and the median area as 'opesium', suggesting an organization like that of anascan cheilostomes in which the frontal membrane is attached to rigid lateral walls and stretches over the opesium (see Taylor 1981). The parietal muscle (whose contraction depresses the frontal membrane and brings about polypide eversion) were possibly attached to the frontal membrane along the well-defined lines between flattened lateral margins and raised median area. Wrinkling and folding of the frontal wall in pyrite casts of zooids in BMNH D 57497 (Pl. 1, fig. 2; Pl. 2, fig. 1) is a further indication of partial collapse during overgrowth. Transverse contraction of the zoid resulted in the relatively non-elastic cuticle being thrown into a series of folds and wrinkles running subparallel to the length of the zoid.

Stratigraphical range. Aalenian (*polyplocus* Zone) to Kimmeridgian (*baylei* Zone).

Genus ARACHNOIDELLA d'Hondt, 1983

Type species. *Arachnoidea amnosciae* d'Hondt and Geraci, 1976.

Discussion. *Arachnoidella* was originally proposed by d'Hondt (1983) as a subspecies of *Arachnoidea* Moore, 1903. However, Gordon (1986) elevated *Arachnoidella* to genus rank because the type species of *Arachnoidea* (*A. raylankesteri* Moore) is a freshwater species in which the zooids are interconnected by anastomosing filaments, absent in marine *Arachnoidella*. As noted on p. 20, the distinction between *Arachnoidella* and *Arachnidium* is not great, and the former may eventually prove to be a junior subjective synonym of the latter. D'Hondt (1983) recognized eight Recent species of *Arachnoidella*. The genus has not been previously recorded as a fossil.

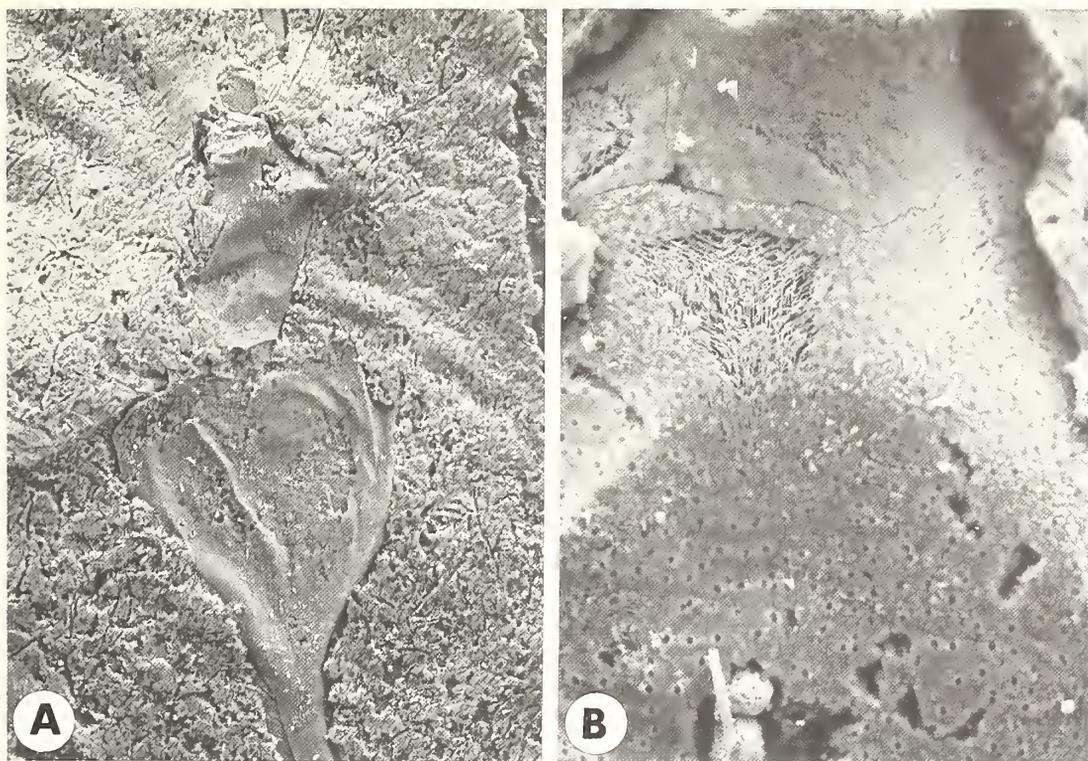
Range. Jurassic (Kimmeridgian) to Recent.

Arachnoidella abusensis sp. nov.

Plate 2, figs. 3-6; text-fig. 3C; text-fig. 4

Holotype. BMNH D 57637, Kimmeridgian, Bed 9 of Birkelund and Calloman (1985) (lower *baylei* Zone), South Ferriby, Humberside, collected by P. D. Taylor, 1987; predominantly a mould bioimmuration (Pl. 2, figs. 3-5) but with a few zooids cast by calcite (Pl. 2, fig. 6) on the attachment area of the bivalve *Deltoideum delta* (Sowerby).

Paratype. BMNH D 57602, details as for holotype; a cast bioimmuration (text-fig. 4) partly exposed by abrasion of the thin overgrowing organism which encrusts a bivalve shell fragment.



TEXT-FIG. 4. *Arachnoidella abusensis* sp. nov., partly collapsed zooids preserved as maturals casts, BMNH D 57602. South Ferriby, Kimmeridgian. A, zoid with distally-directed peristome exposed by abrasion of the bioimmuring organism, $\times 162$. B, distal part of frontal membrane of another zoid showing minute pores which are absent from the peristome base at the top of the figure; note presence of 3 sets of fibres in corroded frontal membrane left of centre, $\times 890$. Back-scattered scanning electron micrographs of an uncoated specimen.

Derivation of name. From *Abus*, Roman name for the River Humber which is close to the type locality of South Ferriby.

Diagnosis. *Arachnoidella* with small zooids having about 30 marginal processes; orifice situated terminally on a distally orientated peristome; caudae account for half or more of total zooid length and increase in length during early branch astogeny.

Description. Colony adnate, consisting of branches of uniseriably-arranged zooids. New branches arise as lateral buds and diverge from the parent branch at an angle averaging about 60° . Frequent branch ramification results in areas of zooid crowding and branch overgrowth (Pl. 2, fig. 3). Ancestrula unknown. Secondary zones of astogenetic change occur in the early parts of new branches: caudal length increases progressively for the first three or four generations of zooids (Pl. 2, fig. 4).

Autozooids pyriform with a cauda of variable length, generally accounting for half or more of the total length of the zooid, succeeded distally by a longitudinally elliptical dilated frontal wall. Autozooid length variable within colonies, observed range 0.42–1.26 mm ($\bar{x} = 0.92$ mm); width ranging from 0.21–0.27 mm ($\bar{x} = 0.25$ mm). Distal frontal wall gently convex (Pl. 2, fig. 5) or flattened (text-fig. 4A) as a result of overgrowth, and bearing minute pores which are absent from the cauda and peristome (text-fig. 4B). Lateral buds arise a little distally of the level of maximum width on the distal frontal wall. Marginal processes visible around the distal frontal walls of some zooids, numbering about 30 per zooid (Pl. 2, figs. 5 and 6). Orifice situated at the extreme

distal end of the zooid on a peristome (text-fig 4A) which is directed distally and is about 0.05 mm wide at its base.

Discussion. This species is distinguished from previously described Jurassic arachnidiids by the extreme distal location of the orifice. Secondary zones of astogenetic change, manifested by progressive increase in zooid length along new branches, are considerably better developed than in other species. In comparison with Recent species of *Arachnoidella*, *A. abusensis* zooids have fewer marginal processes than *A. annosiae* (c. 30 versus 60) but more than all the other species tabulated by d'Hondt (1983).

The preservation of the paratype (text-fig. 4) deserves comment. Naturally-cast zooids are partially visible beneath the thin basal layer of the overgrowing organism. The casting is of a very high quality, and shows clearly the presence of minute pores on the frontal wall and their absence on the cauda and peristome. Although the identity of the casting material is unknown, an abraded area of the cast of one zooid has a fibrous structure (text-fig. 4B). Fibres are arranged in 3 conjugate sets orientated at 120° to one another. One of the sets exactly parallels the long axis of the zooid. This suggests that the fibres may reflect some aspect of the original structure of the zooidal frontal wall. Possibly they are pseudomorphs of one of the organic components of the zooid body wall.

Stratigraphical range. Kimmeridgian (*baylei* Zone).

Genus CARDOARACHNIDIUM gen. nov.

Type species. *Cardoarachnidium bantai* sp. nov.

Derivation of name. *Cardo-*, Latin for hinge, in reference to the apparent presence of a hinged operculum.

Diagnosis. Arachnidiidae in which the autozooidal orifice is D-shaped with a straight proximal edge and a curved distal/lateral edge.

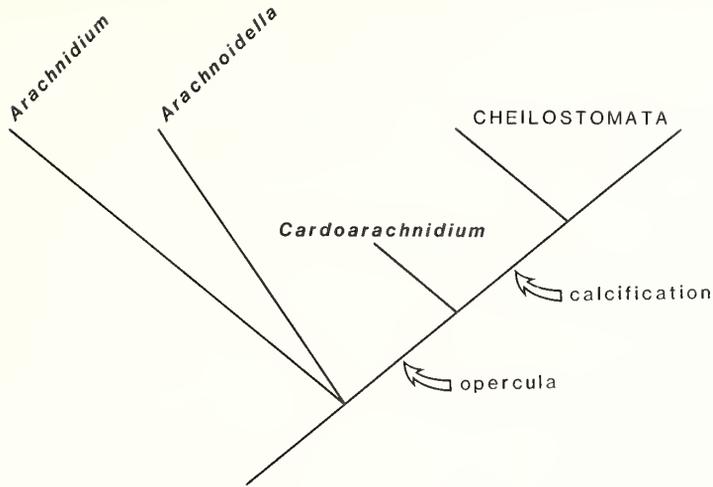
Discussion. This new genus is established for two new species of Jurassic bioimmured ctenostomes which differ from species of *Arachnidium* and *Arachnidiella* in having a D-shaped autozooidal orifice suggesting the presence of a hinged operculum during life. Opercula are generally regarded as being absent in ctenostome bryozoans. However, Banta (1975) notes that structures 'virtually indistinguishable from opercula' occur in the living ctenostome genera *Flustrellidra*, *Elzerina* and *Hislopia*, and d'Hondt (1983) describes the lip of the orifice in *Haywardozoon* as 'simulating an operculum'. An important difference between *Cardoarachnidium* and these Recent genera is that the operculum of *Cardoarachnidium* is a well-defined, univalved structure, whereas those of the Recent genera are bivalved – they are commonly described as bilabiate – with a distal hinged flap as well as a generally larger proximal hinged flap.

Although the phylogenetic significance of the inferred operculum in *Cardoarachnidium* is discussed fully on page 32, it is appropriate to note here that its presence allows *Cardoarachnidium* to be placed within the stem-group of the Cheilostomata. If correct, *Cardoarachnidium* is more closely related (in cladistic terms) to the Cheilostomata than it is to other genera of the Arachnidiidae. The latter family as understood here and by previous authors is almost certainly paraphyletic, and demands future division into its constituent monophyletic clades. Until this is accomplished *Cardoarachnidium* is assigned to the Arachnidiidae.

Cardoarachnidium bantai sp. nov.

Plate 3, figs. 1–3; text-fig. 3D

Holotype. BMNH D 57499 (a), Sandsfoot Clay (sandy top), Upper Oxfordian (*serratum* or *regulare* Zones), below Sandsfoot Castle, Weymouth, Dorset, collected by W. J. Kennedy, N. J. Morris and C. P. Palmer, 1971.



TEXT-FIG. 5. Simplified cladogram showing inferred phylogenetic relationships between genera of arachnidiid ctenostomes present in the Jurassic and the Cheilostomata. *Cardoarachnidium* is depicted as a stem-group cheilostome because it apparently possesses one (opercula) but not the second (calcification) apomorphic feature of the crown-group cheilostomes. The trichotomy between *Arachnidium*, *Arachnoidella* and *Cardoarachnidium* + the Cheilostomata is unresolved.

A mould bioimmuration on the attachment scar of the bivalve *Dehoideum delta* (Sowerby), and intergrown with the holotype of *Cardoarachnidium voighti* sp. nov. (see p. 30).

Derivation of name. In recognition of the bryozoological research of Dr W. C. Banta (The American University, Washington).

Diagnosis. *Cardoarachnidium* with pyriform zooids lacking significant caudae; orifice located subterminally.

Description. Colony adnate, consisting of uniserial branches, often slightly curved, from which daughter branches arise sporadically as lateral buds and diverge at angles of 60–90° to the parent branch (Pl. 3, fig. 1). Ancestrula budding a proximal periancestrular zooid only; no distal periancestrular zooid visible (Pl. 3, fig. 2). Ancestrula of similar shape but smaller than the periancestrular zooid and later zooids, with a length of 0.30 mm, width 0.17 mm and D-shaped orifice 0.06 mm wide.

Autozooids moderately pyriform in outline shape, narrow proximally, rounded distally, achieving maximum width rather distal of mid-length. Length of autozooid about 2.5 times the width, length averaging 0.76 mm (range 0.63–0.93 mm), width averaging 0.32 mm (range 0.27–0.39 mm). Frontal wall gently convex, sometimes with slightly flattened lateral margins. Close to the orifice in one autozooid, the basal layer of the bioimmuring bivalve is penetrated by small pores which may represent a negative impression of an originally spinose or pustulose frontal wall and operculum. Orifice when visible is D-shaped (Pl. 3, fig. 3), wider than long, small, about 0.05 × 0.08 mm in size, situated more-or-less opposite sites of lateral bud origin. The straight proximal edge is less well-defined than the crescentic lateral/distal edge which, together with the shape of the orifice, suggests that an operculum was hinged on the proximal edge of the orifice. In many zooids the orifice cannot be seen, possibly because of poor quality bioimmuration.

Discussion. Colony-form and autozooid shape and size are very similar to *A. smithii*, although the length:width ratio of the autozooids is a little greater in *C. bantai*. However, the D-shaped orifice serves to distinguish *C. bantai* from *A. smithii*.

Stratigraphical range. Oxfordian (*serratum* or *regulare* Zones).

Cardoarachnidium voighti sp. nov.

(Plate 3, figs. 4–6; text-fig. 3E)

Holotype. BMNH D 57499 (b), Sandsfoot Clay (sandy top), Upper Oxfordian (*serratum* or *regulare* Zones), below Sandsfoot Castle, Weymouth, Dorset, collected by W. J. Kennedy, N. J. Morris and C. P. Palmer, 1971. A mould bioimmuration on the attachment scar of the bivalve *Deltoideum delta* (Sowerby), and intergrown with the holotype of *C. bantai* sp. nov. (see p. 28).

Derivation of name. In honour of Professor E. Voigt (Universität Hamburg).

Diagnosis. *Cardoarachnidium* with slender, caudate zooids; orifice located terminally.

Description. Colony adnate, consisting of uniserial branches from which daughter branches arise as lateral buds at an angle of about 45–90° to the parent branch (Pl. 3, fig. 4). Branch ramification occurs frequently, most zooids producing two lateral buds. Growing branches generally terminate on meeting established branches, giving an anastomosing network in some areas of the colony. Ancestrula unknown.

Autozooids slender (Pl. 3, fig. 5), 0.74–1.65 mm long (\bar{x} 1.20 mm), a narrow proximal cauda accounting for a third to three quarters of their length and succeeded distally by a dilated part the shape of a longitudinally elongate ellipse 0.32–0.45 mm long (\bar{x} 0.37 mm) by 0.20–0.29 mm wide (\bar{x} 0.22 mm). Distal frontal wall gently convex or flat-topped; ornamentation not apparent. Laterally-budded daughter zooids often rather shorter than their parental zooids, but clearly-defined secondary zones of astogenetic change not obvious. Lateral budding loci situated a little distally of mid-length on the distal frontal wall. Orifice terminal (Pl. 3, fig. 6), small, slightly raised, a poorly-defined D-shape, about 0.07 mm wide.

Discussion. This species is immediately distinguished from most other Jurassic bioimmured ctenostomes by the long length of the caudae. In this feature it most closely resembles the Maastrichtian *Arachnidium longicauda* Voigt, 1980 which has a roughly circular distal frontal wall, and subcircular orifice situated much further proximally than that of *C. voighti*. Although the caudae of *Arachnoidella abusensis* (see p. 26) may also be long, the orifice of this species is more terminally situated and the zooids often possess marginal processes.

None of the autozooidal orifices are as well-preserved as those of *C. bantai* which shares the same substratum. Nevertheless, *C. voighti* also appears to have a D-shaped orifice suggesting the presence of an operculum hinged on the straight proximal edge of the orifice. This D-shape is apparently not an artefact caused by the overgrowing organism pushing over short peristomes in a distal direction; if it were the D-shape would be better developed in zooids orientated parallel to the growth direction of the overgrowing organism, which is not the case.

Stratigraphical range. Oxfordian (*serratum* or *regulare* Zones).

DISCUSSION

Present-day bryozoan faunas are dominated by species belonging to the order Cheilostomata. For example, in a survey of seven regional faunas (Taylor 1981), the percentage contribution of cheilostome species ranged from 69 to 91. However, cheilostomes are a geologically young order,

EXPLANATION OF PLATE 3

Figs. 1–3. *Cardoarachnidium bantai* sp. nov., holotype, BMNH D 57499 (a), mould bioimmuration, Weymouth, Oxfordian. 1, uniserial branch, $\times 14$. 2, ancestrula (lower left) with proximal ancestrular bud (centre) and its distal bud, $\times 55$. 3, D-shaped orifice of proximal periancestrular zooid, $\times 15$.

Figs. 4–6. *Cardoarachnidium voighti* sp. nov., holotype, BMNH D 57499 (b), mould bioimmuration, Weymouth, Oxfordian. 4, $\times 16$. 5, caudate zooids, $\times 38$. 6, distal part of zooid showing terminal orifice, $\times 120$.

All illustrations are back-scattered electron micrographs of uncoated specimens.



first appearing at the end of the Jurassic (Pohowsky 1973) and not diversifying appreciably until the late Cretaceous (see Taylor 1988). Several hypotheses have been proposed to account for the phylogenetic origin of cheilostomes (Banta 1975). Cheilostome ancestry has been sought in the Fenestrata (Ulrich 1890), Cyclostomata (Dzik 1975) and Ctenostomata (e.g. Banta 1975; Cheetham and Cook in Boardman *et al.* 1983). There are severe difficulties with hypotheses which propose an origin from either of the first two orders which are stenolaemate bryozoans. Similarities do exist between some cheilostome species and fenestrates (which may share box-shaped zooecia), and between other cheilostome species and stomatopodid or corynotrypid cyclostomes (which can both have uniserial colonies with pyriform zooecia), but these are best explained by homoplasy in the first case (Tavener-Smith 1971) and plesiomorphy in the second. Comparative anatomical studies of living bryozoans support the theory of a ctenostome ancestry for the cheilostomes, or more strictly, that 'ctenostomes' (a primitive, paraphyletic grouping of marine bryozoans) include the sister-group of cheilostomes. As Banta (1975) points out, there are extremely few differences between many carnosan ctenostomes and primitive cheilostomes.

The Cheilostomata are very probably a monophyletic clade which can be distinguished from their sister group ctenostomes by two apomorphic characters; calcification of parts of the zooid body walls, and the possession of an operculum to close the orifice on retraction on the tentacles. All living cheilostomes have some degree of calcification, although in certain genera (e.g. *Membranipora*, *Flustra*) this is slight. Most cheilostomes possess opercula; absence of the operculum in the feeding zooids of a few genera (e.g. *Bugula*) is undoubtedly a result of their secondary loss, as shown by the presence in the same colonies of polymorphic zooids (avicularia) which retain opercula. Extinct cheilostomes for which adequate information is available also possess the two apomorphies. Indeed, they are present even in the oldest known cheilostome, *Pyriporopsis portlandensis* from the Tithonian (Portlandian) of southern England, which has thickly-calcified zooid vertical walls, and in which the past presence of a non-calcified operculum can be inferred confidently from impressions on the closure plates of degenerated zooids (Pohowsky 1973; Banta 1975; Taylor 1987). Therefore, current knowledge of living and fossil cheilostomes provides no information on the order of appearance of the two apomorphies; did calcification predate opercula or vice-versa?

The new genus *Cardoaraclnidium* is important because it apparently has one of the two apomorphies of the Cheilostomata. The simple D-shaped opercula of *Cardoaraclnidium* closely resemble the opercula of primitive anascan cheilostomes. However, *Cardoaraclnidium* clearly did not have calcified zooids and therefore lacked the second apomorphy of the Cheilostomata; bioimmured colonies show no trace of calcified zooid walls, and distortion of the zooids during overgrowth, typical of that seen in other bioimmured ctenostomes, implies that the zooids were soft-bodied.

The stem-group concept in phylogenetics has been explained recently by Jefferies *et al.* (1987). Stem-groups are the paraphyletic ancestral groupings of extinct taxa remaining when the crown groups have been subtracted from the total group. They are distinguished by possessing some but not all of the apomorphies that separate any two monophyletic clades with extant representatives (crown groups). By this criterion, *Cardoaraclnidium* can be included in the stem-group of the Cheilostomata. This inferred relationship is expressed in the cladogram depicted in text-fig. 5. Stratigraphical sequence is consistent with the cladogram; arachnidoids date back at least to the Aalenian, *Cardoaraclnidium* occurs in the Oxfordian, and the first cheilostome in the Tithonian. The discovery and phylogenetic placement of *Cardoaraclnidium* solves the problem of the order in which the two apomorphies of cheilostomes appeared; opercula apparently predate calcification.

As the most crownward known representative of the stem-group of the Cheilostomata, *Cardoaraclnidium* is a useful outgroup for inferring character polarities (plesiomorphic versus apomorphic) during studies of phylogenetic relationships within the cheilostomes. Unfortunately, however, relatively few morphological characters are available in bioimmured *Cardoaraclnidium* and these do not, of course, include characters of the calcified skeleton which are generally emphasized during studies of cheilostomes. Nevertheless, *Cardoaraclnidium* does suggest the following plesiomorphic character states in cheilostomes: uniserial pattern of colony growth with

the potential for each zooid to produce a distal and two lateral buds; pyriform zooid shape; and the budding of a proximal periancestrular zooid from the ancestrula. *Pyriporopsis*, *Pyripora* and *Herpetopora* among primitive 'malacostegan' cheilostomes (see Taylor 1987) retain all of these characters, although there is a tendency towards pluriserial growth in *Pyriporopsis*.

Knowledge of Jurassic bryozoans is strongly geographically constrained; very few Jurassic bryozoans have been described outside Europe, and modern studies are mostly concerned with faunas from France and southern England. Within this limited geographical region, however, an interesting pattern of stratigraphical distribution is apparent. Rich cyclostome bryozoan faunas occur locally in the Middle Jurassic (e.g. Gloucestershire Aalenian, Normandy Bathonian), with assemblages containing encrusting and erect tubuliporine and cerioporine cyclostomes. Few ctenostomes are evident, either as borers in the abundant shelly substrata, or as encrusters preserved by bioimmuration. Upper Jurassic bryozoan faunas from southern England and France contain assemblages of encrusting tubuloporine cyclostomes greatly reduced in diversity and abundance. However, ctenostomes are much more prominent than in the Middle Jurassic. They include shell borers as well as the bioimmured encrusters described herein. Considering the fairly low probability of preservation of soft-bodied arachnidiids, their abundance and diversity in the late Jurassic epicontinental sea of north-west Europe may have been substantial, quite possibly exceeding arachnidiid abundance and diversity at the present-day. The origin of the Cheilostomata should be viewed within the context of this time of comparative arachnidiid prevalence.

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PALAEOPERIDINIUM CRETACEUM: A BRACKISH-WATER PERIDINIINEAN DINOFLAGELLATE FROM THE EARLY CRETACEOUS

by I. C. HARDING

ABSTRACT. New SEM observations of topotype material of *Palaeoperidinium cretaceum* from the early Cretaceous of Alberta, Canada have allowed a complete description of this poorly known morphotype, including tabulation and plate overlap patterns. The features displayed by *P. cretaceum* show that, unlike other members of the genus, this morphotype cannot be interpreted as an extrathecal 'exophragm'. The life-cycle stage represented by *P. cretaceum* is discussed in relation to the life-cycle of modern dinoflagellates. It is suggested that *P. cretaceum* may represent a hitherto unknown fossilizable zygotic stage in the dinoflagellate life-cycle.

THIS paper details the unusual morphology displayed by *Palaeoperidinium cretaceum* Pocock (1962) as revealed by the scanning electron microscope (SEM). This morphology is interpreted in the light of recent discoveries regarding this genus and our present knowledge of the dinoflagellate life-cycle.

The genus *Palaeoperidinium* was created by Deflandre (1935, p. 227) to accommodate those dinoflagellate fossils which displayed a similar morphology to that of the modern dinoflagellate genus *Peridinium* (now *Protoperidinium*), but whose tabulation was insufficiently known to allow allocation to an existing genus. No type species was designated and the genus became a 'waiting genus' for incompletely known morphotypes (Sarjeant 1967, p. 242).

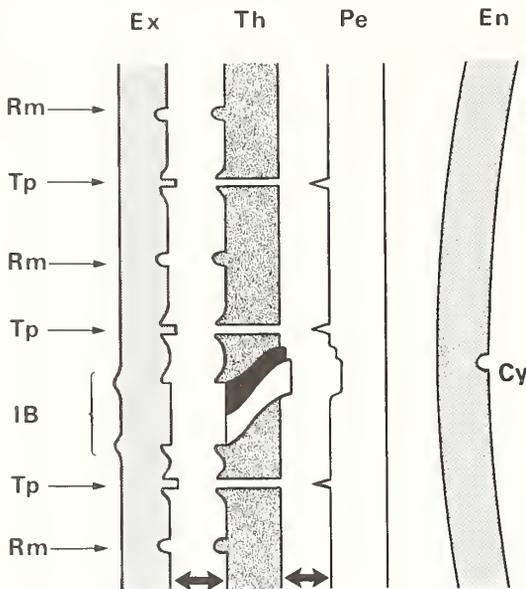
Palaeoperidinium pyrophorum, originally described by Ehrenberg (1838) and allocated to the modern genus *Peridinium*, was selected as the type species of the genus when it was formally emended by Sarjeant (1967).

Interest in the genus *Palaeoperidinium* has been stimulated by the meticulous study of late Cretaceous *P. pyrophorum* (Gocht and Netzel 1976). Utilizing the superior resolution capabilities of the SEM, Gocht and Netzel showed that the prominent sculptural elements of *P. pyrophorum* are located on the internal surface of the fossil and not the external surface as in other known fossil peridiniineans. Previous observations had shown that the dinoflagellate fossil record consisted of intrathecal cysts. Furthermore, tabulation patterns are known to occur on the internal surfaces of modern dinocyst wall layers (cf. *Peridinium limbatum* Evitt and Wall (1968), which led Gocht and Netzel to explain cyst formation and morphology in *P. pyrophorum* in terms of genetic control by the cell protoplast.

However, whereas it does seem reasonable to explain the endocystical tabulation of *Peridinium limbatum* in terms of genetic control (the possibility of the theca acting as a 'template' being precluded), it is unlikely that such a mechanism can be invoked for *P. pyrophorum*. Evitt (1985 pp. 205–207) reasoned that *P. pyrophorum* is unlikely to represent a conventional intrathecal cyst because its single wall layer often contains a two-walled internal body which itself could be interpreted as an intrathecal cyst. He also argued that phenetic influences on the ontogeny of an individual mature theca (represented by pandasutural areas) were unlikely to be found on a body wall independent of the theca. In the case of *P. pyrophorum*, the most elegant interpretation of the negative relief patterns on the internal cyst surface is that they were formed by direct contact with the external surface of the parent theca.

Thus, *P. pyrophorum* was taken to represent a resistant (sporopollenin?) extrathecal structure

(Evitt 1985, p. 206), subsequently termed an 'exophragm' (Evitt *et al.* 1987). The presumed relationships of exophragm, thecal and cyst wall layers can be seen in text-fig. 1. Evitt *et al.* (1987) have subsequently examined *P. basilum* and two as yet undescribed early Cretaceous species and concluded that they too seem to be exophragms. Modern dinoflagellates are not known to produce fossilizable extrathecal wall layers, but some species do form a gelatinous extrathecal sheath (Evitt 1985, p. 206) indicating a mechanism whereby such a layer might be deposited.



TEXT-FIG. 1. Cross-sectional wall layer relationships in a hypothetical dinoflagellate. Ex = 'exophragm', Th = thecal plate, Pm = periphragm, En = endophragm. The first three wall layers are formed closely appressed to one another. The following features are represented in various guises on several of the wall layers: Rm = reticular murus, Tp = trichocyst pore, IB = intercalary growth band, Cy = cell cytoplasm. This cross-section is a composite reconstruction, the 'exophragm' (Ex) is based on that of *Palaeoperidinium pyrophorum*, the thecal plates (Th) on modern *Peridinium*, the periphragm (Pe) on *Subtilisphaera terrula* and the endophragm (En) on modern *Peridinium limbatum* (note parasutural groove on internal surface of endophragm). The plasmalemma, vesicular membranes and pellicle are omitted. N.B., all wall layers shown would not be present at one time.

Palaeoperidinium cretaceum was first described by Pocock (1962) from the Quartz Sand Member of the early Cretaceous Lower Mannville Formation (Imperial McMurray Testhole 6, Alberta, Canada). Davey (1970) made *P. cretaceum* the type species of his new genus *Astrocysta* after studying Albian specimens from the International Yarbo No. 17 borehole, east of Regina, Saskatchewan. Subsequent authors have treated *Astrocysta* as a junior synonym of *Palaeoperidinium* (Lentin and Williams 1976), but Bujak and Davies (1983, p. 134) suggest the retention of *Astrocysta* to accommodate conventional intrathecal cysts presently allocated to *Palaeoperidinium*. More recently the type specimen of *P. cretaceum* has been re-examined by Jansonius (1986).

The present study was prompted by the discovery of abundant specimens of *P. cretaceum*, from 130 ft (39.62 m) in the IGS (now British Geological Survey) Hunstanton Borehole in Norfolk. These specimens were observed during an SEM-based biostratigraphical project on the dinocysts of the western European Barremian (Harding in press). Topotype material of both *P. cretaceum* and '*Astrocysta cretacea*' have been made available to enable an SEM study of this morphotype.

MATERIAL AND METHODS

The topotype material was supplied as a wet residue, prepared following standard palynological techniques, but without oxidation or alkali treatment, in order to keep degradation of this thin-walled taxon to a minimum. Little obscuring amorphous organic matter was present. Other samples mentioned in this paper have been oxidized. For SEM observation, specimens were either strew-mounted or individually picked via micropipette from an aqueous solution on to squares of X-ray film. This minimizes the loss of morphological definition experienced with standard SEM preparation techniques (e.g. Hughes *et al.* 1979). The specimens were found to adhere well to the moistened emulsion, with no sinking of palynomorphs into the mounting medium. The film squares, most bearing scribed reference grids, were cemented on to aluminium pin-stubs with

cyanoacrylate adhesive, and sputter-coated with gold. Observations were made using a Philips 501B SEM; permanent micrographic records were made on 70 mm Ilford FP4 film.

Residues were stained using Saffranin O, but specimens of *P. cretaceum* showed no coloration. This negative staining reaction has been observed in many types of thin-walled dinocysts, raising the question as to whether they are of the same composition as other 'sporopollenin' dinocysts. Lentin (pers. comm.) suggested that *P. cretaceum* might have a wall composed of chitinous material (*n*-acetylglucosamine). In order to test this possibility a chitin-specific stain was added to the residue. This stain consisted of iodine, potassium iodide and hydrated calcium chloride in distilled water, a positive test turning chitin red-violet (Lillie 1965, p. 503). The test proved negative. This result is perhaps unsurprising, given that hot hydrochloric acid is used in the processing of a palynological residue and that chitinous arthropod exoskeletal cuticle will dissolve in such a medium. The precise composition of the wall of *P. cretaceum* therefore remains unclear.

The following descriptions are based on the examination of the topotype material and use conventional dinocyst terminology (see Evič 1985), although the prefix 'para-' is not used (Norris 1978). Illustrated specimens are held in the Sedgwick Museum, Cambridge, England.

PALAEONTOLOGY AND AGE OF THE SAMPLES

In Hunstanton borehole sample HUN 130 was unique amongst the European samples in yielding abundant specimens of *P. cretaceum*. No more than ten specimens were recorded in total from all of the other localities studied: Speeton (Yorks.), Alford (Lincs.), Warlingham (Surrey) and Gott (West Germany) (Harding in press). The microfungal assemblages isolated from HUN 130 suggested that this sample represents a much nearer-shore environment than the other samples in which *P. cretaceum* only rarely occurred. After a light microscope (LM) count of 200 palynomorphs (slide X413/3) the microfungal composition of the sample was found to be as follows (%): saccate gymnosperm pollen, 39; *Classopollis*, < 1; *Eucommiidites*, 1; large trilete fern spores, 10; small trilete fern spores, 18; angiosperm pollen (*Afropollis*), 2; *P. cretaceum*, 3; other dinocysts, 10; foram. linings, 1; fungal bodies, 2; unidentified 'simple sacs', 13.

The single species of angiosperm pollen present in this sample represents a new species of the genus *Afropollis* (Penny 1989). Twenty-six dinocyst taxa were identified in the sample, most of a very low numerical abundance. The limited dinocyst assemblage and the abundance of terrestrial palynomorphs suggest a strong terrestrial input into a marginal area of deposition – probably a brackish-water environment. The sample is of late Barremian age.

In contrast, the microfungal assemblage in the topotype sample (LM slide JANSONIUS 640/4) gave the following composition after a count of 200 palynomorphs (%): saccate gymnosperm pollen, 14; large trilete fern spores, 2; small trilete fern spores, 6; angiosperm pollen, < 1; *P. cretaceum*, 6; other dinocysts, 7; unidentified 'simple sacs', 64.

This sample has a low-diversity dinocyst flora in which ten taxa have been identified at least to generic level. The dinocysts are dominated by *P. cretaceum* with ceratioids, some similar to those described by Bint (1986), forming the next largest group. The large percentage of unidentified 'simple sacs' precludes making accurate environmental statements. However, the remaining microflora and especially the nature of the dinocyst assemblage (see Bint 1986) suggest a low-salinity (at most brackish) origin for the deposition of this sample. This sample was originally dated as Cretaceous by Pocock (1962), but a more precise estimate of Aptian or Albian age was given by Jansonius (1986). The latter age is favoured here from the presence of tricolpate angiosperm pollen with bimodal luminal sizes and by the ceratioid dinocysts.

The sample from the International Yarbo borehole No. 17 (count of 200 palynomorphs from slide CH238/3) yielded a microfungal assemblage as follows (%): saccate gymnosperm pollen, 4; small trilete fern spores, 7; '*Astrocyta*' *cretacea*, 6; *Ovoidinium ostium*, 16; other dinocysts, 17; unidentified palynomorphs, 50 (poorly preserved).

Ten species of dinocyst have so far been recorded. Identified terrestrial palynomorphs are rare, with a far greater percentage of dinocysts present in the assemblage. This leads to the conclusion that this sample was deposited in an environment in which a more normal marine salinity prevailed than in those discussed above. However, as will be seen later, the dinoflagellate from this sample

which Davey (1970) described under the new genus *Astrocysta*, is not the same morphotype as that from the type sample of *P. cretaceum*. Thus, environmental interpretations derived from the International Yarbo sample are not of significance in assessing the life environment of *P. cretaceum*. The age of the sample is late Albian (Davey 1970).

From the analyses of the first two study samples it appears that *P. cretaceum* occurs in residues isolated from samples deposited in restricted salinity environments. The distribution of this morphotype in samples from restricted environments is also corroborated by some samples from offshore Canada where this species comprises 100% of the dinocyst flora (Lentin pers. comm.). It is perhaps unwise to suggest that *P. cretaceum* was a freshwater species. It does seem reasonable, however, to interpret *P. cretaceum* as being formed by a dinoflagellate which was found in low-salinity marginal environments. The presence of marine dinocysts alongside *P. cretaceum* may be due to taphonomic transport of *P. cretaceum* into these areas (i.e. they are allochthonous), or that the morphotype was euryhaline.

MORPHOLOGY OF *PALAEOPERIDINIUM CRETACEUM*

The most striking feature of *P. cretaceum* is its diaphanous nature. The body wall is only $\approx 0.2 \mu\text{m}$ thick and does not absorb staining compounds. Specimens show strong primary dorso-ventral compression and a distinctive peridinioid ambitus (Pl. 1, fig. 1). The apical region is drawn out into a broad-based, tapering, truncated, apical horn (Pl. 2, fig. 7). The antapical region bears two asymmetrical horns, that on the left being the more pronounced (Pl. 2, fig. 9). The cyst consists of a single thin wall layer, the antapical horns are solid and the apical horn is thickened distally.

Surface features

The majority of specimens do not display well developed tabulation – indeed the surface features of many are negligible or extremely indistinct. Tabulation, when discernible, is more distinct on the ventral surface and the dorsal hypocyst, specimens with clearly expressed dorsal epicystal tabulation being rare. This may be interpreted as indicating that tabulation was originally less well expressed on the dorsal epicyst. However, as so many specimens entirely lack definite surface features, it may be that the dorsal epicyst is more prone to post-mortem degradation than the rest of the cyst. Fortunately, the abundance of *P. cretaceum* in the study sample has allowed a reconstruction of the tabulation of this morphotype.

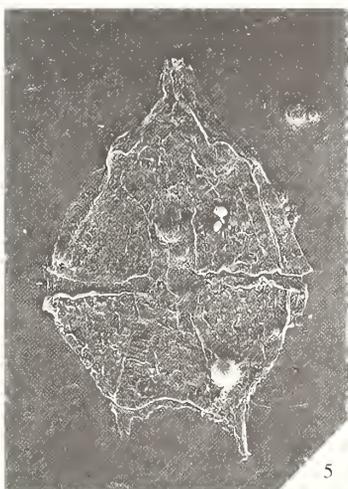
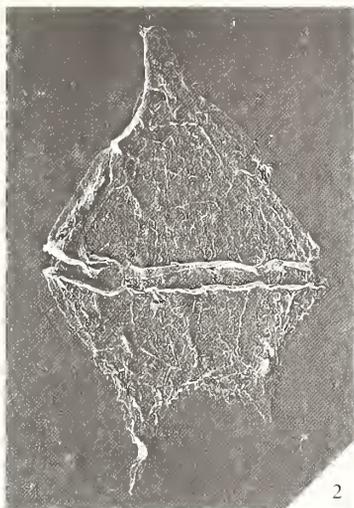
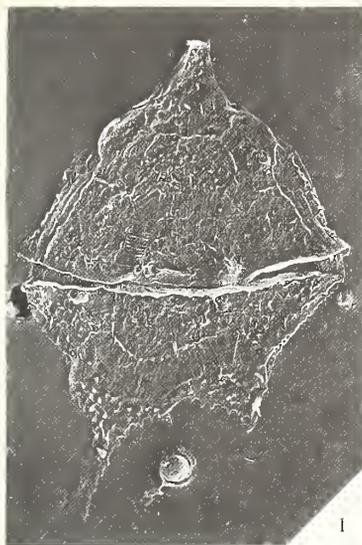
Tabulation is standard ortho-hexa peridinioid type (text-fig. 2), no variation from this pattern having been observed (unlike the aberrant ortho-penta organization found on occasional specimens of *Subtilisphaera terrula* – Harding 1988). The 2a plate is iso-deltaform (Δ , as defined by Bujak and Davies 1985, p. 25).

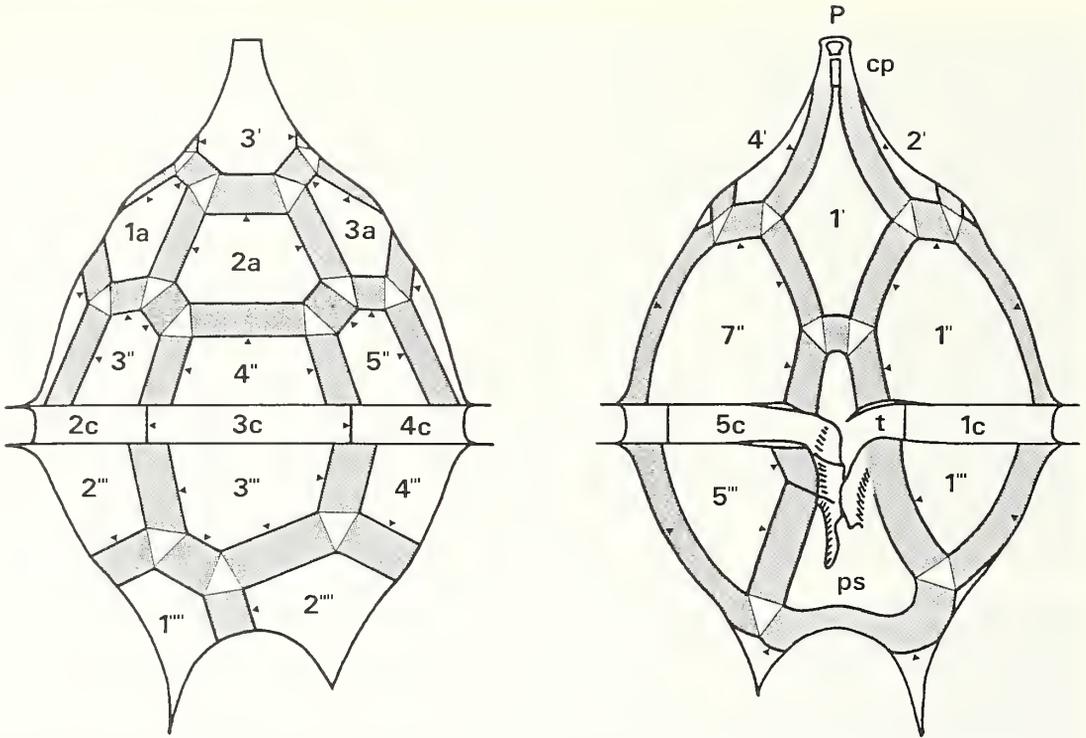
The ventral epicyst displays a large rhomboidal first apical plate (1', Pl. 2, fig. 7), the anterior margins (1'/2' and 1'/4') of which are delineated by low septa up to $1 \mu\text{m}$ high (arrowed in Pl. 2, fig. 7). Anterior to the first apical plate, the septa run parallel along the lateral margins of a small, axially elongated plate, identified as the canal plate of Dodge and Hermes (1981) (Pl. 3, fig. 5). The distal extremity of the apical horn is encircled by a collar formed by the fusion of the lateral septa. This collar, which often possesses subdued denticulation, surrounds a solid cylindrical or conical projection (Pl. 3, fig. 5).

EXPLANATION OF PLATE 1

All figures are from a depth of 640 ft in the Imperial McMurray Testhole 6, Alberta, Canada and preparation JANSONIUS, unless otherwise stated. Also given are the SEM stub numbers (IC-), a 6-figure stub grid reference or specimen number, and film and frame number.

Figs. 1–9. *Palaeoperidinium cretaceum*. Fig. 1, IC517, specimen 1, 3002/72 b. Dorsal view, showing tabulation, $\times 640$. 2, IC517, specimen 2, 3004/72 b. Dorsal view, showing tabulation, $\times 640$. 3, IC447, specimen 1, 3035/73. Ventral view, showing prominent sulcal rostrum, $\times 800$. 4, IC517, specimen 4, 3006/72 b. Ventral view, $\times 640$. 5, IC517, specimen 3, 3008/72 b. Ventral view, $\times 640$. 6, IC458, 133/078, 3013/74. Oblique ventral view, note elongate left antapical horn, $\times 800$. 7, IC456, 114/054, 3027/75. Ventral view, $\times 800$. 8, IC456, 124/064, 3032/75. Left lateral view, $\times 800$. 9, IC448, specimen 14, 3041/73. Ventral view, $\times 800$.





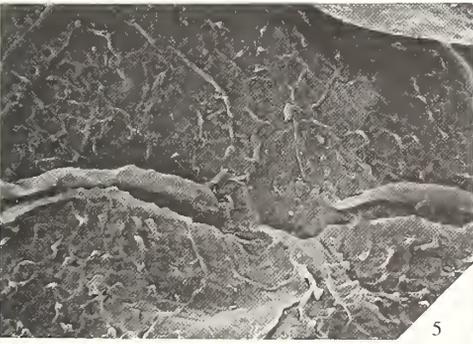
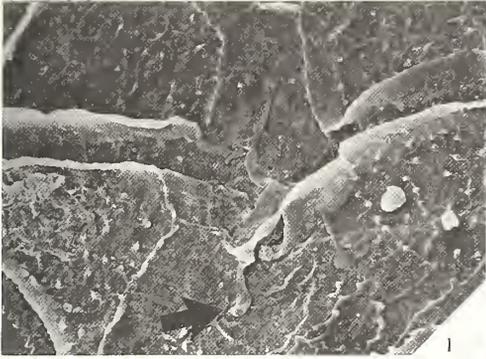
TEXT-FIG. 2. Idealized reconstruction of the tabulation of *Palaeoperidinium cretaceum*, left = dorsal view, right = ventral view. Intercalary bands are stippled. Direction of plate overlap in the thecate organism is shown by the arrowheads, which also indicate the side of the intercalary band which bears the more pronounced bounding ridge. P = apical projection, t = transitional cingular/sulcal plate, cp = canal plate, rostrum indicated by solid arrow, left sulcal list indicated by open arrow.

The planar cingulum is a prominent depression bordered by distally denticulate septa on both posterior and anterior margins, the septa having a maximum height of $\approx 4 \mu\text{m}$ (Pl. 2, figs. 1 and 4). The septa at the right-hand and anterior left-hand terminations of the cingulum decrease in height as they approach the sulcus. However, the posterior left-hand septum is directed antapically into the sulcus, forming what neontologists would call a 'sulcal list' (Pl. 2, figs. 1–6). There is also a similar structure developed on the left-hand margin of the right sulcal plate, this 'list' being extended onto the posterior sulcal plate in the form of a rostrum (Pl. 2, figs. 1–6). This latter 'list' in particular is convex and arches over the left sulcal plate.

The sculpture of the plate area is subdued and reticulate (often very poorly preserved), the junctions of the reticulum (in particular) often bear distal outgrowths of a lobate or conical nature (Pl. 2, fig. 8). These distal

EXPLANATION OF PLATE 2

Figs. 1–9. *Palaeoperidinium cretaceum* Fig. 1, IC449, specimen 1, 3040/73. Ventral view, detail showing high cingular lists, left sulcal list and rostrum (arrowed), $\times 1600$. 2, IC457, 105/031, 3037/75. Ventral view, detail of sulcal area, left sulcal list is well shown (arrow), $\times 1600$. 3, IC447, specimen 1, 3036/73. Ventral view, detail of sulcal area, left sulcal list and rostrum well developed, $\times 3000$. 4, IC449, specimen 7, 3044/73. Ventral view, detail of hypocyst, lists prominent, $\times 1600$. 5, IC456, 168/044, 3024/75. Ventral view, detail of sulcal area, note plate reticulation and cingular lists, $\times 1600$. 6, IC515, specimen 4, 3026/72a. Ventral view, detail of sulcal area, $\times 1600$. 7, IC457, 133/054, 3040/75. Ventral view, detail of rhomboidal 1' plate and apical horn, $\times 1600$. 8, IC458, 127/054, 3017/74. Detail of plate 5'', showing reticulation, $\times 3000$. 9, IC456, 120/050, 3028/75. Dorsal view, showing tabulation, striate intercalary bands and hypocystal ambital denticulation, $\times 1360$.



outgrowths give a denticulate outline to the hypocyst ambitus, especially pronounced on the antapical horns (Pl. 3, fig. 2 – this feature is not seen on the epicyst as the ambitus here is occupied by plate-bounding septa).

All specimens displaying tabulation possess intercalary ('pandasutural') bands. These bands are prominent, plate-bounding areas $\approx 4 \mu\text{m}$ in width with strongly developed cross-striations (Pl. 2, fig. 9) except at the triangular junctions between adjacent intercalary bands (Pl. 3, fig. 6). There is no evidence of a feature reflecting a suture-plane between adjacent plates. The two lateral margins of an individual intercalary band are dissimilar. One margin is bordered by a low ridge, often distally denticulate especially on the hypocyst (Pl. 2, fig. 9). This ridge is developed into the lateral septa found on the ventral epicyst. The opposite margin has a less distinct boundary, but in some instances may appear to be folded over the adjacent plate area. This differential development of intercalary band margins clearly reflects the mode of thecal plate overlap. Netzel (1982) showed that one of the methods for analysing the direction of plate overlap was to recognize an overlapping plate margin by the development of crests or ridges of differing heights. In the case of *P. cretaceum*, the margin of the intercalary band bearing the denticulate ridge can be identified as the overlapping plate, allowing the reconstruction of the overlap pattern (text-fig. 2). This reconstruction shows that the keystone (Evitt 1985) or ridge-tile (Netzel 1982) plates are 4" and 3"', the conventional arrangement for modern peridinioid dinoflagellates. This contrasts with the arrangement determined for the early Cretaceous dinocyst *Subtilisphaera terrula* (Harding 1988), in which the 3" and 3"' plates were involved.

The archaeopyle

A low percentage of specimens (10% of 200 specimens observed in LM) have been discovered which display an archaeopyle, but this may be due in part to the nature of the opening. Jansonius (1986) described the archaeopyle found on the holotype of *P. cretaceum* as being A313Pa (3', 1–3a, 3–5"). This is a transapical archaeopyle (Bujak and Davies 1983, p. 21). This definition shows that the dorsal epicystal plates remain attached, as a compound operculum, via the cingulum to the rest of the cyst after release of the cell contents. Thus, theoretically, the presence of an archaeopyle can only be recognized when this operculum is laterally displaced (as in the holotype) or is removed mechanically. However, those specimens illustrated in Pl. 3, figs. 5, 6, 11, show no sign of a mechanical removal of the operculum, a conventional suture accounting for the loss of the operculum. Furthermore, specimens have been found which appear to show the initiation of the archaeopyle suture along the precingular–cingular junction (Pl. 3, fig. 4). It may be inferred from this that the archaeopyle type in *P. cretaceum* is A313P, hemiepicystal rather than transapical, the operculum sometimes remaining adnate along the cingulum (*sensu* Evitt 1985).

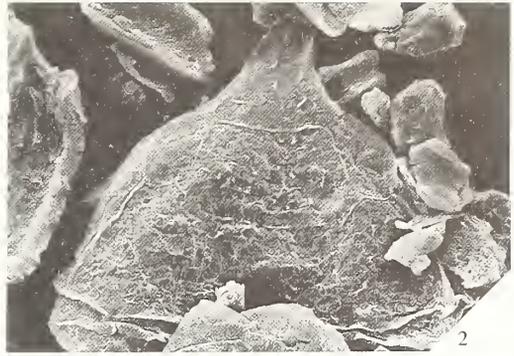
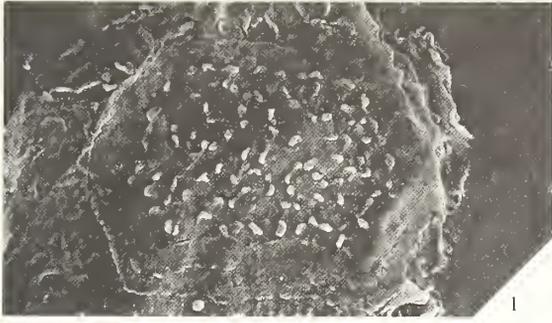
It should be noted at this point that on specimens from which the operculum has been lost, the inner surface of the body wall can be examined. In all instances the inner surface has been found to be devoid of sculpture, even when tabulation is expressed on the external surface of the body wall (Pl. 3, figs. 3, 7, 8).

AFFINITIES

Palaeoperidinium cretaceum, based on the morphology described above, belongs to the tribe Palaeoperidinioideae of Bujak and Davies (1983). Further elucidation of its affinities can be made by determining the number of cingular plates developed. Boltovskoy (1979) showed a strong

EXPLANATION OF PLATE 3

Figs. 1–9. *Palaeoperidinium cretaceum*. Fig. 1, IC456, 106/035, 3026/75. Dorsal view, detail of deltaform 2a plate, intratabular reticulum subdued although distal outgrowths from this reticulum are prominent, $\times 2400$. 2, IC456, 146/007, 3001/74. Dorsal view, detail of epicyst, note 2a plate, $\times 1040$. 3, IC475, 146/077, 3001/74. Dorsal view, detail of epicyst showing archaeopyle, note lack of ornamentation on the interior of the epicyst, $\times 1200$. 4, IC515, specimen 5, 3027/72a. Dorsal epicystal detail showing operculum detached along the cingulum, $\times 880$. 5, IC457, 124/037, 3038/75. Ventral view of apical horn showing canal plate and apical projection, $\times 3000$. 6, IC517, specimen 5, 3009/72b. Detail of triple junction between adjacent striate intercalary bands, $\times 3000$. 7, IC457, 104/076, 3035/75. Dorsal view, archaeopyle well displayed, $\times 800$. 8, IC457, 117/059, 3036/75. Dorsal view, archaeopyle well displayed, $\times 800$. 9, topotype specimen of '*Astrocyista*' *cretacea*. IC513, specimen 3, 3028/72a. Detail of dorsal epicystal intercalary bands, note lack of striation, $\times 1600$.



HARDING, *Palaeoperidium*

correlation between the number of cingular plates and the nature of the intercalary bands found in the adcingular plate series amongst modern dinoflagellates. From the six broad intercalary bands of *P. pyrophorum* (then still believed to be a cyst), Boltovskoy inferred the presence of six cingular plates. Bujak and Davies (1983) later reinterpreted this cingular tabulation as being one transitional cingular/sulcal and five cingular plates. According to the method outlined by Boltovskoy (1979), *P. cretaceum* should also have five cingulars and a transitional plate. However, Taylor (1987, p. 52) has pointed out that Boltovskoy's method is fallible, as some modern species of *Protoperidinium* have only three cingulars but produce six broad intercalary bands. Hence, Boltovskoy's method is an unreliable way of determining the number of cingular plates in modern dinoflagellates and it seems unwise to apply it to fossil cysts as suggested by Bujak and Davies (1983, p. 35). Greater use of SEM observation is likely to allow the number of cingular plates in fossil dinocysts to be determined with more certainty. This study shows that the cingular tabulation of *P. cretaceum* is the same as that represented on the exophragm of *P. pyrophorum*.

P. cretaceum, therefore, is a peridiniinean characterized by an ortho-hexa style of tabulation, a linteloid second anterior intercalary plate and an epicystal tabulation displaying symmetry about the dorsal midline. These features clearly show that *P. cretaceum* is morphologically more closely related to the modern freshwater genus *Peridinium sensu stricto* than to the marine genus *Protoperidinium* (which has only three cingular plates). The dorsal epicystal symmetry narrows this attribution further to the bipesiod group of *Peridinium sensu stricto*, the cinctioid group having no such symmetry (Bujak and Davies 1983). *P. cretaceum* is the oldest peridiniinean dinoflagellate fossil described from sediments deposited in environments of less than normal marine salinity. Peridiniinean dinocysts have not previously been *conclusively* identified in such sediments prior to the Oligocene, although other groups of dinocysts have now been reported from reduced salinity environments of the early Cretaceous of southern England (Hughes and Harding 1985; Batten 1985; Lister and Batten 1988), the USA (Bint 1986) and China (Lentin *et al.* 1988).

SYSTEMATIC PALAEOLOGY

Genus PALAEOPERIDINIUM Deflandre (1935) emend. Sarjeant (1967)

Palaeoperidinium cretaceum Pocock (1962)

- 1962 *Palaeoperidinium cretaceum* Pocock, p. 80, pl. 14, fig. 219.
 1970 *Astrocysta cretacea* (Pocock); Davey, p. 359.
 1986 *Palaeoperidinium cretaceum* Pocock; Jansonius, p. 214, pl. 5, fig. 6.

Emended diagnosis. Shape. Typically pentagonal peridinioid ambitus. Prominent broad-based apical horn, two antapical horns of which the left-hand is the more pronounced. Epicyst usually longer than hypocyst. Greatest width across cingulum. Strong primary dorso-ventral compression. *Phragma.* Autophragm, very thin ($\approx 0.2 \mu\text{m}$ thick), when well preserved shows corrugated intercalary bands delineating tabulation. Septa developed bordering cingulum, sulcus, ventral apical region. Plate areas have subdued reticulate sculpture. *Tabulation.* Ortho-hexa peridinioid type, 4', 3a, 7", 5c, 5"', 4s. Iso-deltaform second anterior intercalary. Apical structure indicates an apical pore plate and a small ventral canal plate. A cingular/sulcal transitional plate also present. *Archaeopyle.* Type (A313P), hemiepicystal, operculum often remains adherent along the cingulum. *Cingulum.* Planar, with five plates and one transitional. Bordered by distally denticulate septa. *Sulcus.* Consists of four plates; right sulcal plate bears a convex sulcal 'list' which is prolonged onto the posterior sulcal in the form of a rostrum. Less prominent 'list' is found on the left sulcal.

Dimensions. Length = (68) 80 (101) μm . Number of specimens measured = 30.

Remarks. The description of this species is revised following the examination of topotype material. Although the type species of the genus has been shown to be a fossil of extrathecal origin, *P. cretaceum*, is retained in the same genus. Bujak and Davies (1983) suggested that the genus

Astrocysta Davey be retained for those species of *Palaeoperidinium* which were shown not to be extrathecal structures. This practice is unnecessary as there is an obvious phylogenetic relationship between the taxa. Such a practice would lead to the same problems of dual nomenclature presently experienced with modern motile dinoflagellates and their corresponding cyst stages.

The morphotype described by Davey (1970) as the type of his new genus *Astrocysta* is not synonymized with *P. cretaceum* in this work. Unfortunately, the poor preservation of the Saskatchewan topotype specimens does not suit them to SEM analysis, but the resulting micrographs do show that the morphotype is a conventional intrathecal cyst and not an 'exophragm' (Pl. 3, fig. 9). The morphology of the cyst does reveal that '*Astrocysta*' is a junior synonym of *Palaeoperidinium* (as envisaged above). Measurement of twenty-two specimens of '*A. cretacea*' has resulted in the following: length = (90) 112.5 (135) μm . The minimum and maximum dimensions comply with those given by Davey (1970), but the mean of Davey's measurements is 10 μm less than that determined here from a greater number of specimens. Thus, the average specimen from Davey's material is a full 30 μm (37.5%) longer than the average specimen of *P. cretaceum*. Whilst this could indicate an evolutionary increase in the size of the organism through Albian time, it is felt more likely that the morphotype described by Davey (1970) is referable to a separate taxon, albeit within the genus *Palaeoperidinium*. Judging from the associated palynoflora, '*Astrocysta*' *cretacea* appears to have occupied a more saline environment than *P. cretaceum*.

NATURE OF THE FOSSIL

The general morphology of *P. cretaceum* presents an aspect unlike that of most cyst-types, in that it appears to be outwardly similar to the motile, thecate stage of many modern peridiniinean dinoflagellates. This raises the question: which stage in the dinoflagellate life cycle does *P. cretaceum* represent?

SEM examination reveals that sculptural elements on the body wall of *P. cretaceum* are located on the external surface, the internal surface being laevigate (e.g. Pl. 3, fig. 3). In this respect it is unlike other recently studied species currently placed in this genus (Gocht and Netzel 1976; Evitt *et al.* 1987). *P. pyrophorum* is also known with internal bodies which have been interpreted as conventional intrathecal hypnozygotic cysts (Evitt 1985). Pocock (1962; p. 80) mentioned that occasional specimens of *P. cretaceum* contained 'spherical cysts' but an LM study of 200 specimens for this study has not revealed any such structures. It would therefore appear that *P. cretaceum* is not an extrathecal mould or exophragm.

The striking morphology of *P. cretaceum* allows comparison with the motile thecate stages of modern dinoflagellates, in the same manner as Evitt (1985, pp. 267–268) likened fossil *Dinogymnium* and modern *Gymnodinium*. There is a strong resemblance between the *P. cretaceum* and modern peridiniinean thecae. Evitt (1985) stated that for the two gymnodinioid genera previously mentioned, there is 'complete compatibility between the form of the depressions here considered to be flagellar furrows and actual occupation of the depression by flagella of design and function typical for dinoflagellates'. However, the presence of an archaeopyle in *P. cretaceum* would argue against interpretation as a vegetative theca. In this case, the 'archaeopyle' may be interpreted as an ecdysial opening formed in the vegetative theca to allow release of the cell contents in response to vegetative reproduction (eleutheroschisis) or adverse conditions. Boltovskoy (1973) detailed ecdysial openings (which he erroneously referred to as 'archaeopyles') in several modern *Peridinium* species. A strong correlation exists between the plates involved in thecal ecdysial openings and those involved in archaeopyle formation.

Against interpretation of *P. cretaceum* as a vegetative motile stage are the facts that the theca would have to have been impregnated with sporopollenin or a similar resistant organic compound, a feature unknown amongst modern thecae, and that pore-structures representing trichocyst pores, apical pore complexes and flagellar pores were not detected on the fossil. The first condition may not be a difficulty given that 'diversity is the hallmark of dinoflagellates' (Evitt 1985, p. 268) and that other types of sporopollenin-impregnated membranes occur in the palaeoperidinioid lineage.

More serious is the presence of a cylindrical projection at the end of the apical horn, where a pore might be expected. This projection is similar to the first preapical (P) plate of cribroperidinioid dinocysts which has been interpreted as a plug-like infilling of the apical pore (Evitt 1985, p. 75). The lack of trichocyst pores and flagellar pores is similarly disquieting. Also, if *P. cretaceum* were a thecate organism, the thecal plates would have dissociated when subjected to Javelle water (discounting the unknown effects of diagenesis or sporopollenin impregnation). This is not the case. Thus, it seems unlikely that *P. cretaceum* represents a fossilized vegetative theca.

If not a vegetative thecate stage, is it possible that *P. cretaceum* might represent an individual, resistant component of the dinoflagellate amphiesma (as defined by Loeblich 1970)? The pellicle is the only component of the amphiesma in modern dinoflagellates with any likelihood of being fossilized. The pellicular layer is found in modern thecate dinoflagellates lying inside the vesicular layer, which encloses the thecal plates (Loeblich 1970, see also text-fig. 1). Pellicles are possessed by most thecate dinoflagellates and many are acid-resistant (Morrill and Loeblich 1981). Modern species, especially of *Peridinium*, have acetolysis-resistant pellicles with a presumed sporopollenin component in their fibrous wall-structure (Morrill and Loeblich 1981).

The pellicle and the inner vesicular membrane form the outer wall of ecdysial cysts (also referred to as temporary, vegetative and pellicular cysts) after the shedding of the theca (see Dürr and Netzel 1974 and the 'spheroplasts' of Adamich and Sweeney 1976). The pellicular layer has fossilization potential, but lacks prominent sculptural features other than subdued ridges and pore openings. The simple sac-like morphology of modern dinoflagellate pellicles argues against *P. cretaceum* being a fossilized pellicular layer or an ecdysial cyst.

From the discussion above, interpretation of *P. cretaceum* as a stage in the vegetative part of the dinoflagellate lifecycle cannot be accepted. Thus it must represent part of the sexual phase: the planozygotic theca, the hypnozygotic theca or the hypnozygotic cyst. Corroboration of the involvement of the sexual phase is given by the broad intercalary bands of *P. cretaceum*. Studies by Pfeister and Skvarla (1979, 1980) of the vegetative and sexual theca of species of modern *Peridinium* have shown that, at most, vegetative thecae produce only very narrow intercalary bands. It is the plano- and hypnozygotic thecae that display extremely broad intercalary bands, indicating plate growth to accommodate the growing cell protoplasm.

It seems improbable that the fossil can be identified as a conventional hypnozygotic cyst as the surface features are incompatible with the wall layer having been deposited beneath the amphiesmal vesicles. The cyst of *Subtilisphaera terrula* clearly shows evidence of having been formed adpressed to the inside of the thecate organism (Harding 1988), but the thin, delicate cingular and sulcal 'lists' of *P. cretaceum* are entirely compatible with their having been functional and thus external features.

P. cretaceum appears to represent a resting stage, presumably formed after sexual reproduction, but its morphological features argue against it being viewed as a conventional subthecal hypnocyst. Given our relative lack of knowledge regarding present-day zygotic cysts, it is suggested that *P. cretaceum* may be a hitherto unknown fossilizable zygotic stage in the dinoflagellate life-cycle. Given the structural innovations already known within the lineage containing *P. cretaceum*, and the morphological experimentation (especially with archaeopyle types – Bujak and Davies 1983) amongst early Cretaceous Peridiniineae, this conclusion may not be an entirely untenable notion.

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This manuscript was submitted before the recent presentation on *Palaeoperidinium* given by Evitt *et al.* (1989) at the DINO4 conference at Woods Hole, Massachusetts. This elegant presentation used sophisticated microcasting and SEM image-processing techniques to reveal the details of the internal surface of specimens referred to *Palaeoperidinium pyrophorum*. The internal surface of *P. cretaceum*, studied using scanning electron microscopy, has not revealed any similar features to those displayed by the material illustrated at DINO4. Further investigation has failed to identify any internal membrane/conventional cyst wall adpressed to the internal surface of the wall of *P. cretaceum* which could obscure such features. The evidence presented is that *P. cretaceum* represents a dinoflagellate fossil of a different organizational nature to those described by Evitt *et al.* (1989).

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NEW PERMIAN CRINOIDS FROM AUSTRALIA

by G. D. WEBSTER

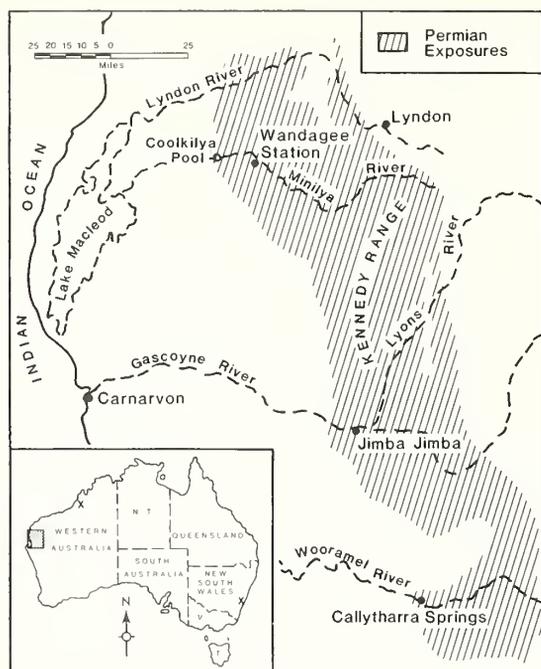
ABSTRACT. Thirteen taxa of Permian crinoids are reported from Australia. These crinoids increase our knowledge of the cooler water Australian late Palaeozoic faunas, are dominantly sand substrate dwellers, and provide new fossils which support earlier correlations of recognized Permian strata in eastern and Western Australia. The early Permian age of several Australian species, which are also found in Timor, supports earlier views that the previously assigned late Permian age of the Timor crinoid-bearing Basleo Beds of the Maubisse Formation may be incorrect. Taxonomic reassignment of families previously placed in the Lophocrinacea are: the Pachylocrinidae to the Texacrinacea, based on the similarities of the radial facets and arms branching patterns; the Stellarocrinidae to the Texacrinacea, based on dorsal cup similarities; and the Laudonocrinidae to the Pirasocrinacea, based on dorsal cup and arm morphology. Taxonomic reassignment of four genera previously placed in the Pelecocrinidae, all based on similarity of morphological characters of the dorsal cup of the genus and the family, are: transfer of *Forthocrinus* to the Stellarocrinidae; *Tetrabrachioocrinus* to the Laudonocrinidae; and *Malaiocrinus* and *Depaocrinus* to the Pachylocrinidae. Inadunates recognized for the first time in Western Australia are *Eoindocrinus praecontignatus* and *Tapinoocrinus spinosus*. New taxa described are the camerates *Dichocrinus? gerringongensis* sp. nov., *Neocamptocrinus occidentalis* sp. nov., and *Stomiocrinus ferruginus* sp. nov., and the inadunates *Occiduoocrinus australis* gen. et. sp. nov., *Anechoocrinus nalbiaensis* gen. et sp. nov., *Skaioocrinus granulosus* gen. et sp. nov., and *Jimbacrinus minilyaensis* sp. nov.

PERMIAN crinoids were first reported from eastern Australia by M'Coy (1847), Ratte (1885, 1887), Etheridge (1892), and Jack and Etheridge (1892). In 1915, Etheridge described plates of the crinoid *Calceolispongia*, from Western Australia, mistaking them for parts of a sponge. Sieverts-Doreck (1942) reported the stems of two inadunate genera from Tasmania. Teichert (1949) demonstrated the early Permian stratigraphic significance of 14 species of *Calceolispongia* within the Carnarvon Basin of Western Australia and, in 1954, recognized *Jimbacrinus*, another genus of the calceolispongiids, from Western Australia. Three inadunates were reported from Queensland in papers by Dickins (1968) and McKellar (1969).

More recently Willink (1978, 1979a, b, 1980a, b) described 35 species, systematically reallocated most of the species previously named from eastern Australia, and demonstrated the stratigraphic utilization of several genera in the Permian of eastern Australia. Webster (1987) described an early Permian crinoid fauna (40 species) from the Callytharra Limestone of Western Australia and considered it closely related to the late Permian fauna reported from Timor by Wanner (1916, 1924, 1937, among others).

At present there are 104 species of Permian crinoids recognized from Australia, 51 from eastern Australia and 53 from Western Australia, with no species common to both regions. These Permian crinoids are very important because they are the only recognized cooler water faunas from the Palaeozoic, they support the concept of seaway connections around northern Australia or across the continental interior during the Permian, and they contain some of the same species as the faunas of Timor.

The purpose of this paper is to describe Artinskian to Tatarian crinoids from Australia, especially from the Quinannie Shale and Wandagee Formation of the Minilya River drainage, the Wandagee Formation of the Lyndon River drainage, and the Cundlego Formation in the Gascoyne River drainage of Western Australia (text-fig. 1). Unfortunately, precise stratigraphic horizon or detailed locality information is not available for many of the specimens. However, most are embedded in distinctive lithologies and it is possible that precise locality and stratigraphic details can be determined in the future. The material is described at this time because it adds significantly to the



TEXT-FIG. 1. Locality map showing general location of Permian crinoids described from Australia. Enlarged section of Western Australia modified after Teichert 1949. Specific locality information given under each species in systematics section.

known Permian crinoid faunas and to bring it to the attention of future workers for their applied use. Some taxa add to the increasing number of faunal elements used for correlation between eastern and Western Australia, some raise further questions about the late Permian age of part of the Timor crinoids, and some led to revision of generic and family assignments within the superfamily Lophocrinacea.

SUBSTRATE PREFERENCE

The Permian strata of Western Australia are dominantly clastic sediments; sandstones, graywackes, siltstones, and shales with minor limestones (Trendall *et al.* 1975, among others). Eastern Australian Permian sediments are also dominantly clastic sediments with some volcanoclastics, limestones and coal (Brown *et al.* 1968, among others). The Permian age and series equivalency of the strata in these two areas (text-fig. 2) are based on the occurrence of goniatites and other fossils which have been described in a number of papers since the late 1940s (Teichert 1949; Glenister and Furnish 1961; Thomas Dickins 1954; Dickins 1963; among others).

All specimens reported here, except the mudstone mould of *Dichocrinus?* *gerringongensis* sp. nov. from eastern Australia and the marl-enclosed unnamed new genus of the Rhenocrinidae from Western Australia, are embedded in fine-grained sandstones or mudstones with interbedded sand stringers, are preserved as hydrous iron oxide replacements of the original calcite, and weather a rust yellow or orange to dark red. Most specimens are interpreted to have lived at, or in close proximity to, the site of burial on a sand or silt substrate. Those specimens with arms or proximal lengths of stem attached were buried rapidly, probably the result of storm kills. The few specimens lacking arms and proximal columnals show no abrasion and may have been transported short distances or undergone a brief time of exposure on the sea floor before burial.

Willink (1979a, b, 1980a) reported species of *Gissoerinus?*, *Nowracrinus*, *Tribrachyoerinus*, *Calceolispongia*, and *Meganotocrinus* from sandstones, some very coarse-grained, of eastern Australia. In the same publications or two others Willink (1978, 1980b) reported other species of these same genera and species of *Dichocrinus?* and *Notiocatilloerinus* from mudstones, siltstones

SERIES	WESTERN AUSTRALIA		NEW SOUTH WALES
	CARNARVON BASIN	CANNING BASIN	SOUTHERN SIDNEY BASIN
TATARIAN		LIVERINGA FORMATION	ILLAWARRA COAL MEASURE
KAZANIAN		HARDMAN MBR. CONDREN MBR? LIGHT JACK MBR	GERRINGONG VOLCS. BERRY FM.
KUNGURIAN	KENNEDY GROUP		NOWRA SANDSTONE
ARTINSKIAN	BYRO GROUP BAKER FM. NALBIA GW. WANDAGEE FM. QUINNANIE SH. CUNDLEGO FM. BULGADOO SH. MALLENS GW. COYRIE FM.	NOONKANBAH FORMATION	WANDRAWANDIAN SILTSTONE ?
	WOORAMEL GROUP	POOLE SANDSTONE	YADBORO CONGL.
	CALLYTHARRA FM.	NURA NURA MBR	PIDGEON HOUSE CREEK SILTSTONE
	LYONS GROUP	GRANT FORMATION (part)	

TEXT-FIG. 2. Correlation chart of Permian stratigraphic columns for areas in Australia from which crinoids are reported herein. Columns for Western Australia modified after Trendall *et al.*, 1975; that for New South Wales modified after Willink 1980b.

and volcanoclastic rocks of the same region. With the exception of the fauna from the limestones of the Callytharra Formation (Webster 1987), Permian crinoids previously reported from Western Australia were found in terrigenous derived sediments, mostly siltstones and fine-grained sandstones (Etheridge 1915; Teichert 1949, 1954). Fifty-one of the 104 Permian crinoid species from Australia are reported from fine- to coarse-grained clastic rocks.

It is unusual to find crinoids on quartz sand substrates as most Palaeozoic crinoids are found in fine- to coarse-grained limestones, claystones and marls (Lane *in* Moore and Teichert 1978, p. 344). Some inadunates in the late Palaeozoic were moderately common in terrigenous derived muds (Lane *in* Moore and Teichert 1978, p. 344). Ausich *et al.* (1979) reported an early Carboniferous community dominated by poteriocrine inadunates which occurs in interdistributary siltstones and distributary channel fine-grained sandstones in the Borden Delta of Indiana and Kentucky.

The adaptation to life on a sand substrate by some poteriocrinid inadunates and a few camerates occurred in or before the early Carboniferous (Ausich *et al.* 1979). The adaptation of other poteriocrinid, cyathocrinitid, and rhenocrinid inadunates as well as other camerates in the Permian of Australia apparently accompanied an adaptation to the cooler waters of the more southerly position of Australia during the late Palaeozoic.

The crinoids described are dominantly poteriocrine inadunates, seven species, but include four species of camerates and one cyathocrinitid inadunate. Other than being fairly robust forms, no morphologic feature which might be interpreted as an adaptation to a sand substrate was found to be common to all sand substrate dwelling species. The abundance and diversity of the sand substrate faunas of the Permian of Australia are the greatest known in the Palaeozoic. Additional study of these faunas is needed as most of the earlier collections were made for stratigraphic purposes and sedimentological data necessary for palaeocological studies were not recorded.

CORRELATION

Teichert (1951) pointed out the Tethyan affinities of the marine Permian faunas of Western Australia, noting their diversity, abundance and widespread occurrence. Western Australian crinoid faunas described by Teichert (1949) and Webster (1987) also show Tethyan similarity in kind, are most closely related to the Timor faunas, and have noted affinities to eastern Australian faunas.

Although the Western Australian crinoids are most closely related to the Timor faunas, correlation of the two faunas is problematic. Timor crinoids are reported from several localities and horizons within the Maubisse Formation, such as the Basleo Beds, etc. (Wanner 1914-1949). The Maubisse Formation is a sequence of highly fossiliferous limestones containing some reefal buildups and eruptive rocks including many vesicular basalts (Audley-Charles 1965). The Maubisse Formation occurs in allochthonous thrust blocks, that were thrust southward from an unknown northern source area (Audley-Charles 1965). Furthermore, Audley-Charles (1965) considers the Maubisse Formation to represent the northern margin of the Westralian geosyncline during part of Permian time. Contemporaneous southern shelf margin deposits included the Permian strata of the Canning Basin and Carnarvon Basin of Western Australia.

In a series of papers between 1914 and 1949 Wanner described the crinoid faunas of Timor and reported them to be of early and late Permian age, mostly the latter. Webster (1987) questioned the late Permian age of the Timor faunas because: there are several mutual species in the crinoid faunas from the Callytharra Limestone and the Basleo Beds; crinoid genera and species are generally short lived, geographically restricted, and good index fossils; and the goniatite control on the Permian section of Western Australia is well documented whereas the stratigraphy of the Timor crinoid-bearing beds is not defined.

Species of *Stomiocrinus*, a camptocrinitid, and an indocrinid in the Wandagee Formation show close relationship to species of these same taxa in the Timor faunas. *Tapinocrinus spinosus* occurs in both the Wandagee Formation and the Basleo Beds. The eastern Australian Artinskian species *Dichocrinus? australis*, *D? darlingtonensis*, *Neocatillocrinus oakiensis*, *N. nerimberae*, *Neocamptocrinus bundanoonensis*, *N. wardenensis* and *N. millerensis* show relationship to the Timor 'late Permian' faunas. These mutual occurrences provide additional support for a coeval age and paleogeographic proximity for the crinoid-bearing beds of Timor, eastern Australia, and Western Australia. Until the internal stratigraphic and structural relationships of the allochthonous blocks of Timor are completely understood, the late Permian age of the Timor crinoid bearing beds should be questioned.

The relationship of the Permian marine faunas of Western Australia and eastern Australia has been discussed in several papers in the past 25 years (Teichert 1951; Wass 1969, 1970; Stehli 1971; McClung 1975; Runnegar and Campbell 1975; among others). Permian crinoid genera common to eastern Australia and Western Australia are *Neocamptocrinus*, *Notiocatillocrinus*, and *Calceolispongia*. Although no crinoid species occurs in both areas, species such as *Neo. millerensis* and *Neo. occidentalis*, *Neo. bundanoonensis* and *Neo. sp. nov.*, *No. nerimberae* and *No. callytharraensis*, and *C. lizziensis* and *C. spinosa* are closely related. Crinoids strongly support earlier views that migration pathways around the northern margin or across the central interior of the Australian continent were actively open during part of the Permian.

SYSTEMATIC PALAEOLOGY

Crinoid terminology follows the Treatise on invertebrate paleontology, pt. T, Echinodermata (Moore and Teichert 1978). All measurements are linear and in mm. Specimens are deposited in the University of Western Australia (UWA) and the Australian Bureau of Mineral Resources (CPC).

Subclass CAMERATA Wachsmuth and Springer, 1885
 Order MONOBATHRA Moore and Laudon, 1943
 Family DICHOCRINIDAE Miller, 1889

Diagnosis. Crown elongate, usually small. Calyx bowl- to globose- to truncated cone-shaped. Basals two, equal, with A-CD interbasal suture. Radials five, separated on posterior side by primanal in line of radial circlet. Tegmen low to inflated, with hypertrophied wing plates, or secondarily simplified to five orals, in advanced genera. Free arms primitively uniserial, two to four in each ray, becoming biserial, four to six in each ray in advanced forms. Stem round transversely and straight, or coiled and bilaterally symmetrical.

Remarks. Broadhead (1981) recognized three subfamilies of the Dichocrinidae: (1) the Dichocrininae Miller, 1889, have the second primibrachial axillary, and the transversely round stem is uncoiled; (2) the Camptocrininae Broadhead, 1981, are similar except the stem is coiled, bilaterally symmetrical and cirrae-bearing; and (3) the Talarocrininae Ubaghs, 1953, are characterized by an inflated tegmen, axillary first primibrachials, and a transversely round stem. The Dichocrininae and Talarocrininae are most diverse in the early Carboniferous, whereas the Camptocrininae are most diverse in the Permian. Permian camptocrinids have been reported from Timor (Wanner 1916, 1924, 1937), Australia (Willink, 1980*a, b*; Webster 1987) and Russia (Yakovlev 1927). Their abundance and diversity in Permian strata of Australia offer potential for correlation.

Subfamily DICHOCRININAE Miller, 1889

Genus DICHOCRINUS Münster, 1839

Dichocrinus? gerringgongensis sp. nov.

Plate 3, fig. 1

Diagnosis. Monocyclic, bipartite base, basal flange on cup, and non-aligned nodes on basal and radial plates, second primibrachial axillary, isotomous branching, 10 uniserial arms, stem uncoiled.

Type and locality. An external mould (UWA 62961) found by Dr J. E. Glover in a gray mudstone in Permian strata, on the coastal platform 0.8 km south of Gerringgong, New South Wales. The precise locality and horizon were not recorded.

Etymology. The trivial name is taken from the town of Gerringgong, near where the specimen was found.

Description. Crown moderately large (estimated 5 cm length), elongate. Cup bowl-shaped, higher than wide (estimated 2 cm to radial summit, 1.6 cm wide), widest a little below radial facets; prominent basal flange; basals two, form base of bowl, slightly impressed proximally, upward and slightly outflaring distally, subhorizontally projecting flange slightly below midheight, interbasal suture from middle of primanal to middle of A radial; radials five, higher than wide, gently convex transversely and longitudinally, in contact laterally except on primanal, facet below distal tip; primanal elongate longitudinally, gently convex transversely and longitudinally; coarse node and short oblique ridge ornamentation on basals, radials and primanal; tegmen not exposed. Arms ten; brachials strongly convex transversely, gently to moderately convex longitudinally, wider than high, uniserial, cuneate, isotomous division on IBr₂, no further subdivisions; pinnules slender, one per brachial alternating on sides of arm. Stem round (approximately 12 cm preserved), heteromorphic, alternating nodal and internodal proximally, distally homeomorphic; strongly rounded epifacet, articulum unknown, cirri unknown.

Remarks. *D? gerringgongensis* is the third species questionably assigned to the genus from Permian strata of eastern Australia. Willink (1980) described *D? australis* (late Artinskian from New South Wales) and *D? darlingtonensis* (early Artinskian from Maria Island, Tasmania). These three species form an evolutionary lineage and are closely related in cup shape and coarse noded ornamentation. *D? gerringgongensis* is distinguished by the presence of a prominent basal flange with non-aligned nodes. It is intermediate between *D? darlingtonensis*, which lacks the prominent basal flange and the nodes are non-aligned, and *D? australis*, which has aligned nodes on the basals and radials with a weak basal flange. Although the exact horizon is not known for *D? gerringgongensis*, the morphological affinities to *D? darlingtonensis* and *D? australis* suggest an Artinskian age, with *D?*

gerringgongensis evolving from *D? darlingtonensis* by development of the basal flange. *D? australis* evolved from *D? gerringgongensis* with the alignment of the nodes on the basals and radials.

D? darlingtonensis is from a limestone, whereas *D? australis* is from the Wandrawandian Siltstone (Willink 1980) and *D? gerringgongensis* is from a mudstone. Each is thought to have lived in or very near the site of burial, because they have associated brachials and columnals. Thus these Permian forms apparently had a wide tolerance for substrate type or the three species represent adaptive radiation into different environments.

Broadhead (1981) reviewed the subfamily Dichocrininae and considered the morphology of the tegmen to be an important generic character. Unfortunately, the tegmen is unknown for all three Australian species resulting in the questionable assignment to the genus.

Of the 29 species of *Dichocrinus* that Broadhead (1981) recognized, only two, from the Westphalian of Texas, are known from post early Carboniferous strata and all are known from Europe, North America or Russia. The three Permian species from Australia represent radiation into cooler water environments from a common ancestor.

Subfamily CAMPTOCRININAE Broadhead, 1981

Genus NEOCAMPTOCRINUS Willink, 1980a

Diagnosis. Calyx generally large, subquadrangular in lateral view. Basals bipartite, weakly upflared; radials and equal-sized primanal in second cirlet, strongly upflared. Radial articular facets trifascial. Tegmen inflated, composed of orals, interambulacral and anals symmetrically arranged about A-CD plane of symmetry. Orals five, CD enlarged, dome-like, deltoid or semi-cylindrical, madreporitic. Interambulacral variable in number, commonly two or more in each interray. Anals numerous, serially arranged to form protuberance at posterior. Arms uniserial, isotomously branched, usually on IBr_2 and $IIBr_2$. Stem coiled, bilateral for entire length. Nodal pairs bear solitary or bundled marginal cirri. Rudimentary cirri present or absent. (After Willink, 1980a.)

Neocamptocrinus occidentalis sp. nov.

Plate 1, figs. 1-6, 12-14

Diagnosis. A *Neocamptocrinus* with an inverted V-shaped ridge on the posterior oral immediately above the anal opening; coarse central nodes on all orals; no ornament or with fine granular ornament on the basals, radials and primanal; and four to seven arms per ray.

Types and locality. The paratypes, four partial crowns (CPC 27449-27452) and a pluricolumnal (CPC 27453) are from a single slab containing associated crowns of *Jimbacrinus bostocki*. The holotype (CPC 27448) is a partial crown on a small slab. Both slabs are from an unspecified horizon in the Cundlego Formation, late Artinskian, along the Gascoyne River two miles upstream from the Jimba Jimba Homestead. This is the type locality for *J. bostocki* and the slabs are part of the original material studied by Teichert (1954) when he described *Jimbacrinus*.

Etymology. The trivial name *occidentalis* is Latin for western and refers to the Western Australian occurrence of the species.

EXPLANATION OF PLATE I

Figs. 1-6, 12-14. *Neocamptocrinus occidentalis* sp. nov. 1-4, A ray, oral, basal, and CD interray views, respectively, of paratype CPC 27450; $\times 2$. 5, 6, oral and CD interray views, respectively, of paratype CPC 27449; $\times 2$. 12, exterior view of paratype CPC 27453; $\times 1$. 13, 14, CD interray and A ray views, respectively, of Holotype CPC 27448; $\times 1.5$.

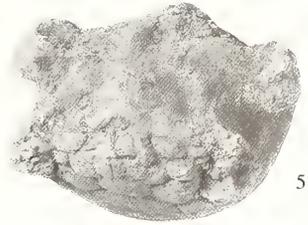
Figs. 7-11. *Neocamptocrinus* sp. nov. 7, D and E ray view, CPC 27455; $\times 1.5$. 8-11, oral, CD interray, A ray, and basal views, respectively, of CPC 27454; $\times 1.5$.



1



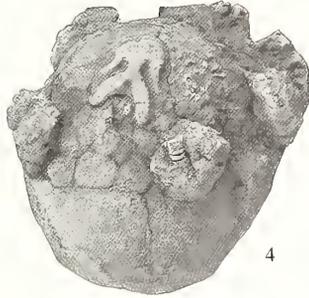
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5



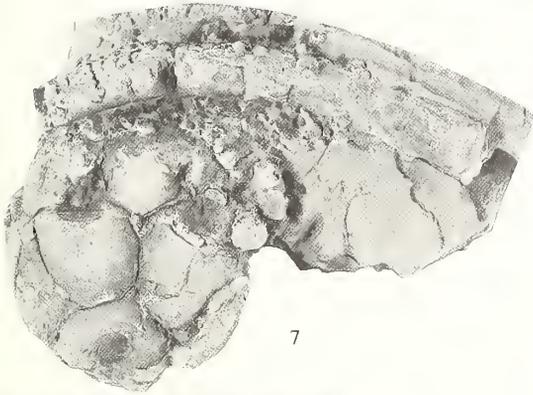
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6



7



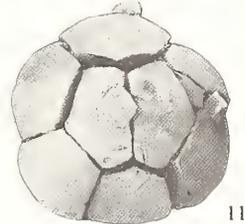
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9



10



11



12



13



14

Description. Crown of moderate size, elongate, widest where arms branch on secundibrachials. Calyx elongate bowl-shaped, higher than wide; fine granular ornament on basal circlet, radials and primanal, or lacking ornament. Basal circlet large, gently upflared, visible in lateral view, bipartite, suture in A ray-posterior plane of bilateral symmetry. Radials five, higher than wide, widest below base of arm facets, steeply upflared to subvertical, gently convex transversely and longitudinally, strongly incurved distally, basal sutures concave adorally. Arm facets angustary, two-fifths width of radial slightly below distal shoulder of radials, gently slope outward; transverse ridge extends full width of facet; outer facet area crescent-shaped with low marginal ridge and low ligament ridge separated by shallow ligament furrow; inner facet area not exposed. Primanal in radial circlet, same size and shape as radials, distally adjoined by three plates in tegmen.

Tegmen gently arched, formed of multiple interambulacra, five large orals, and multiple anals in posterior interray. Interambulacra a series of 8–12 plates, with variable number of small plates in two or three rows above a basal row of three plates. Orals form central circlet at top of tegmen; posterior oral largest, adjoined by other four, with a prominent inverted V-shaped ridge along the proximal edge immediately above the anal opening, may have a centrally adjoined parallel ridge distally. A and E orals smallest, B and D orals of intermediate size, all bearing coarse central node. Anal series 3:5:6+; anal opening central, slightly protruded in third row, surrounded by numerous small plates.

Arms slender, retaining same width until distal tips, 4–7 per ray, first and second branches isotomous, endotomous thereafter; all branching on second brachial of series. Brachials strongly convex transversely, uniserial proximally, cuneate medially, biserial distally. Second primibrachs much wider than long, laterally fixed to interambulacral plates. Secundibrachs wider than long, more strongly convex transversely than primibrachs, first secundibrach may be fixed to interambulacra. Tertibrachs through pentibrachs more strongly convex transversely than primibrachs or secundibrachs. Pinnules slender, one per brachial.

Stem facet impressed in basal circlet, elliptical with long axis at an angle of less than 90° to the plane of bilateral symmetry. Proximal columnals homeomorphic, gently convex latera, symplectial articulation; articulum flat, areola wide, crenularium narrow, twice width of latus; lumen small, round. Measurements are given in Table 1.

TABLE 1. Measurements of *Neocamptocrinus occidentalis*

	Holotype CPC 27448	Paratype CPC 27449	Paratype CPC 27450
Crown			
Height (incomplete)	—	39.9	—
Width	—	21.1	—
Calyx			
Height	25.4	—	20.5
Width (average)	19.6	18.3	13.8
Diameter BB circlet	14.0	—	10.8
Height R (A ray)	14.6	13.2	11.9
Width R (A ray)	10.8	10.8	8.6
Height IBr ₁	1.2	1.5	1.2
Width IBr ₁	4.7	5.1	3.7
Height IBr ₂	1.2	1.0	0.9
Width IBr ₂	5.0	5.8	4.2
Length proximal columnal	4.6	5.3	4.0
Width proximal columnal	3.5	3.8	3.0

Note: All specimens slightly crushed or distorted.

Remarks. *Neocamptocrinus* was described from eastern Australia (Willink 1980a) and is distinguished from other Camptocrininae by the presence of numerous interambulacral plates and five large orals in the tegmen. Three of the species described by Willink (1980a) are based on calyces. Two, *N. bundanoonensis* and *N. wardenensis* have calyx plates bearing different types of coarse ornament, neither of which are developed on *N. occidentalis*. The third species, *N. millerensis*, although probably based on a juvenile, has more elongate radials, a higher basal circlet and lacks the ornament on the orals that is present on *N. occidentalis*.

The fine granular ornament on the basals, radials and primanal of paratypes CPC 27451 and 27452 is poorly preserved. It is uncertain if fine granules were present on all the specimens, but not preserved in the hydrous-iron oxide replacement of the calcite, or if this is an intraspecific or specific character.

The excellent preservation of the tegmen on three of the specimens shows the spatial relationships of the interambulacra and oral plates. Ambulacral trackways into the calyx were directed under the proximal end of each of the orals, which were elevated above the radials by the interambulacra. The coarse inverted V-shaped ridge on the posterior oral is interpreted as a diverting structure, directing faeces away from the oral surface of the tegmen.

Associated pluricolumnals within the same slab as the calyces are subrectangular in lateral section, heteromorphic with 9–11 internodals per noditaxis. Cirri are circular in transverse section laterally extended for several centimetres, and initiate at paired nodals, overlapping slightly onto the adjacent two internodals. None of the pluricolumnals is attached to the proximal columnals and intermediate columnals were not found in the disarticulated material in the matrix.

Broadhead (1981) suggested that the small cup size and enrolled stem with protecting cirri indicated that the Camptocrininae were moderately rheophilic to moderately rheophobic feeders. The dense feeding net that would have been present on *N. occidentalis* when in the feeding posture, larger cup size, and occurrence in a fine-grained sandstone suggest that it was a rheophilic feeder in a moderate current condition. Neocamptocrinids from eastern Australia (Willink 1980a) were reported from mudstones (*N. bmidanoonensis*), siltstones (*N. wardenensis*, *N. gremialis*), and sandstones (*N. millerensis*). All were probably living in moderate energy environments and rheophilic feeders. The burial of multiple specimens of both *N. occidentalis* and *Jimbacrinus bostocki* in a single slab with only moderate disarticulation of the column and loss of distal parts of the arms for both species suggests a mass kill during a storm with rapid burial. There is no suggestion of extensive transport before burial.

Neocamptocrinus sp. nov.

Plate 1, figs. 7–11

Material and locality. Four specimens (CPC 27454–27457) from the late Permian, Tatarian, Hardman Member of the Liveringa Formation, from an undesignated locality in the Millyit Range, Fitzroy Trough of the Canning Basin, Western Australia; Wapet Collection, Bureau of Mineral Resources. The specimens are placed in open nomenclature because the precise stratigraphic and geographic localities are not known. There is strong probability that future collecting in the Canning Basin will establish the stratigraphic position and possibly the original locality for the species.

Description. Calyx globose, bowl-shaped, slightly higher than wide. Bipartite basal cirlet low, distal tips gently upflared, visible in lateral view. Radials and primanal slightly longer than wide, moderately convex longitudinally, slightly convex transversely. Tegmen strongly arched, composed of five prominent orals, four interambulacra and four anal plates in a series of 3:1. Posterior oral largest, with gently rounded ridge adjacent to anal opening; adjoined laterally by other four orals. Proximal columnal large, elliptical in cross-section. No ornamentation on basals or radials. Some orals have a gently rounded central node.

Remarks. Three of the four crushed and partly disarticulated specimens of *Neocamptocrinus* sp. nov. have closely associated parts of the coiled column, which relates them to the camptocrinines, not the dichocrinines. The enrolled column with numerous cirri are slightly separated from the calyces, but are considered to have been attached prior to compaction of the enclosing sediment and concurrent distortion, crushing, and disarticulation. The specimens are enclosed in a claystone with thin interbeds of fine-grained sandstone.

One specimen (CPC 27454) was reconstructed after removing the plates from the matrix (Pl. 1, figs. 8–11). The slight difference in size of each of the radials and primanal and unique length and angles of plate sutures between the radials and basal cirlet simplified the reconstruction of the cup and oral cirlet. Absence of the anals, most intrambulacral plates, and small parts of two of the orals precluded a precise reconstruction and positioning of the tegmen. The globose shape of the theca

and inflated tegmen approximate the original form sufficiently to permit shape interpretations and comparisons with other known forms.

These specimens are referred to *Neocamptocrinus* because they have one interambulacral plate per interray between the radials and the orals, and multiple plates in the anal series above the primal. Among the Camptocrininae only *Neocamptocrinus* has interambulacrals and multiple anals in the tegmen (Broadhead 1981).

Neocamptocrinus sp. nov. is very similar in shape, but lacks the ornament and more numerous interambulacrals and anals present on *N. bundanoonensis*. The latter species is a Kazanian form from New South Wales (Willink 1980a). The morphological similarities and late Permian age of *N.* sp. nov. and *N. bundanoonensis* suggest seaways were open between eastern and Western Australia in the late Permian and that both forms were derived from a common ancestor.

Genus STOMIOCRINUS Wanner, 1937

Diagnosis. Crown small to medium in size, elongate, slender. Calyx elongate, globose to truncated cone-shaped. Basals bipartite, subequal. Radials large form two-third of dorsal cup. Solitary anal plate in radial circlet, narrower than radials. Radial facets oval in outline, angustary, elevated producing radial notches, slope outward. Orals large, slightly inflated, do not meet at centre of tegmen; CD oral largest, projects slightly beyond centre of tegmen. Ambulacral grooves along mutual shoulders of adjacent orals. Arms ten, uniserial. Brachials cuneate, inflated, IBr_2 axillary, bear one pinnule each on alternate sides of arm. Stem bilaterally symmetrical bearing cirri, coiled.

Stomiocrinus ferruginus sp. nov.

Plate 3, figs. 4 and 5

Diagnosis. A *Stomiocrinus* with truncated base, high conical cup, ten uniserial arms with cuneate brachials and one pinnule per brachial on alternating sides of arms.

Type and locality. The holotype (UWA 27006), is imbedded in fine-grained sandstone associated with gastropod and bivalve fragments from the upper part of the Wandagee Formation along the Lyndon River, Western Australia. Precise horizon and locality not recorded.

Etymology. The trival name refers to the preservation of the specimen. All plates are replaced with hydrous iron oxides.

Description. Crown slender elongate, widest at three-quarters height; cup nearly cylindrical high truncated cone expanding gently above basals, unornamented, sutures gently impressed, crushed parallel to A-CD symmetry plane; basal circlet half again as wide as high, walls subvertical, formed by two equal plates, one each on either side of symmetry plane; five RR over half as long again as wide, gently convex longitudinally, moderately convex transversely, angustary radial facets project above the distal surface, facet details not observable; anal plate similar to but narrower and slightly shorter than RR; Brr cuneate uniserial, wider than high becoming more pronounced distally, strongly convex transversely, proximal IIBrr gently convex longitudinally, distal IIBrr strongly convex longitudinally with lateral blunt spinose projection in zig-zag manner along arm; Brr facets much deeper than wide, ambulacral groove small, narrow V-shaped; arms ten, IBr_2 axillary in all rays, one pinnule per brachial, projecting on alternate sides of the arm. Stem facet round, large, no details preserved; oral plates not observable.

Measurements: Crown height 33.2, width 12.6; cup height, 8.4, maximum width 6.7, minimum width 5.5, average width 6.1; basal circlet diameter 3.9, height 2.8; R height, 6.2, width 3.7; anal height 5.7, width 1.9; IBr_1 height 1.2, width 2.1; $AxIBr_2$ height 2.0, width 2.5; $IIBr_1$ height 1.4, width 1.8; diameter stem facet 2.4.

Remarks. *Stomiocrinus* is known from Artinskian deposits of Russia (Yakovlev *in* Yakovlev and Ivanov 1956) and the Basleo Beds of Timor (Wanner 1937). *S. ferruginus* shows affinity with both

the Russian and the Timor species, but is most similar to *S. minimus* Wanner, 1937 from Timor. The more nearly vertical walled basal circlet and relatively narrower anal plate distinguish *S. ferruginus*. All other species of the genus, based on the thecae and reported from carbonate substrates, have basal circlets that flare moderately to strongly up and out. The excellent state of preservation in a fine-grained sandstone and abundant associated invertebrate fauna suggests little if any transport of the fauna after death.

This is the first knowledge of the arms of *Stomiocrinus*. The occurrence of two primibrachs and isotomous branching on the second primibrach are features typical of most dichocrinids. A rheophilic feeding pattern is suggested by the lengthy arms and slender pinnule development.

The classification of *Stomiocrinus* is somewhat uncertain. Yakovlev (*in* Yakovlev and Ivanov 1956) reported disassociated thecae and bilaterally symmetrical columns that he referred to *Stomiocrinus*. Broadhead (1981) accepted Yakovlev's interpretation of *Stomiocrinus* and assigned it to the subfamily Camptocrininae, which have bilaterally symmetrical columns that enroll. Until articulated theca and columnals of *Stomiocrinus* are found some uncertainty remains about the subfamily affinity.

Order CLADIDA Moore and Landon, 1943

Suborder CYATHOCRININA Bather, 1899

Superfamily CYATHOCRINITACEA Bassler, 1938

Family CYATHOCRINITIDAE Bassler, 1938

Comments. Four cyathocrinitid genera are recognized by Moore *et al.* (*in* Moore and Teichert 1978). They share the common features of a laterally positioned, short, stout anal sac with a vent at or near the apex, a single large pramanal in the cup and angustary arm facets. Two of the four genera are known from very few specimens and restricted in geological and geographical distribution. *Anarchocrinus* is monotypic, of middle Ordovician age, and known from Estonia. The two species of *Ceratocrinus* are of late Permian age from Timor. A third genus *Gissocrinus* has 27 reported species (Bassler and Moody 1943; Webster 1973), is of late Silurian to early Devonian age and found in North America, Europe and Russia. *Cyathocrinites*, the fourth genus, has 96 species assigned to it (Bassler and Moody 1943; Webster 1973, 1986), a range of Silurian to Permian, a cosmopolitan distribution, and is in dire need of a systematic review.

Since a thorough review of *Cyathocrinites* is beyond the scope of this investigation, a few comments on the morphology of the cup as shown on the 96 species currently assigned to the genus will suffice for comparison to *Occiducrinus* gen. nov., proposed herein, and to be included in the Cyathocrinitidae. The shape of the cup of *Cyathocrinites* varies from a low, shallow, widely expanding bowl to an impressed, flat to rounded, upflaring-based, moderately high bowl to an upflaring, steep-walled cone. Forms with the bowl shape are by far the most common and show considerable latitude in slope of the walls from incurved to vertical to outflared. The five infrabasals (very rarely fused) may be nearly fully visible, only show the distal tips in lateral view, or be confined to the basal plane or basal invagination and not visible in lateral view. Ornamentation of the cup plates varies from smooth (rare) to finely granulate (most typical) to coarsely noded or spined (rare) to striate or ridged (rare). Sutures may be flush or more commonly weakly to moderately impressed. The stem, where known, may be pentagonal or circular in outline, sometimes grading from pentagonal to circular distally, and is normally heteromorphic. The tegmen (known on less than half the species assigned to the genus), is generally flat but may protrude gently to moderately and may or may not have a central opening. The anal sac, where known, is invariably a short to moderately high, stout tube projecting above the posterior interradius with an opening at or near the apex.

In summary, the generic concept of *Cyathocrinites* is based principally upon the presence of five infrabasals, narrow arm facets and a stout anal sac positioned laterally on the tegmen. At present species assigned to the genus show an extremely wide latitude of morphological features, undoubtedly representing intraspecific variation in part. A study of Silurian *Cyathocrinites* by Frest (1977) resulted in the recognition of three subgenera and three new species, knowledge of the palaeoecology of the genus, and a proposed phylogeny of the Silurian species of *Cyathocrinites*.

Webster and Lane (1987) pointed out the need for a systematic review of *Cyathocrinites*. Such a review would unquestionably enhance the stratigraphic, palaeogeographic, and phylogenetic value of the species assigned to the genus.

Genus *OCCIDUCRINUS* gen. nov.

Type species. Occiducrinus australis sp. nov. here designated.

Diagnosis. Cup elongate high cone, dicyclic, 3–4 IBB visible in side view, single anal in line of RR resting on pB, sutures slightly impressed, fine granular ornamentation on all cup plates; anal sac offset posteriorly; tegmen formed of double circlet of plates, inner circlet five large noded projecting 00; arms round, branching pattern unknown, numerous cover plates on ambulacral track.

Etymology. The generic name is derived from the Latin term *occidens*, meaning to the left or west, and refers to Western Australia where the specimens were found.

Description. See description of *Occiducrinus australis*.

Occiducrinus australis sp. nov.

Plate 2, figs. 1–3

Diagnosis. See diagnosis for the genus.

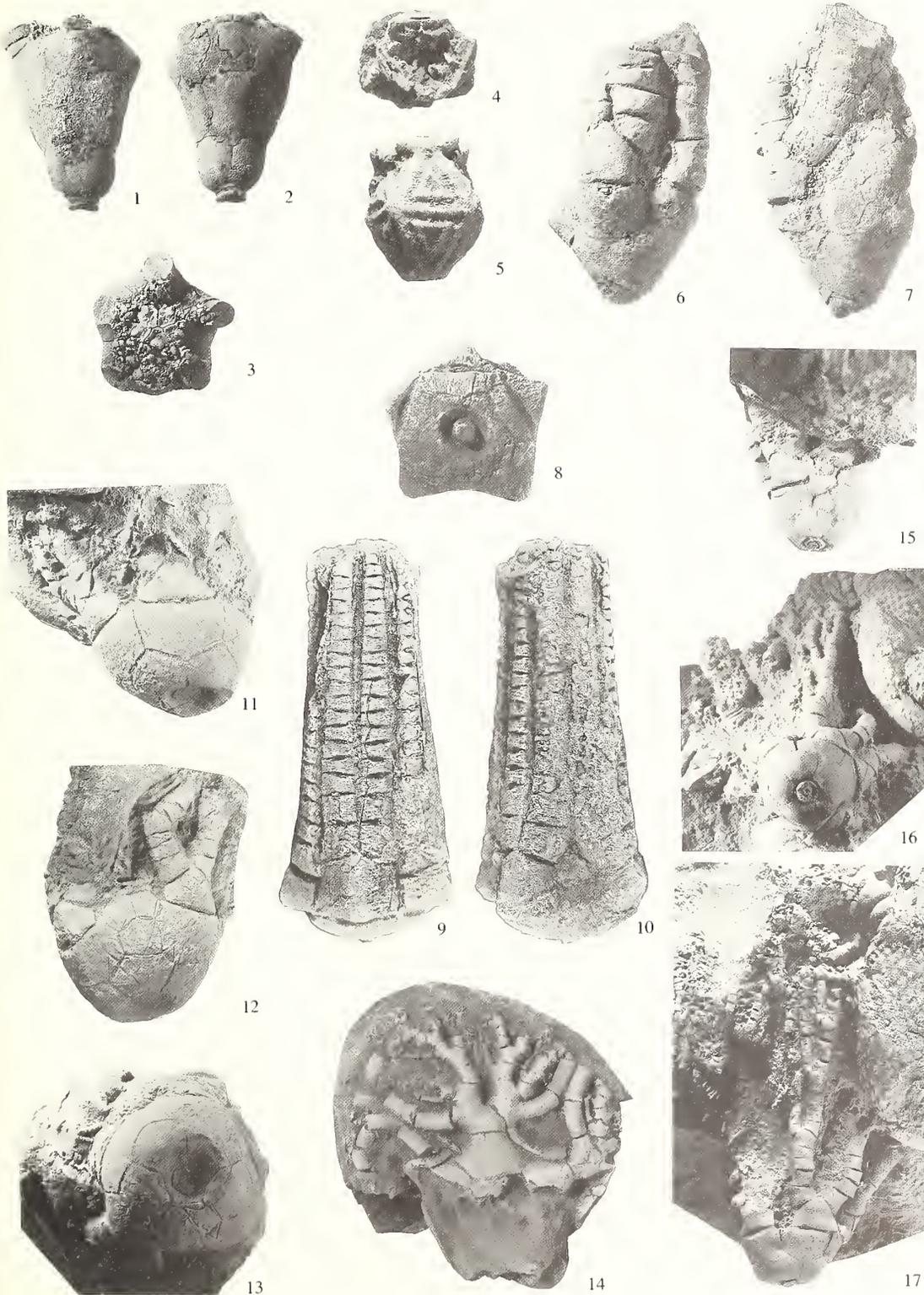
Types and locality. One partial crown, the holotype (UWA 27001) has tegmen, proximal brachials of three arms, and proximal three columnals preserved. Three partial cups, one designated a paratype (UWA 26996) has a part of the two subjacent basals and the A radial lacking but has well preserved radial facets and the stem facet; the other two (UWA 26999 and 27002) are so badly leached by solution and weathering that they are of no value other than they show radial facets. The specimens, except 27002, are from a calcareous sandstone in the upper part of the Wandagee Formation on the northeast side of a syncline along the North bank of the Minilya River, east of Coolkilya Pool, Western Australia. Specimen 27002, found by Dr Curt Teichert, was reported to occur 156 feet (48 m) above the red beds, from the southeastern part of S-Hill, West Kimberly, Western Australia. Precise horizon and locality not recorded.

Etymology. The trivial name, *australis*, is a Latin term meaning southern and the derivation of the term Australia. Thus the type species *Occiducrinus australis* could be loosely translated Western Australian crinoid.

Description. Cup elongate, high, gradually expanding with gently impressed sutures and fine granular ornamentation on all cup plates. IBB three or four, smaller in A radius if three, large ones in D and E radius when four; form high, nearly vertical-walled, rounded base with shallow invagination for stem attachment. BB five, hexagonal except heptagonal pB, slightly longer than wide, widest at distal ends of lateral sutures, gently

EXPLANATION OF PLATE 2

- Figs. 1–3. *Occiducrinus australis* gen. and sp. nov.; A ray, CD interray, and oral views, respectively, of holotype UWA 27001; $\times 2$.
 Figs. 4, 5. *Eoindocrinus praecontignatus* Arendt 1981; oral and A ray views, respectively, of UWA 27003; $\times 2$.
 Figs. 6, 7. Rhenocrinidae gen. and sp. nov.; A ray and CD interray views, respectively, of UWA 83761; $\times 1$.
 Figs. 8–10. *Tapinoerinus spinosus* (Wanner 1924); basal, A ray, and CD interray views, respectively, of UWA 27000; $\times 2$.
 Figs. 11–13. *Anechocrinus nalbiaensis* gen. and sp. nov.; B ray, CD interray, and basal views, respectively, of holotype UWA 27008; $\times 1$.
 Fig. 14. Indeterminate inadunate crinoid; lateral view of partly preserved crown, UWA 83762; $\times 1.5$.
 Figs. 15–17. *Skaioerinus granulatus* gen. and sp. nov.; CD interray, basal, and B ray views, respectively, of holotype UWA 21187; $\times 1$.



outflaring, moderately tumid transversely, gently tumid longitudinally. RR five, as wide as long, gently outflaring proximally, strongly incurved from base of facet, distal tips nearly horizontal, horseshow-shaped with oval to subcircular facet. Articular facet half as wide as radial, moderate to strong outward slope, shallowly excavated, interior smooth with weakly developed transverse ridge and central muscle area dividing facet into two ligament areas, an inner U-shaped area bordering the notch for the aboral coelomic canal and an outer half moon shaped area; transverse ridge divided into three parts, inner nodes and short ridges separated by irregular pits and short grooves, and two mirror image elongate lens-shaped ridges transverse to the central mass, no nerve canals present.

Anal plate large, rectangular, within radial circlet, adjoins pB and two adjacent radials, supports four small anal tube plates above, gently convex transversely and longitudinally, three-quarters as wide as high. Anal tube not preserved except for basal circlet of 11, possibly 12, small plates in posterior interradius between oral plates of tegmen adorally and C and D radials laterally and above anal plates externally. Tegmen formed of a double circlet of plates; outer circlet consists of 12 plates, three in each interradius, central one bridges interradiial suture and adjoins oral plate of inner circlet, two lateral plates border on the central plate of the outer circlet and the radial supporting cover plates of ambulacral canal leading from brachials to the mouth beneath the inner circlet 00; elevated inner circlet of five 00, posterior largest adjoining anal sac and all four other 00, all other 00 bordered by one plate of outer circlet, two adjacent 00 and several cover plates of ambulacral canal, each 0 ornamented with a coarse node on outer ridge of flat distal surface, sutures between 00 slightly projecting along ridges. Only three arms have brachials preserved; primibrachs of A through C rays and secundibrach of B ray; all short, strongly convex outer surface nearly three times as wide as high; facets elliptical, deeper than wide; ambulacral tracks small, U-shaped.

Stem circular, heteromorphic, nodals with strongly rounded smooth latera or epifacets; internodal with smooth vertical latus; nodals four times as high as internodals; articular surface poorly preserved, on base of IBB circlet shows wide articulum of faint crenulae; lumen circular. Measurements are given in Table 2.

Remarks. *Occiducrinus* is distinguished by the high, elongate dorsal cup and three or four infrabasal plates, in contrast to the bowl-shaped or conical cup and five infrabasal plates in *Cyathocrinites*. The radial facets of *O. australis* resemble those of *Platycrinites hemisphericus* as described and illustrated by Van Sant (*in* Van Sant and Lane 1964, p. 56, fig. 17-4). However *P. hemisphericus* has short

TABLE 2. Measurements of *Occiducrinus australis*

	Holotype UWA 27001	Paratype UWA 26996
Cup		
Height (top orals)	29.2	32.7*
Width IBB circlet	11.1	14.0
Width BB circlet	18.8	22.4
Width RR circlet	22.4	24.8
Height IBB circlet	9.2	10.0
Height B (AB interray)	12.0	13.2*
Width B	10.0	11.6
Height pB	12.1	13.3
Width pB	10.3	9.6
Height R (B ray)	10.7	11.4
Width R	10.6	12.0*
Height anal X	8.1	7.9
Width anal X	5.9	7.0
Height IBr (A ray)	2.2	—
Width IBr	5.5	—
Height IIBr	2.8	—
Width IIBr	4.5	—
Diameter stem	5.2	—

* Estimated.

crenulae on the edge of the facet which are lacking in *O. australis* and *O. australis* has a central muscle area which is absent on *P. hemisphericus*. Preservation of the stereom on the holotype and paratype is excellent and even under higher magnification ($\times 64$ to $\times 100$) on standard stereoscopic binocular microscopes the fine mesh stereom for muscle attachment (Lane and Macurda 1975) can be seen to be confined to the transverse ridge with the coarse mesh stereom flooring the ligament areas.

Suborder POTERIOCRININA Jaekel, 1918
 Superfamily RHENOCRINACEA Jaekel, 1918
 Family RHENOCRINIDAE Jaekel, 1918

Rhenocrinidae gen. et sp. nov.

Plate 2, figs. 6 and 7

Material. One partial crown (UWA 83761) and a partial set of arms (UWA 27009), both from a yellow marl in the Wandagee Formation, south of Barrabiddy Dam, Wandagee Station, Western Australia; found by Dr Curt Teichert. Precise horizon and locality not recorded.

Remarks. A partial crown with a high broad turbinate-shaped cup, five? upflaring infrabasals, five upflaring basals, five highly upflaring radials, angustary radial facets with inset radial notches, three anals mostly in the cup, probably ten or more uniserial arms, strongly transversely convex cuneate brachials, large pinnules, and a slender prominent anal tube is assigned to the rhenocrinids as currently recognized in the Treatise (Moore and Teichert 1978, p. 673). Unfortunately the specimen lacks the stem and most of the A through C rays including some cup plates, making it unacceptable as a holotype.

Most rhenocrinids are of Devonian and early Carboniferous age and are known from Europe and North America. Only *Araeocrinus* is known from Upper Carboniferous strata of Texas. The rhenocrinids are not well defined and in need of study, as suggested by Webster and Lane (1987), thus a rhenocrinid from the Permian of Australia extends the stratigraphic and geographical range of the family, but the full significance of such a discovery must await the study of the superfamily and hopefully additional material from Western Australia.

Superfamily LOPHOCRINACEA Bather, 1899

Remarks. The discovery of specimens assigned to the Indocrinidae, Pachylocrinidae and Stellarocrinidae in the study material resulted in a comparison of the morphological features of the Lophocrinacea and related cladid inadunates.

The Lophocrinacea are defined in the Treatise by Moore *et al.* (in Moore and Teichert 1978) as having a conical cup with the infrabasals readily visible in lateral view, among other morphologically significant characters. Yet four of the six families assigned to the Lophocrinacea have all or most of the genera in each family with low to moderately high, bowl-shaped cups with the infrabasals downflaring (rarely), subhorizontal (commonly), or barely upflaring (rarely). Cup shape and character of the infrabasal circlet are two of the more important morphological features used in the classification of the cladid inadunates at the superfamily, family and generic levels (Moore and Teichert 1978). Thus it is surprising to find a superfamily defined on a set of morphological characters and more than half the genera assigned to it not conform. With the exception of the Pelecocrinidae, each family of the Lophocrinacea is considered by me to have unifying morphological characters that allow the proposal of phylogenetic lineages within the family. Above the family level, the Lophocrinacea are a heterogeneous group which requires reclassification. The following changes are recommended.

Morphological affinities of the Texacrinidae and Pachylocrinidae were recognized by Moore and Strimple (in Moore and Teichert 1978) when they considered the pachylocrinids to be the progenitor of the texacrinids. The pachylocrinids have peneplenary arm facets whereas the texacrinids have plenary arm facets and arm branching patterns are modified in the texacrinids. The Pachylocrinidae

are judged to be more closely allied to the texacrinids than the lophocrinids and therefore placed in the Texacrinacea.

Moore *et al.* (*in* Moore and Teichert 1978) suggested that the Stellarocrinidae were derived from the Pachylocrinidae. The cup structure of the two families is more closely related than that of the stellarocrinids and the lophocrinids. The arm structure of the stellarocrinids is different from both the pachylocrinids and lophocrinids, but could easily be modified from the pachylocrinids by outflaring and development of biserial brachials. The stellarocrinids are also transferred to the Texacrinacea.

The Laudonocrinidae are assigned to the Pirasocrinacea. Similarities of the Laudonocrinidae and the Pirasocrinidae were discussed and the validity of the former justified by Moore and Strimple (*in* Moore and Teichert 1978). The Laudonocrinidae are considered the progenitor of the Pirasocrinidae.

Four genera previously assigned to the pelecocrinids are transferred to other families. *Forthocrinus* has a low, bowl-shaped cup and interplate ornamentation similar to *Stellarocrinus* and other stellarocrinids, and is therefore assigned to the Stellarocrinidae. *Tetrabrachioocrinus* is assigned to the Laudonocrinidae because it has a low, widely expanding cup, among other features, similar to *Bathronocrinus* and *Paianocrinus*. *Malaiocrinus* and *Depaocrinus* are transferred questionably to the Pachylocrinidae because of similarity of cup features with a lack of knowledge of the arms. This leaves only two genera, *Pelecocrinus* and *Exoriocrinus*, in the Pelecocrinidae, which along with the Lophocrinidae, are accepted in the Lophocrinacea.

The Indocrinidae were removed from the Lophocrinacea and placed in the superfamily Cromyocrinacea by Arendt (1981) as he considered that they were derived from *Ureocrinus*. I tentatively concur with Arendt's assignment.

Superfamily CROMYOCRINACEA Bather, 1890

Family INDOCRINIDAE Wanner, 1916

Genus EOINDOCRINUS Arendt, 1981

Eoindocrinus praecontignatus Arendt, 1981

Plate, figs. 4 and 5

Material and locality. One cup, UWA 27003, from a fine grained sandstone in the upper part of the Wandagee Formation, northeastern side of a syncline, north bank of the Minilya River east of Coolkilya Pool, Western Australia. Precise horizon and locality not recorded.

Remarks. The cup referred to *Eoindocrinus praecontignatus* is crushed inward on the CD interray destroying partly the BC through DE basals. Three small anal plates below the radial summit are weathered and recognizable but rather difficult to define. Grooves and ridges which extend across plate boundaries form a radiating triangular ornamentation pattern. Primary ridges converge in the centre of the basals. Secondary ridges form triangles between the primary ridges. The triangles are not always well developed as some legs tend to curve inward and end before reaching another leg of the triangle.

The ornamentation pattern is very similar to that of specimens of *E. praecontignatus* Arendt, 1981 (pl. 18) from the upper Artinskian of the Ural Mountains. This is the first report of *Eoindocrinus* from an area outside Russia. *E. praecontignatus* supports a late Artinskian age for the Wandagee Formation. Indocrinids are moderately common in the Timor faunas. Thus an indocrinid in the Western Australian faunas shows additional affinities with the Timor faunas.

Superfamily ERISOCRINACEA Wachsmuth and Springer, 1886

Family GRAPHIOCRINIDAE Wachsmuth and Springer, 1886

Genus TAPINOCRINUS Webster, 1987

Tapinocrinus spinosus (Wanner, 1924)

Plate 2, figs. 8–10

Material and locality. One crown, UWA 27000, from a fine-grained sandstone in the upper part of the Wandagee Formation along the Lyndon River, Western Australia. This is the same general locality and stratigraphical interval given for *Stomiocrinus ferruginus*. It is unknown if these species were associated or from different horizons.

Remarks. One crown of *T. spinosus* shows the distal arm structure of the species which was based on an incomplete partial crown (Wanner 1924). There are ten arms with the primibrachs axillary in all rays. The A and D primibrachs are higher than the other three primibrachs. All secundibrachs are slightly cuneate with a pronounced, blunt to moderately sharp, short spine or node in the centre of the plate. The blunt spined primibrachs form a good pentagonal outline in basal or oral view.

T. spinosus is an advanced member of the genus with a low, discoid cup lacking ornamentation. This is the first report of *T. spinosus* outside Timor. Webster (1987) reported two species, *T. macurdai* and *T. ingrami*, from the Callytharra Formation at Callytharra Springs, Western Australia. These species have higher cups that are ornamented. Species of *Tapinocrinus* are potential zone fossils for the Permian strata of Western Australia.

Measurements. Crown height 31.9, width 14.7; cup height 3.0, width 11.3; H/W ratio 0.27; B height 2.1, width 2.9; R height 3.1, width 6.0; IBr (A ray) height 5.6, width 6.6; B ray IBr height 4.0, width 6.5; IIBr₁ A ray height 2.9, width 3.3; IIBr₂ height 2.4, width 3.2; IIBr₃ height 1.3, width 3.1; IIBr₁₀ height 1.0, width 2.2; diameter stem impression 2.0.

Superfamily TEXACRINACEA Strimple, 1961

Emended Diagnosis. Crown tall and slender, cup bowl-shaped with basal concavity and steep sides near rim, arm facets penepenary to plenary, one to three anals in cup, anal sac tall, composed of longitudinal rows of plates, arms uniserial or biserial, long, commonly many (up to 40) but five or ten in some. Carboniferous–Permian.

Remarks. The Pachylocrinidae and Stellarocrinidae are transferred to the Texacrinacea as explained in the remarks under the superfamily Lophocrinacea.

Family PACHYLOCRINIDAE Kirk, 1942

Genus SKAIOCRINUS gen. nov.

Type species. *Skaioocrinus granulosis* sp. nov., here designated.

Diagnosis. Crown elongate, expanding distally; cup low, truncate bowl-shaped, base slightly concave, small impressions at apices of basals and radials; infrabasals gently downflared, not visible from side, mostly covered by proximal columnal; radial facets wide, penepenary, bearing transverse ridge and ligament pits; arms branching isotomously on axillary first primibrach, branch exotomously at least three times; brachials strongly convex transversely, slightly cuneate; one pinnule per brachial on alternate sides of arm; three anals in cup; granular ornamentation on cup plates and proximal brachials; proximal stem transversely round, lumen pentalobate.

Etymology. The generic name, *Skaioocrinus*, is derived from the Greek word *skaios*, meaning left and western. It is used in reference to Western Australia.

Description. See description of *S. granulosis* gen. et sp. nov.

Remarks. When Moore and Plummer (1940) named *Texacrinus* they recognized that it was similar to *Pachylocrinus*, but differed by having plenary radial facets and an exotomous arm branching pattern. *Skaiocrinus* is transitional between the two genera, that is, the arms branch exotomously like *Texacrinus* and the radial facets are peneplenary as in *Pachylocrinus*. Arguments could be made to include *Skaiocrinus* in the Texacrinidae because of the exotomous arm branching pattern. Because the type of radial facet, angustary to plenary, is used at the superfamily level in the classification of the Inadunata, *Skaiocrinus* is placed in the Pachylocrinidae.

Skaiocrinus granulosis sp. nov.

Plate 2, figs. 15–17

Diagnosis. Characters of the genus.

Type and locality. One crown and two fragmentary arms of a second specimen associated with a large specimen of the productid brachiopod *Taeniothaerus* in a single block of calcareous siltstone, UWA 21187, found by Dr Curt Teichert in the east limb of a syncline north of the Minilya River, west of Coolkilya Pool, Western Australia. Precise horizon not recorded.

Etymology. The trivial name refers to the granular surface ornament on the cup and proximal brachial plates.

Description. Crown medium size, slender at base expanding upward with additional arm branchings. Cup medium high, truncate, bowl-shaped, walls slope gently outward, basal invagination slight; granulose ornamentation, small pits at apices of BB and RR. IBB five, small, confined to basal invagination, subhorizontal to slightly downflaring, proximal parts covered by proximal columnal, not visible in lateral view. BB five, pentagonal (BC basal hexagonal) moderately convex transversely, strongly convex longitudinally, downflaring proximally and upward outflaring distally. RR five, wider than high, moderately convex transversely and straight to gently convex longitudinally, radial facet peneplenary, small radial gape; facets slope gently out and downward; B radial facet partly exposed by broken IBr showing large denticulate outer marginal ridge, very narrow ligament furrow and outer ligament ridge externally to fairly large ligament pit; denticulate outer marginal ridge visible in lateral view of all rays, no other details observable. Anals, three in cup, pA largest bordered by C radial, BC basal, CB basal, D radial and two overlying anal plates; anal X second largest, distal portion above cup summit; right tube plate or tertanal small, less than half below summit of cup, barely adjoins pA. Brr strongly convex transversely, slightly concave longitudinally on IBr and IBr₁₋₃ and straight on all more distal Brr, usually wider than high, arm branching isotomous on axillary IBr in all rays, exotomous thereafter on IBr_{5or7}, IIBr₆, IVBr₅, and VBr₆ in visible E ray, possibly one higher branching, thus 50 or 60 arms probable. Poorly preserved column transversely round, with well-developed crenularium and areola; lumen pentalobate, probably heteromorphic.

Measurements. Crown height 59.5; cup height 7.6, width maximum 14.8, width minimum 13.6, width average 14.2; diameter IBB circlet 4.2; BB height 4.8, width 5.0; RR height 5.3, width 7.5; AIBr₁ height 4.6, width 6.8; IIBr₁ height 3.5, width 4.6; IIBr₂ height 2.7, width 3.2; IIBr₃ height 1.9, width 3.0; AllBr₅ height 2.8, width 3.0; diameter columnal 3.2.

Family STELLAROCRINIDAE Strimple, 1961

Genus ANECHOCHRINUS gen. nov.

Type species. *Anechocrinus nalbiaensis* sp. nov. here designated.

Diagnosis. Stellarocrinid with medium high, unornamented, bowl-shaped cup; five IBB confined to weak basal invagination; sutures flush; three anals in cup; radial facets peneplenary, outflaring radial notches visible in dorsal or ventral view; arms uniserial branching isotomously on first primibrach and fourth secundibrach; stem facet roundly pentalobate, lumen pentalobate.

Etymology. The name is from the Greek *anecho*, meaning hold back or retain, in reference to the primitive nature of three anals retained within the cup.

Remarks. The outflaring, widely branching arms of *Anechocrinus* are typically developed in the stellarocrinids. Only two other genera of the stellarocrinids have three anals in the cup, these are *Heliosocrinus* Strimple, 1951 (Upper Mississippian, North America) and *Pedinocrinus* Wright, 1951 (Lower Carboniferous, Scotland), both of which have low cups with slightly cuneate brachials and weakly peneplenary arm facets. *Heliosocrinus* has coarse interplate ridge ornamentation on the cup whereas *Pedinocrinus* is smooth. *Anechocrinus* has a higher cup than either *Heliosocrinus* or *Pedinocrinus* and more obvious radial notches.

The cup of *Anechocrinus* resembles the four-rayed cup of *Depaocrinus* Wanner, 1937, agreeing in the shape, basal invagination, smooth surface and presence of three anals in the cup; unfortunately the arms of *Depaocrinus* are unknown. Wanner (1937, p. 153) pointed out that it is not known if the four-rayed condition of the only known specimen of *Depaocrinus* is an abnormality or of generic character as several other genera in the Permian of Timor are four-rayed. Until the arm structure of *Depaocrinus* is known its family assignment remains uncertain.

Stellarocrinids are most abundant in the late Carboniferous of North America. *Anechocrinus* is interpreted to be a conservative member of the family which apparently adapted to a sand substrate in the Permian of Western Australia.

Anechocrinus nalbiaensis sp. nov.

Plate 2, figs. 11–13

Diagnosis. Characters of the genus.

Types and locality. One slightly distorted crown (the holotype, UWA 27008), crushed along the E-ray, protruded along C-ray, and one partial cup with proximal brachials UWA 27030. The holotype, found by Dr Curt Teichert, is from the *Lingula* horizon in the Quinannie Shale, Carnarvon Road, Nalbia Paddock, south of Wandagee Station, Western Australia. No locality information is available for the partial cup. Both specimens are from fine-grained sandstones of similar lithology, suggesting a common locality and horizon.

Etymology: The trivial name refers to Nalbia Paddock where the holotype was found.

Description. Crown low, widely splayed, isotomously branching arms. Cup medium high, bowl-shaped, unornamented, weak basal invagination, walls gently outflaring becoming vertical to slightly inturned at summit; five IBB small, downflaring, confined to basal invagination, mostly covered by stem impression; five BB pentagonal except hexagonal pB, downflaring proximally, strongly recurved, moderately outflaring distally, gently convex laterally, slightly wider than high; RR half again as wide as high, gently convex longitudinally and transversely, facets peneplenary sloping outward, facet surface not exposed, radial notches obvious in lateral view, weakly concave in basal view; three anals in cup, primanal pentagonal adjoining C radial, posterior basal, D radial and two overlying pentagonal anal plates both of which project half above cup summit; primaxils strongly convex transversely, gently convex longitudinally, form gape with radials along suture, IIBrr and all subsequent Brr strongly convex transversely, straight to weakly convex longitudinally, weakly cuneate; IIBr₄ axillary; all branchings isotomous, widely splayed, probably at least one additional branching after that on IIBr₄; stem impression roundly pentagonal, crenularium of 35 rounded crenulae, areola pentagonal, lumen pentalobate; anal sac unknown.

Measurements. Crown height 37·0 incomplete; cup height 11·9, maximum width 15·8, minimum width 13·8, average width 14·8; width IBB circlet 8·0; BB height 8·0, width 9·6; pB height 7·8, width 9·8; RR height 8·4, width 13·9; IBr height 6·5, width 10·0; IIBr₁ height 4·2, width 5·8; IIBr₂ height 2·6, width 4·5; IIBr₃ height 2·3, width 4·0; AIIBr₄ height 2·8, width 4·0; anal × height 6·2, width 6·3; stem impression diameter 4·7

Superfamily CALCEOLISPONGIACEA Teichert, 1954

Family CALCEOLISPONGIIDAE Teichert, 1954

Genus CALCEOLISPONGIA Etheridge, 1915

Calceolispongia abundans Teichert, 1949

Plate 3, figs. 6–9

Material and locality. Five cups and crowns (UWA 83756–83760) from a boulder of fine-grained sandstone of the Wandagee Formation in the bed of Minilya River between Coolkilya Pool and Curdmuda Well, Western Australia. Teichert (1949) reported *C. abundans* as particularly common in a sandstone bed between 120 and 135 feet (37–41.5 m) above the *Calceolispongia* Stage of the Wandagee Formation in the syncline west of Coolkilya Pool. The boulder of this study was probably eroded from that interval and transported downstream to the locality where it was found, which was not precisely recorded.

Remarks. A block of fine-grained sandstone of the Wandagee Formation yielded five specimens of *C. abundans*, one with the proximal parts of the arms and stem still articulated. In addition the remainder of other arms are closely associated possibly from this same specimen. Two other specimens from the same block have the proximal part of the stem attached.

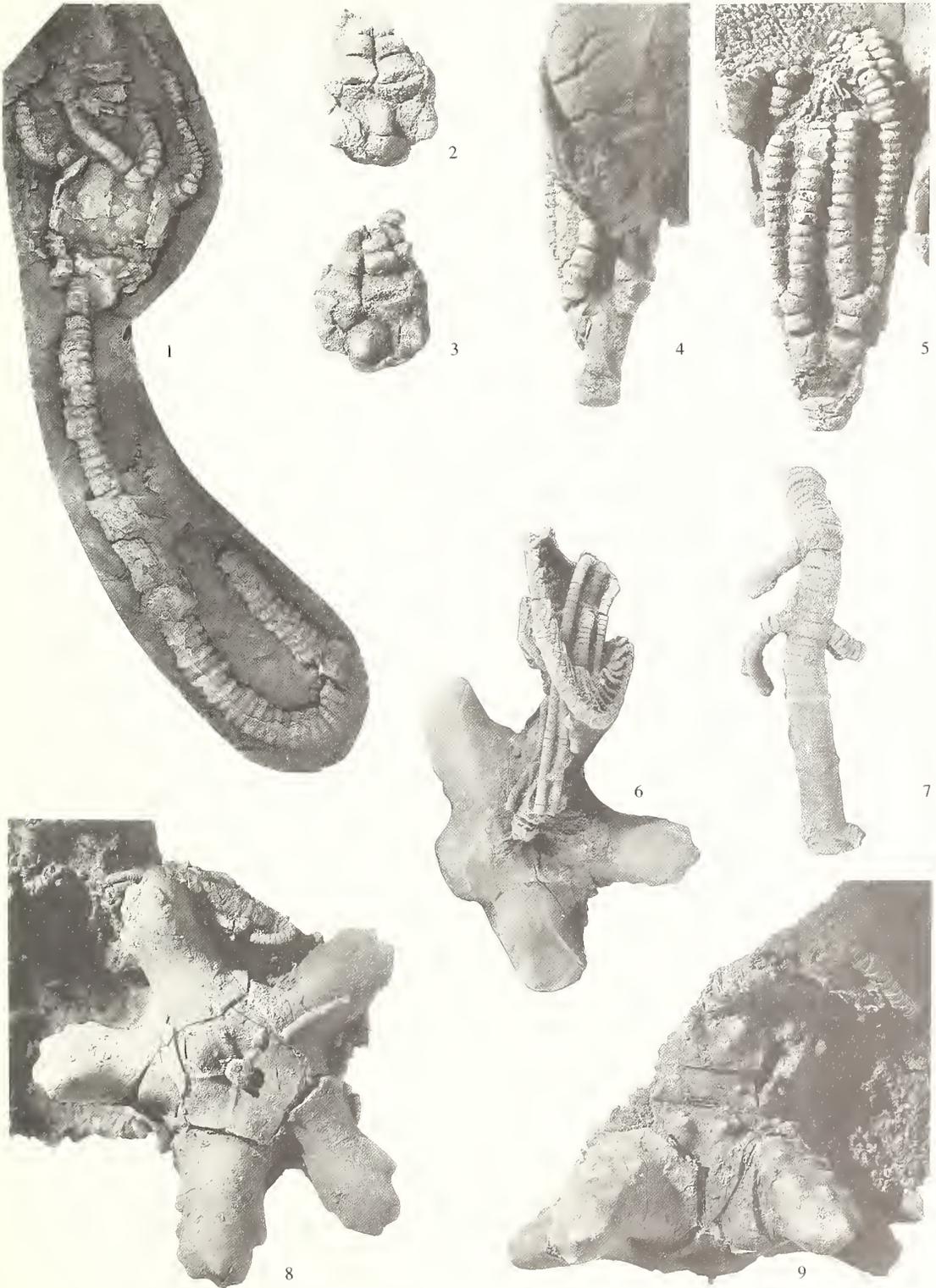
No morphological detail can be added to Teichert's description (1949, p.54) of the cup and arms of *C. abundans*, however, some information can be added to the interesting proximal stem. One crown has 34 mm and one cup has 106 mm of proximal stem preserved. These consist of a heteromorphic series of nodals and priminternodals (pluricolumnal pattern Type II, Webster 1974). In a pluricolumnal series 60 mm from the cup measurements of heights of plates are: nodal 1.1 mm; priminternodal 0.7 mm; and secundinternodal 0.5 mm. All columnals have rounded epifacets and symplectial articulation. Articulum divided into crenularium and areola. Crenularium narrow (width one-eighth of stem diameter) with straight coarse rounded crenulae. Areola wide (diameter 3 mm with stem diameter of 4 mm), shallow depression. Lumen pentagonal. Proximal columnals weakly pentagonal in outline, distal columnals circular in outline. Attached cirri are homeomorphic with straight smooth latera. Proximal cirri short, 5 mm to 14 mm, composed of very short cirrals, distally tapering to pointed ends; distal cirri long, at least 45 mm (incomplete), composed of long cirrals, believed to also taper on distal tips. Articulum of cirri same as that of columnals.

Teichert (1949, p. 58) listed the subpentagonal outline of the column of *C. abundans* as one of the possibly important distinguishing features of the species. From the description of the stem given above it is obvious that this is true only for proximal parts of the stem. More complete stems of the different species of *Calceolispongia* are needed to understand their relationships fully.

Teichert (1949, p. 30) speculated that the stem of *Calceolispongia* was entirely functionless. The size of *C. abundans* and extended development of the basals suggest that it rested the expanded central part of the basals on the substrate. Study of modern stemmed crinoids by Macurda and Meyer (1974) has shown that for some forms the distal cirri are used to burrow into soft substrate and anchor the animal while other medial cirri on the same individual may act only as props. The extended stem and lengthy cirri on *C. abundans* undoubtedly served as an anchoring device in the

EXPLANATION OF PLATE 3

- Fig. 1. *Dichocrinus? gerringongensis* sp. nov., CD interray view, holotype UWA 62961; $\times 1$.
 Figs. 2, 3. *Jimbacrinus minilyaensis* sp. nov., B–C rays and D–E rays views, respectively, holotype UWA 83763; $\times 2$.
 Figs. 4, 5. *Stomiocrinus ferruginus* sp. nov., CD interray and B–C rays views, respectively, holotype, UWA 27006; $\times 2$.
 Figs. 6–9. *Calceolispongia abundans* Teichert 1949. 6, basal view of crown showing attached proximal column and an associated arm fragment; UWA 83756, $\times 0.75$. 7, lateral view of pluricolumnal segment originally attached to specimen of fig. 6, UWA 83756, $\times 1.5$. 8, 9, basal and A ray views, respectively, of UWA 83757, $\times 1$.



fine-grained sand substrate where they lived. Using the proximal cirri as props they may have elevated themselves a few centimetres above the sediments. This would have allowed them to obtain a more favourable feeding position and to move upward keeping pace with sedimentation. This supports the feeding posture as interpreted by Willink (1979*b*) for species of *Calceolispongia* studied in eastern Australia.

Species of *Calceolispongia* are common in Western Australia, eastern Australia, and Timor. They are of stratigraphic use in eastern Australia and Western Australia (Willink 1979*b*; Teichert 1949) and were perhaps the most successful evolutionary lineage in the colder water and sand substrate environments of Australia. They clearly indicate migration pathways were open between eastern and Western Australia in the early Permian. They also raise further questions on the late Permian age of the Basleo faunas.

Genus JIMBACRINUS Teichert, 1954

Jimbacrinus minilyaensis sp. nov.

Plate 3, figs. 2 and 3

Diagnosis. A *Jimbacrinus* with granular ornamentation on all cup plates and first primibrachs, basals bulbous to bluntly spinose, no coarse nodes on radials.

Types and locality. Two partial crowns, the holotype UWA 83763 and the paratype UWA 83764 from a sandstone in the Wandagee Formation, northeast side of syncline north of Minilya River, east of Coolkilya Pool, Western Australia. Precise horizon not recorded.

Etymology. The trivial name is derived from the Minilya River, along which both specimens were found.

Description. Crown slender, elongate; dorsal cup bowl-shaped, base gently convex; five IBB very weakly upflared, proximal quarter covered by stem impression; five BB hexagonal, except heptagonal posterior B, slightly higher than wide, moderately to strongly convex with pronounced central enlargement or blunt node. Five RR pentagonal, half again as wide as high, subvertical, gently convex transversely; cup sutures flush except pit at apices of RR and BB; radial facets plenary, surfaces not exposed; primanal nearly equidimensional, distal end may project slightly above radial summit, adjoined by two tube plates, both C and D radials and posterior B; fine granular ornamentation on all cup plates.

Arms, five, atomous; IBr_1 nearly twice as wide as high, narrowing distally; IBr_2 rectangular, half again as wide as high; may possess two blunt coarse nodes laterally to one another; all higher Brr strongly cuneate, convex transversely, with pinnule facet on wide side, very rounded in oral view with wide V-shaped ambulacral tract.

Anal sac composed of thin plates extending at least to IBr_4 in height. Stem impression round, column not preserved. Measurements are given in Table 3.

Remarks. *Jimbacrinus minilyaensis* is a much smaller form and lacks the coarse nodes or spines on the radials of *J. bostocki* Teichert, 1954. Both the holotype and paratype are slightly crushed. The paratype is smaller than the holotype and is considered to be an immature form. Immaturity of the paratype is reflected in the near absence of the nodes on the second brachial and lesser development of the central enlargement or blunt node on the basals. The granular ornamentation is poorly preserved on the basals and infrabasals.

Family and genus indeterminate

Plate 2, fig. 14

Material and locality. One partial crown, UWA 83762, from a red claystone in the Wandagee Formation, south of Barrabiddy Dam, Wandagee Station, Western Australia; found by Dr Curt Teichert.

TABLE 3. Measurements of *Jimbacrinus minilyaensis*

	Holotype UWA 83763	Paratype UWA 83764
Cup height*	5.7	3.7
Diameter IBB circlet	4.8	—
Height B	3.8	3.3
Width B	3.2	3.3
Height R	2.6	1.8
Width R	4.2	3.6
Height pA	1.8	1.4
Width pA	2.4	1.3
Height IBr ₁	2.2	1.7
Width IBr ₁	3.8	3.4
Height IBr ₂	1.4	1.0
Width IBr ₂	2.7	2.0
Diameter stem impression	1.8	—

* Crushed specimens.

Description. Crown low, as wide as long. Cup medium cone, base impressed, approximately half (16 mm) height of estimated crown height (31 mm). Radials with elevated angustary facets. Arms ten or more per ray, inner eight weakly zigzag, outer two gently convex laterally; all brachials strongly convex transversely, gently convex to straight longitudinally. IBr₁ wider (4.5 mm) than long (2.8 mm), axillary; IIBr₁ wider (3.4 mm) than long (2.2 mm), axillary. Outer IIIBr slightly more than twice as long (4.0 mm) as wide (1.9 mm), strongly rounded exterior; succeeding 3 brachials of same shape, but becoming shorter distally, Inner IIBr₁ wider (3.2 mm) than long (2.2 mm), axillary; succeeding brachial slightly cuneate, longer (2.2 mm) than wide (1.8 mm), bearing slender elongate pinnule on outer side. At least two additional branchings on IIBr₃ and IVBr₁. Stem unknown.

Remarks. This specimen is crushed and has been partly destroyed by erosion. However, the cup shape and dicyclic condition are recognizable from the outline and trace of the plates along the edges where eroded. The arms are distinctive. The unbranched outer two arms of each ray are enlarged pinnules which form a horseshoe-shaped structure with the zigzag arms inside. Several cladid inadunates have weakly zigzag arms, such as species of *Ramulocrinus* and *Gilmocrinus*. However, these Lower to Middle Carboniferous forms have only ten arms, the crowns are elongate, and the cups lack basal invaginations. The basal invagination and branching of the arms on the single primibrachials and secundibrachials in each ray are advanced conditions. Unfortunately the specimen cannot be assigned to any known cladid family without question.

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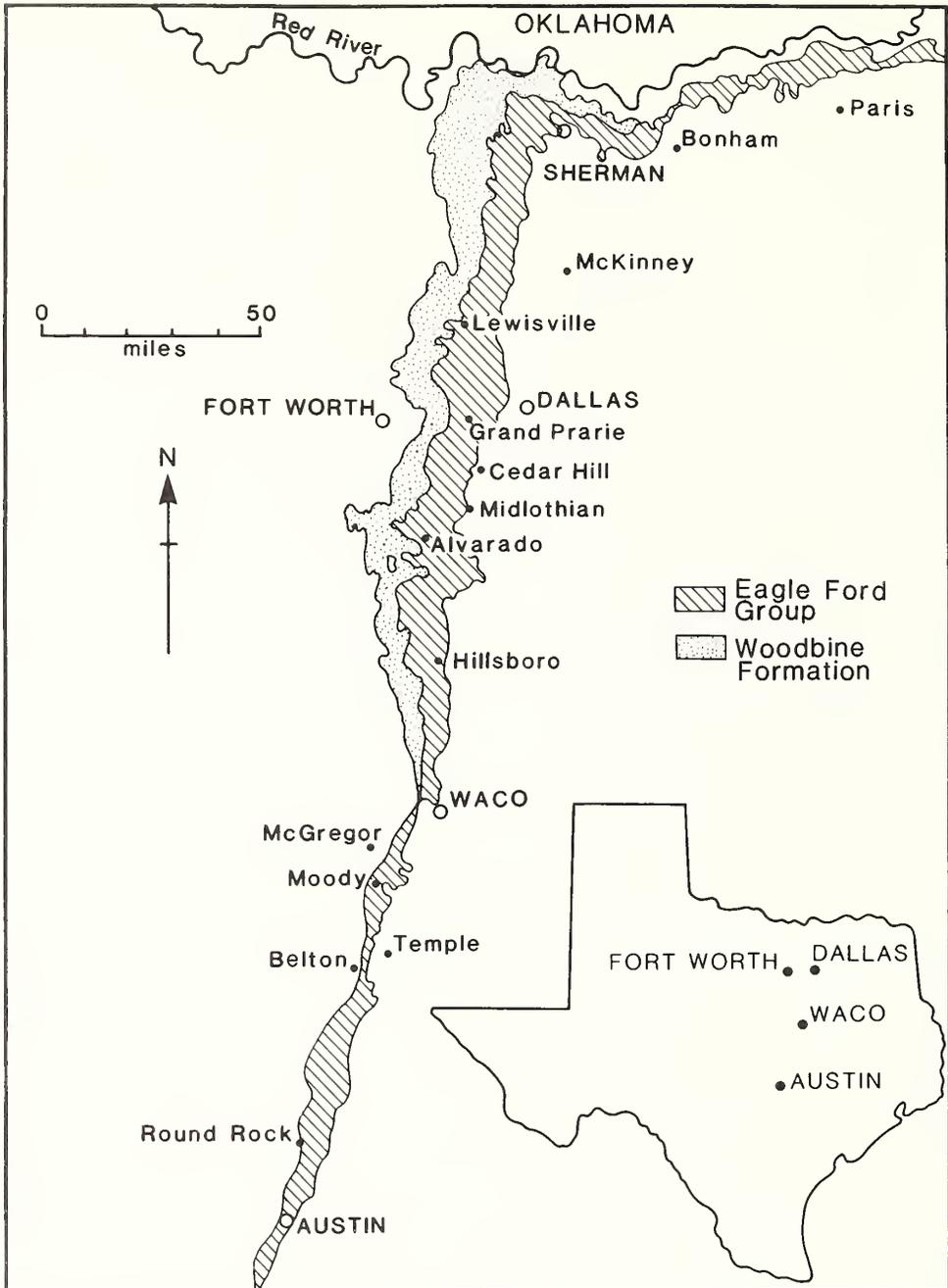
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CENOMANIAN AMMONITE FAUNAS FROM THE WOODBINE FORMATION AND LOWER PART OF THE EAGLE FORD GROUP, TEXAS

by W. J. KENNEDY and W. A. COBBAN

ABSTRACT. The ammonite faunas of the Woodbine Formation and lower part of the Eagle Ford Group of north-east and central Texas can be referred to five successive zonal assemblages of the standard sequence recognized for the southern part of the US Western Interior. The upper lower Cenomanian *Forbesiceras brundrettei* zone is represented by a limited assemblage in old collections believed to be from the Pepper Shale Member of the Woodbine, and from the Waco area. The middle Cenomanian *Conlinoceras tarrantense* zone is represented in the Tarrant Formation of the Eagle Ford in the area west of Dallas. The succeeding *Acanthoceras bellense* zone is a new biostratigraphic unit in the area, occurring only at the base of the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group near Belton in Bell County. It yields *Anagandryceras involvulum* (Stoliczka, 1865), *Puzosia* (*Puzosia*) sp., *Forbesiceras* cf. *chevillei* (Pictet and Renevier, 1866), *Acanthoceras bellense* Adkins, 1928, *Calycoceras* (*Newboldiceras*) sp., *Conlinoceras* sp., *Paraconlinoceras leonense* (Adkins, 1928), *Cunningtoniceras lonsdalei* (Adkins, 1928), *Hamites cimarronensis* (Kauffman and Powell, 1977), *Sciponoceras?* sp., and *Turrilites* (*Turrilites*) *acutus* Passy, 1832. The *Acanthoceras amphibolum* zone is represented by the type species in the Lewisville Member of the Woodbine. The Six Flags Limestone Member of the Woodbine and the lower part of the bentonitic member of the Eagle Ford Group yield the index species and *Tarrantoceras* west of Dallas. A more diverse assemblage occurs in the basal Eagle Ford Group of Johnson and Tarrant Counties and the Lewisville Member from Bell County southwards. The highest fauna described is that of the *Plesiacanthoceras wyomingense* zone, known only from the Templeton Member of the Woodbine in the northeastern part of the study area. Two genera, *Paraconlinoceras* and *Plesiacanthoceratoides*, are new.

Rocks of mid-Cenomanian age outcrop widely in north-east and central Texas from the Red River on the Texas/Oklahoma border in the north to the Austin area 400 km (250 miles) to the south (text-fig. 1). They encompass the Woodbine Formation and its southerly correlative the Pepper Shale; the Tarrant Formation and lower part of the Britton Formation of the Eagle Ford Group; and correlative parts of the Lake Waco Formation of the Eagle Ford Group to the south. Ammonites were first described from this interval by Shumard (1860), Cragin (1893) and Hyatt (1903). The first comprehensive account was that of Adkins (1928). The fauna of the Woodbine Formation was monographed by Stephenson (1953*a, b*) and that of the basal Eagle Ford Group in Johnson and Tarrant counties by the same author in 1955. As detailed below, unravelling the relative stratigraphic position of the faunas is complicated by the fact that beds with ammonites are of limited stratigraphic and geographic extent, especially in the Woodbine Formation, the bulk of which is of fluvio-deltaic and marginal marine origin (Oliver 1971), and the sequence is cut through by regional unconformities (Stephenson 1929). Whereas precise ammonite zonation has been established for the mid-Cenomanian of the US Western Interior (Cobban 1984), it has thus far proved impossible to extend this to central Texas (Young and Powell 1978). As we show below, the bulk of the Texas faunas are readily placed in the standard zonation. The taxonomic revision of the fauna reveals interesting patterns of evolution in certain of the endemic taxa which mirror those of contemporaneous Old World faunas.



TEXT-FIG. 1. Locality map showing the outcrop of the Woodbine Formation and Eagle Ford Group, and some of the more important localities mentioned in the text.

AMMONITE ZONATION

Adkins (1933) was unable to recognize a satisfactory zonation in the Woodbine. He recognized three zones in his Cenomanian part of the Eagle Ford; in ascending order these had *Acanthoceras tarrantense* Adkins, 1928, *Acanthoceras wintoni* Adkins, 1928 and *Eucalycoceras bentonianum* (Cragin, 1893) as indices. As will be shown below the first two are synonyms, and *E. bentonianum* is a *Sumitomoceras* of the *Sciponoceras gracile* zone. Moreman (1942) proposed a more complex system for the Tarrant Formation; it was referred to an *Acanthoceras inaequiplicatus* zone, subdivided in ascending order into subzones of *Mantelliceras sellardsi* Adkins, 1928, *Acanthoceras wintoni* Adkins, 1928, *Acanthoceras sherborni* Spath, 1926a, *Acanthoceras alvaradoense* Moreman, 1942 and *Metoicoceras swallovi* Shumard, 1860. *Acanthoceras inaequiplicatus* of Moreman is a synonym of *Conlinoceras tarrantense*, as is *A. wintoni*; the *A. sherborni* of Moreman is a synonym of *A. bellense* Adkins, 1928, and *A. alvaradoense* is a synonym of *Acanthoceras amphibolum* Morrow, 1935. The species are thus in the correct stratigraphic sequence except for *M. sellardsi*, which is a *Tarrantoceras* that co-occurs with *A. amphibolum*. The most recent zonation is that of Young and Powell (1978):

Upper Cenomanian	{	<i>Kanabicerias septemseriatum</i> zone <i>Acanthoceras alvaradoense</i> zone <i>Eucalycoceras bentonianum</i> zone <i>Conlinoceras tarrantense</i> zone
Lower Cenomanian	{	<i>Forbesiceras brundrettei</i> zone <i>Budaiceras lyatti</i> zone <i>Graysonites lozoi</i> zone <i>Plesioturrilites brazoensis</i> zone

It should be noted that Young (1986) has since referred to the *F. brundrettei* zone as the lowermost zone of the middle Cenomanian. As will be shown below, *F. brundrettei* is best regarded as lower Cenomanian, and as already noted, *E. bentonianum* is a *Sciponoceras gracile* zone *Sumitomoceras* (e.g. *septemseriatum* Zone of Young and Powell).

We used a modified version of the standard southern Western Interior zonal sequence of Cobban (1984), Cobban *et al.* (1989) and Kennedy (1988), as follows:

Upper Cenomanian	{	<i>Nigericeras scotti</i> zone <i>Neocardioceras juddii</i> zone <i>Burroceras clydense</i> zone <i>Sciponoceras gracile</i> zone <i>Metoicoceras mosbyense</i> zone <i>Calycoceras canitaurinum</i> zone
Middle Cenomanian	{	<i>Plesiakanthoceras wyomingense cobbani</i> zone <i>Acanthoceras amphibolum</i> zone <i>Acanthoceras bellense</i> zone <i>Conlinoceras tarrantense</i> zone
Lower Cenomanian (part)	{	<i>Forbesiceras brundrettei</i> zone <i>Acompsoceras inconstans</i> zone <i>Budaiceras lyatti</i> zone

Two subzones can be recognized in the *A. amphibolum* zone, characterized by the restricted form of the zonal index below and the subspecies *fallense* above. Characteristic faunas of, and criteria for recognizing, this sequence are to be found in Cobban (1984) and Kennedy (1988). The only departure is the insertion of an *A. bellense* zone into the sequence. This is based upon the presence, in Bell County, of a distinctive assemblage immediately below the *A. amphibolum* zone with the

following fauna: *Anagaudryceras involvulum* (Stoliczka, 1865), *Puzosia* (*Puzosia*) sp., *Forbesiceras* cf. *chevillei* (Pictet and Renevier, 1866), *Acanthoceras bellense* Adkins, 1928, *Calycoceras* (*Newboldiceras*) sp., *Conlinoceras* sp., *Paraconlinoceras leonense* (Adkins, 1928), *Cunningtoniceras lonsdalei* (Adkins, 1928), *Hamites cimarronensis* (Kauffman and Powell, 1977), *Sciponoceras*? sp. and *Turrilites* (*Turrilites*) *acutus* Passy, 1832.

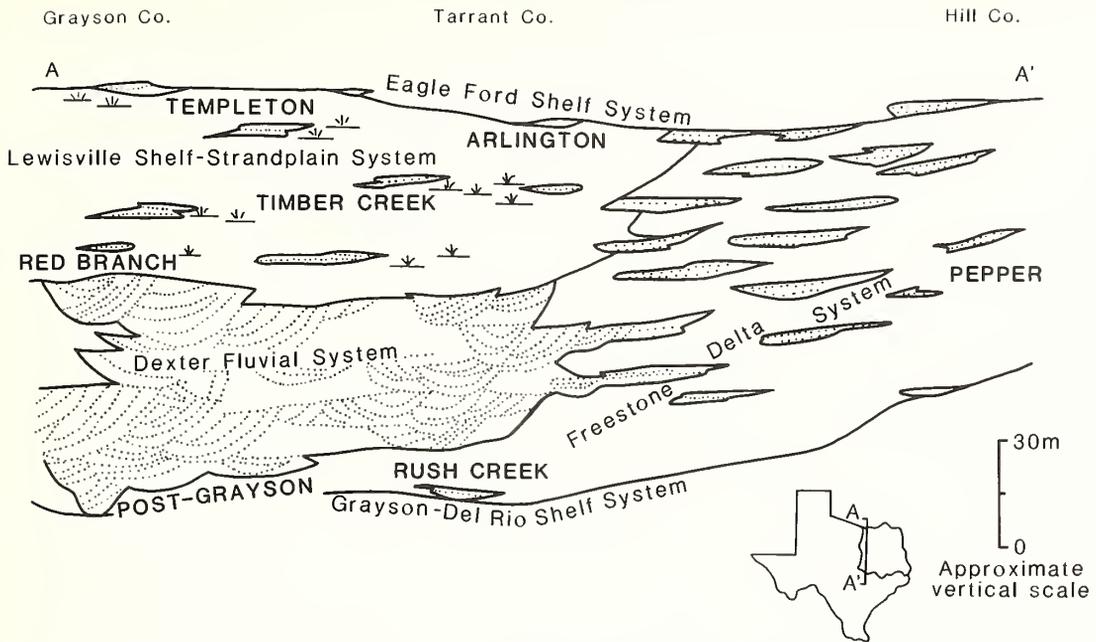
STRATIGRAPHY

Woodbine Formation

The name Woodbine was first used by Hill (1902) for exposures at Woodbine in eastern Cooke County, Texas. Detailed accounts of previous work and measured sections are to be found in Adkins (1933), Bergquist (1949), Adkins and Lozo (1951), and Stephenson (1953a, b). Dodge (1969) summarized the complex nomenclature of the various members recognized by previous workers (reproduced here as text-fig. 2). The Woodbine rests unconformably on upper Albian Main Street Formation or lower Cenomanian Grayson Marl from the Texas/Oklahoma border south to Bosqueville in McLennan County, beyond which it rests upon the lower Cenomanian Buda Limestone through the remainder of the study area. Its upper limit is also a discontinuity. Identifiable ammonites are of limited distribution within the Woodbine, the bulk of the formation being of fluviodeltaic origin. Text-figure 3 shows a diagrammatic representation of the outcrop stratigraphic relations taken from the work of Oliver (1971). The formation is 152 m (500 feet) thick in the Red River area, 91 m (300 feet) at the Tarrant-Johnson county line and reduced to less than 10 m south of the Brazos River, where it is replaced by a wholly shale sequence, the Pepper Shale. Adkins and Lozo (1951) cite 5.5 m (18 feet) on the Johnson-Hill County Line and reduction to zero on the San Marcos arch (for definition see Adkins 1933, p. 266) between Austin and San Antonio. Oliver (1971) recognized three principal depositional systems in the Woodbine: a fluvial system, a high-destructive delta system and a shelf-strandplain system. The fluvial system is represented at outcrop by the Dexter fluvial system, which is dominant north and northeast of a line from Dallas to Tyler. It yields no ammonites. Migration of the drainage network to the east throughout Woodbine delta building and continued subsidence of the area previously occupied by the fluvial system resulted in submergence of much of that area during deposition of the Lewisville shelf-

	Taff 1893	Hill 1901	Adkins 1932	Hazzard et al. 1947	Bergquist 1949	Stephenson 1953a	Dodge 1969
	Eagle Ford Formation	Eagle Ford Formation	Eagle Ford Formation	Eagle Ford Formation	Eagle Ford Formation	Eagle Ford Formation	Eagle Ford Formation
Dakota Formation	Timber Creek Beds	Lewisville Beds	Lewisville Formation	Lewisville Formation Pine Bluff Member	Templeton Member Lewisville Member	Templeton Member Lewisville Member	Wanting Arlington Member
	Dexter Sands	Dexter Formation	Dexter Formation	Eules Formation	Red Branch Member Rainbow Clay	Eules Member Red Branch Member	Lewisville Member Dexter Member
	Basal Clays			Dexter Sandstone Member	Dexter Member Unnamed post-Grayson shale	Dexter Member	Dexter Member Rush Creek Member
	Grayson Formation	Grayson Formation	Grayson Formation	Grayson Formation	Grayson Formation	Unnamed post-Grayson shale Grayson Formation	Grayson Formation

TEXT-FIG. 2. Stratigraphic nomenclature of the Woodbine Formation of previous workers, redrawn from Dodge (1969).



TEXT-FIG. 3. Diagrammatic Woodbine outcrop section, Grayson to Hill County, Texas, redrawn from Oliver (1971).

strandplain system. This yields a few specimens of the early form of *Acanthoceras amphibolum* Morrow, 1935 on Walnut Creek, 0.3 miles north of Gordonville in Grayson County. To the south and southwest, the high-destructive delta system, the Freestone Delta System of Oliver, persists throughout the Woodbine section; portions outcrop in Johnson to Falls Counties, but most of the unit is subsurface. There are no ammonites.

The Tarrant problem. Beds between typical sandstones of the Woodbine and typical shales of the Britton Formation of the Eagle Ford Group in Tarrant County were described by Moreman (1933) as the 'Tarrant sandy clay and limestone' and as the 'Tarrant formation' by the same author in 1942, where he regarded them as the basal unit of the Eagle Ford. Adkins and Lozo (1951, p. 123) refer to it as a 'fictitious lithic unit'. Stephenson (1953a, p. 14) believed the Tarrant to be part of the Lewisville Member of the Woodbine, and described the ammonite fauna as such, presenting, in the same year (1953b, p. 53) clear evidence that the Tarrant was older than the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group in Bell County. Moreman and some others equated the Tarrant and the base of the Eagle Ford in Bell County, and some faunal lists in the literature (e.g. Moreman 1942) include elements from both units. Brown and Pierce (1962), Norton (1965) and Powell (1968) all return to Moreman's view, classifying it with the Eagle Ford. Resolution of this dichotomy of opinion is beyond the scope of this discussion, and irrelevant to it. The unit is referred to as the Eagle Ford here for convenience only. The critical section for this account is that described by Powell (1968), between the north- and south-bound lanes of Texas Highway 360 between Randol Mill Road and the Dallas-Fort Worth Turnpike and Six Flags Park in northeast Arlington, between Dallas and Fort Worth:

Britton Member

Clay: dark-grey weathering pale greyish-orange calcareous, hard and rather brittle when dry, bentonitic; contains thin, discontinuous lenses of qtz siltite and calcisiltite along with streaks and beds of white to orange bentonite up to 8 inches thick.

Feet

Sandy flags: reddish-brown quartz-bearing calcarenite, calcite cement, locally hard and resistant, 1 inch to 3 inches thick; contains fish debris, mainly *Ptychodus whipplei*, lamnid shark and teleost fragments; lucinid clams, *Inoceramus pictus*, *Acanthoceras* cf. *A. wintoni* impressions, *Eucalycoceras?* sp. and *Tarrantoceras?* impressions. Calcareous clay as above. 1

Silty clay and flags: silty clay, light olive-grey to dark-grey, non-calcareous, with silt laminae and tuffaceous? sand. Flags, quartz-bearing, reddish-brown calcisiltite as above, occurring in top 3 feet of unit. 7

Sandy clay: light to dark bluish-grey, silty streaks, mottled and streaked with limonite stain and jarosite; top of unit is 1 to 4 inches tuffaceous? sandstone, with feldspar and mica. Base of unit is soft, clayey quartz sand. 5

Tarrant Member

Sandstone: yellowish- and greyish-brown, very fine to fine quartzose, with few chert pebbles and locally abundant phosphatic granules; burrowed, local calcareous cement; grades downward into grey to yellowish-brown gypsiferous sandy clay (2 feet). 4-5

Sandstone: yellowish-grey to brown, very fine quartzose, with large crustacean burrows (*Callianassa?*), *Acanthoceras wintoni*, *Eucalycoceras* sp., tellinid clams; contains wave ripples trending N-S, and current cross-laminations. 2

Sandstone and shale: sandstone, yellowish-brown, very fine to fine quartzose, in beds ranging in thickness from 3 to 8 inches. Shale, bluish-grey and yellowish-grey, silty with calcareous quartz siltstone flags 1 to 3 inches thick. Shale and sandstone complexly interbedded and contain *A. wintoni*, *A. tarrantense*, *Epengonoceras dumbli*, *Phleopteria dalli*, *Exogyra columbella*, *Ostrea subradiata*, mactrid and other clams. Base of Tarrant not exposed. 6

Total section measured 43-5

Brown and Pierce (1962) showed the base of the Tarrant to be a marked unconformity with a basal phosphatic conglomerate in the Dallas area. Observations by J. M. Hancock and W. J. Kennedy in 1972 indicate that the 'Sandy flags' of the Britton Member of Powell's section correspond to the 'Six Flags limestone' of Norton (1965). The base includes phosphatic pebbles and vertebrate debris, and may be an unconformity. It yields *Tarrantoceras* and *Acanthoceras* of the *amphibolum* group, as do the overlying shales; a prominent bentonite 1.5 m (5 feet) above the Six Flags Limestone Member is identified as the X bentonite of the Western Interior (itself an *A. amphibolum* zone marker) by Kauffman, Hattin and Powell (1977, p. 26).

It should be noted that Norton (1965) draws the Tarrant/Britton boundary at the top of the Six Flags limestone and Powell (1968) 3.65 m (12 feet) below it.

The Templeton Member. Higher biostratigraphic horizons are indicated by the ammonites from the Templeton Member of the Woodbine, a clay and shale unit up to 24 m (80 feet) thick and present from central Denton County northwards to Grayson County and east to eastern Lamar County. Ammonites occur in three different and widely separated parts of the outcrop and it is impossible to put them all in relative sequence from evidence from Texas alone.

The first occurrence is at locality 1540 of Stephenson (1953a) (= USGS localities 14092, 14560, 17163, 18236 and 18971, also represented by OUM KT3937-3989), gullies just south of the old Sherman Highway, 4.5 km (2.8 miles) south-east of the centre of Whitesboro, Grayson County, some 13.7 m (45 feet) below the base of the Eagle Ford. The fauna is: *Metengonoceras dumbli*, *Tarrantoceras cuspidum* (Stephenson, 1953a), *Metoioceras latoventer* Stephenson, 1953a, and *Hamites* sp. *M. dumbli* first appears in the *Conlinoceras tarrantense* zone in Texas and ranges to the *Sciponoceras gracile* zone in western Europe (Kennedy *et al.* 1981; Kennedy and Juignet 1984; Cobban 1987a). *Metoioceras* aff. *latoventer* is recorded from west-central New Mexico by Cobban (1977a) in association with what may be a *Calycoceras canitaurinum* zone fauna, providing a possible date for this assemblage.

Ammonites are abundant at the type locality of the Templeton, locality 164 of Stephenson (1953a) (= USGS locality 20314, also represented by OUM KT4300–4346), bluffs along Templeton Branch of Cornelius Creek, Cooke County, some 37 km (23 miles) to the east. Stephenson places this 6.1 m (20 feet) above the top of the Lewisville Member, and thus probably a little lower in the lithologic sequence than the previous locality. The fauna is: *Metengonoceras dumbli* (common), *M. latoventer* (as represented by USNM 105986, a paratype of *Plesiacanthoceras* [*Mammites*] *bellsanum* (Stephenson, 1953a)), *Metoicoceras crassicostrae* Stephenson, 1953a and *Plesiacanthoceras bellsanum* (Stephenson, 1953a). The last named is closely allied to but distinct from the form described by Cobban (1977a, p. 25, pl. 13, figs 1 and 2) as *P. aff. wyomingense* and later named *P. wyomingense cobbani* Atabekian, 1985 (p. 87). *Metoicoceras* comparable to *crassicostrae* occur in the *P. wyomingense* zone of the northern part of the Western Interior (Cobban, 1987a, p. C5). We conclude that this is a *P. wyomingense* zone assemblage.

The third assemblage is the most problematic. It comes from localities around Arthur City and on the banks of the Red River in Lamar County, 112.6 km (70 miles) east-north-east of the others, corresponding to localities 201, 202, 203 and 207 of Stephenson (1953a), including the celebrated outcrop at Slate Shoals in the bed of the Red River, 13 km (8 miles) east of Arthur City, and now completely overgrown. The fauna is *Metengonoceras dumbli* and *Metoicoceras swallowi* (Shumard, 1860). The former is long-ranging (see above), the latter is known only from this area, and we cannot place it in sequence.

The Pepper Shale. This unit extends from the Brazos River southwards until it is cut out on the San Marcos arch between Austin and San Antonio. The type locality is in bluffs along Bird Creek (also referred to as Pepper Creek in the literature), 6.4 km (4 miles) east-north-east of Belton in Bell County, where it is 7.2 m (23.5 feet) thick, and rests unconformably on lower Cenomanian Del Rio Clay. Ammonites from the unit were discussed by L. F. Spath in 1933 (*in* Adkins 1933, p. 419), foraminifers by Plummer (*in* Adkins 1933) and Loeblich (1946), and molluscs by Stephenson (1953b). The last named and Adkins and Lozo (1951) provide detailed descriptions of the type and other sections. Spath's observations on the ammonites he examined for Adkins give no indications of precise age, whilst we have failed to relocate the material. Stephenson (1953b) described only a baculitid and an indeterminate acanthoceratid fragment. Our own collecting from the type locality yielded only an indeterminate turrilitid (OUM KT4985). All that can be said with certainty is that the Pepper is post-Del Rio Clay and pre-*Acanthoceras bellense* zone, for the latter fauna occurs at the base of the Bluebonnet Member of the overlying Lake Waco Formation. As noted below, old USGS collections with a lower Cenomanian *Forbesiceras brundrettei* zone fauna from the Waco area may be from the Pepper.

Eagle Ford Group

Dallas–Fort Worth area. Relations of the lower part of the Eagle Ford Group to the Woodbine Formation in the Dallas–Fort Worth area are discussed by Kennedy (1988). The Tarrant Formation of Moreman (1927, 1942) is a concretion-bearing sandy shale unit usually less than 15 m (50 feet) thick. As already noted, Stephenson (1953a) included it in the Lewisville Member of the Eagle Ford. The Tarrant rests with a sharp contact on what Dodge (1969) termed the Arlington Member (of the Woodbine) and yields (in the lower part) a *Conlinoceras tarrantense* zone fauna; the index species is common as is *Metengonoceras dumbli*, with *Paraconlinoceras barcusi* (Jones, 1938), *Cunningtoniceras inermis* (Pervinquier, 1907) (= *Acanthoceras eulessanum* (Stephenson, 1953a)), *Forbesiceras conlini* Stephenson, 1953a and *Turrilites dearingi* Stephenson, 1953a rare. The Six Flags Limestone Member (Norton 1965) and at least the basal 1.5 m of the succeeding bentonitic sub-member of the Britton Formation are of *A. amphibolum* zone age, yielding the index species and *Tarrantoceras sellardsi* (Adkins, 1928). No higher zonal indicators are known up to the *Sciponoceras gracile* zone.

Johnson and Tarrant Counties. Stephenson (1955) described a small fauna from the lower part of the

Eagle Ford Group at four localities in these two counties. The most important is on Walnut Creek, 7.6 km (4.75 miles) east-north-east of Mansfield in Tarrant County (Stephenson 1955, p. 54).

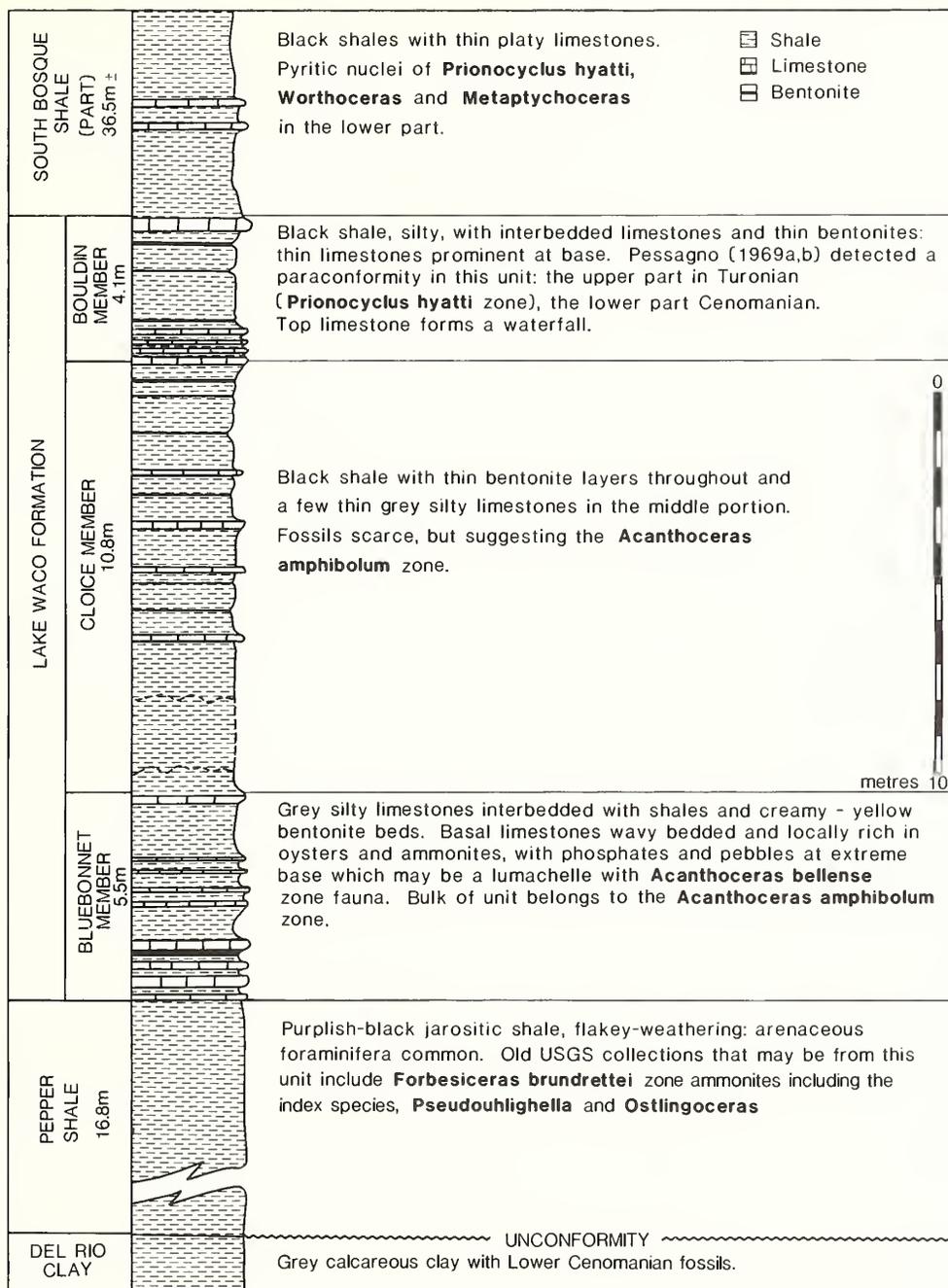
The Woodbine/Eagle Ford contact is an unconformity, and loose concretions from Stephenson's bed 5 of the Eagle Ford yield an abundant fauna. Many concretions are a solid mass of imbricated valves of *Inoceramus arvanus* Stephenson, 1953a, with rarer ammonites of the *Acanthoceras amphibolum* zone: *Borissiakoceras orbiculatum* Stephenson, 1955, *Moremanoceras straini* Kennedy, Cobban and Hook, 1988, *Acanthoceras amphibolum*, *Cunningtoniceras johnsonianum* (Stephenson, 1955), *Plesiacanthoceratoides vetula* (Cobban, 1987b), *Turrilites* (*Turrilites*) *acutus* Passy, 1832, and *Anisoceras* cf. *plicatile* (J. Sowerby, 1819). Stream outcrops at a higher horizon yield a similar fauna in interbedded shales and shelly sandstones.

The Waco area. The Eagle Ford Group in this area is described in detail by Adkins and Lozo (1951), with important additional observations in Brown and Pierce (1962) and Pessagno (1969a, b). The sequence differs markedly from that around Dallas, with the appearance of significant developments of limestones in the lower part of the succession. The *Forbesiceras brundrettei* zone is represented by old collections from a number of localities in this area. Although labelled 'Del Rio' they are from the Woodbine/Eagle Ford outcrop, but cannot be referred with confidence to Woodbine versus Eagle Ford, although probably from the Pepper Shale (Woodbine equivalent). The old brickpit on Cloice Branch yielded, to L. W. Stephenson, T. W. Stanton and J. B. Reeside, Jr. in 1927 the following from '12–15 feet below top of Del Rio' (USGS locality 14592): *Moremanoceras elgini* (Young, 1958), *Forbesiceras brundrettei* (Young, 1958), *Ostlingoceras brandi* Young, 1958. A collection from USGS locality 14598 'Upper Member of Del Rio Clay $\frac{1}{2}$ mile east of South Bosque, near railroad' includes *Ostlingoceras davisense* Young, 1958 and *F. brundrettei*. The Eagle Ford rests with marked unconformity on Pepper Shale (text-fig. 4). The basal shale of the Eagle Ford 45 cm (1.5 feet) thick on Pepper Creek (Adkins and Lozo 1951, p. 130, figs. 8, 13), is overlain by the Lake Waco Formation, some 18–24 m (60 to 80 feet) thick, and divided into three members. The lowest, Bluebonnet Member, is discussed in detail by Silver (1963), who described it as 3 to 6 m (10 to 20 feet) of limestones, shales and bentonites, restricted to all or portions of Bell, Falls, McLennan, Limestone and Hill Counties. He interpreted it as a lagoonal sequence, and noted that ammonites were restricted to the lower part. He gives a series of detailed sections, which supplement those of Adkins and Lozo (1951). The key section is on Bird Creek (Pepper Creek) and environs, 6.4 km (4 miles) east-north-east of Belton in Bell County. A discontinuous concretionary phosphatic pebble/shell conglomerate no more than 30 cm thick yields a diverse *Acanthoceras bellense* zone fauna: *Anagaudryceras involvulum*, *Puzosia* sp., *Forbesiceras* cf. *chevillei*, *Acanthoceras bellense*, *Cunningtoniceras lonsdalei*, *Calycoceras* (*Newboldiceras*) sp., *Conlinoceras* sp., *Paraconlinoceras leonense*, *Hanites cimarronensis*, *Turrilites acutus*, and *Sciponoceras?* sp.

Ammonites of the *A. amphibolum* zone are common in the succeeding flaggy limestones at this locality, and for several metres above. The OUM collections include the index species, numerous *Tarrantoceras sellardsi* and *Moremanoceras straini*. This same assemblage occurs widely elsewhere in the Waco area. A collection from USGS locality 14591, labelled 'Lower part of Eagle Ford Clay, 7.5 feet above base of Eagle Ford' and presumably from the Bluebonnet Member in an old brickpit on Cloice Branch, 1.3 km (0.8 mile) east of South Bosque, McLellan County, yielded abundant *M. straini*, *A. amphibolum*, *T. sellardsi* and *Hanites cimarronensis*.

The Cloice Member of the Lake Waco Formation is predominantly shale, 10.8 m (35.5 feet) thick at the type locality on Cloice Branch; Adkins and Lozo (1951) cite it as yielding similar faunas to the Bluebonnet.

The Bouldin Member of the Lake Waco Formation is a sequence of interbedded greyish white to brownish silty limestones and silty shales with bentonites, 2.8 m (9.25 feet) thick at the type locality on Bouldin Creek between Milton Street and Barton Springs Road, Austin (Adkins and Lozo 1951, p. 121), and 4.1 m (13.5 feet) on Cloice Branch, east of South Bosque (Adkins and Lozo 1951, fig. 18). Adkins and Lozo (1951, p. 142) record '*Encalycoceras*, *Metoicoceras* and *Mantelliceratidae*'. Pessagno (1969a, b) concluded that there was an unconformity 3–4.25 m (10–14



TEXT-FIG. 4. The Pepper Shale (Woodbine equivalent) and lower part of the Eagle Ford Group on Cloice Branch, southwest of Waco, McLennan County (after Adkins and Lozo 1951).

feet) from the top of the Lake Waco Formation. The Blue Cut section (Adkins and Lozo 1951, p. 136) shows *Prionocyclus hyatti* occurring in the top Lake Waco/basal South Bosque Formation transition; there are no records of post-*A. amphibolum* and pre-*P. hyatti* zone fossils in this area and the break may thus be of this extent.

Austin area. Adkins (1933, p. 436) records 3·7 m (12 feet) of black limestone flags and shale with '*Exogyra columbella*, *Mantelliceras* n.sp. (compressed), *Acanthoceras* sp. (strongly cornute), *Eucalycoceras leonense* Adkins, *Austiniceras* n.sp., *Eucalycoceras bentonianum* Cragin (?), *Metoicoceras* sp. (?)'. From his usage elsewhere, this is an *A. amphibolum* zone fauna, confirmed by a fine specimen of *Tarrantoceras sellardsi* from USGS Locality 14609, Public Road 1·8 km (1·1 miles) south-south-east of Round Rock in Williamson County approximately 10 miles north of Austin.

SYSTEMATIC PALAEOLOGY

Location of specimens. The following abbreviations are used to indicate the location of specimens mentioned in the text:

BMNH: British Museum (Natural History), London.

MNHP: Muséum National d'Histoire Naturelle, Paris.

OUM: University Museum, Oxford.

USNM: National Museum of Natural History, Washington D.C.

TMM: University of Texas Memorial Museum, Austin, Texas.

UMM: University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

Suture terminology. The system of Wedekind (1916) as propounded by Kullmann and Wiedmann (1970) is used here. E = external lobe, L = lateral lobe, U = umbilical lobe, I = internal lobe.

Dimensions. All dimensions are given in millimetres; D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus, c = costal, ic = intercostal. Figures in parentheses refer to percentages of diameter. The term rib index as applied to heteromorphs is the number of ribs in a distance equal to the whorl height at the mid-point of the interval counted.

Synonymies. Only citations that include illustrations of material or important systematic, stratigraphic or geographic information are included.

Order AMMONOIDEA Zittel, 1884, pp. 355, 392

Suborder LYTOCERATINA Hyatt, 1889, p. 7

Superfamily TETRAGONITACEAE Hyatt, 1900, p. 568

Family GAUDRYCERATIDAE Spath, 1927, p. 66

Genus ANAGAUDRYCERAS Shimizu, 1934, p. 67

(= *Paragaudryceras* Shimizu, 1934, p. 67; *Murphyella* Matsumoto, 1972, p. 208)

Type species. By original designation: *Ammonites sacya* Forbes, 1846, p. 113, pl. 14, fig. 9.

Anagaudryceras involvulum (Stoliczka, 1865)

Plate 1, figs. 17–19

1865 *Ammonites involvulus* Stoliczka, p. 150, pl. 75, fig. 1 (*involutus* in explanation of plate).

1865 *Ammonites sacya* Forbes; Stoliczka, p. 154, pl. 76, fig. 3 only.

1895 *Lytoceras (Gaudryceras) involvulus* (Stoliczka); Kossmat, p. 32.

1935 *Gaudryceras (Anagaudryceras) utatureense* Shimizu, p. 176.

1956 *Anagaudryceras involvulum* (Stoliczka); Collignon, p. 68.

1966 *Anagaudryceras involvulum* (Stoliczka); Howarth, p. 219, pl. 1, figs. 1 and 2.

1975 *Anagaudryceras involvulum* (Stoliczka); Kennedy and Juignet, p. 77, fig. 1.

1976 *Anagaudryceras involvulum* (Stoliczka); Juignet and Kennedy, p. 49, pl. 1, figs. 1 and 2.

1984 *Anagaudryceras involvulum* (Stoliczka, 1865); Wright and Kennedy, p. 50, pl. 2, fig. 2; text-figs. 1C and F.

Type. Holotype is Stoliczka's original specimen (1865 pl. 75, fig. 1) from the Utatur Group of Odium, South India, by monotypy.

Material. USNM 420184, from the basal shell bed of the Bluebonnet Member on Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County, middle Cenomanian *Acanthoceras bellense* zone.

<i>Dimensions</i>	D	Wb	Wh	Wb:Wh	U
USNM 420184	68.5 (100)	28.5 (41.6)	29.3 (42.8)	0.07	23.5 (34.3)

Description. Coiling is moderately involute with U = 34% of diameter, and of moderate depth. Whorl section is slightly compressed (Wb:Wh = 0.97), with greatest breadth just outside the umbilical shoulder. The umbilical wall is rounded, the inner flanks broadly rounded, the outer flanks flattened and convergent, the venter broadly arched. The shell surface is worn, and no trace of ornament survives, nor are the sutures visible.

Occurrence. The species is known from both the lower and middle Cenomanian, with records from southern India, Angola, Haute-Normandie in France, Devon, England, and central Texas.

Suborder AMMONITINA Hyatt, 1889, p. 7
 Superfamily HAPLOCERATACEAE Zittel, 1884, p. 463
 Family BINNEYITIDAE Reeside, 1928, p. 4
 Genus BORISSIAKOCERAS Arkhanguelsky, 1916, p. 55

Type species. By original designation: *Borissiakoceras mirabilis* Arkhanguelsky, 1916, p. 55, pl. 8, figs. 2 and 3.

Borissiakoceras orbiculatum Stephenson, 1955

Plate 1, figs. 1–14

- 1955 *Borissiakoceras orbiculatum* Stephenson, p. 64, pl. 6, figs. 1–4.
 1961 *Borissiakoceras orbiculatum* Stephenson; Cobban, p. 750, pl. 88, figs. 15–44; text-figs. 5a–f.
 1988 *Borissiakoceras orbiculatum* Stephenson; Kennedy, p. 18, pl. 1, figs. 23–26 (with synonymy).

Holotype. USNM 108832 from the basal Eagle Ford Group on Walnut Creek, 7.6 km (4.75 miles) north-east of Mansfield, Texas, *Acanthoceras amphibolum* zone.

Material. Ten specimens, USNM 420185 to 420191 from USGS Mesozoic locality D12626, loose concretion at roadside 8.9 km (5.5 miles) north-east of Mansfield, Johnson County. Nine specimens, USNM 420192 to 420193 from USGS Mesozoic locality D9502, concretion in field 0.5 km (0.3 mile) north-north-west of Lillian, Johnson County. USNM 420194 from a concretion in a crop field, 1.6 km (1 mile) north of Lillian, Johnson County. Horizon as for type.

Discussion. This species is described at length by Cobban (1961). Stephenson (1955) based his description on 3 specimens only; the present collection includes both smooth and nodate variants as in the largest, Black Hills assemblage of the species (Cobban 1961, p. 750, pl. 88, figs. 15–41; text-figs. 5a–f).

Occurrence. *Acanthoceras amphibolum* zone of Wyoming, Colorado, Kansas and Texas. *Sciponoceras gracile* zone of north-central Texas.

Genus JOHNSONITES Cobban, 1961

Type species. *Johnsonites sulcatus* Cobban, 1961, p. 743, pl. 87, figs. 1–18; text-figs. 3a–g, by original designation.

Johnsonites sp.

- 1953a *Euhoplites* sp. Stephenson, p. 198, pl. 45, figs. 5 and 6.

Material. USNM 105961, from the Lewisville Member of the Woodbine Formation on Timber Creek, 3.5 km (2.25 miles) south-west of Lewisville, Denton County.

Discussion. Cobban (1961, p. 746) notes that this specimen differs from *J. sulcatus* only by the forwardly arched growth lines on the venter. *J. sulcatus* is best known from the *Conlinoceras gilberti* zone of Wyoming and southern Colorado.

Occurrence. As for material.

Superfamily DESMOCERATACEAE Zittel, 1895, p. 426

(*nom. transl.* Wright and Wright, 1951, p. 18; *ex* Desmoceratidae Zittel, 1895, p. 426).

Family DESMOCERATIDAE Zittel, 1895, p. 426

Subfamily DESMOCERATINAE Zittel, 1895, p. 426

(*nom. transl.* Matsumoto, 1938, p. 190; *ex* Desmoceratidae Zittel, 1895)

Genus MOREMANOCERAS Cobban, 1972, p. 465

Type species. *Tragodesmoceras scotti* Moreman, 1942 (p. 208, pl. 33, fig. 8; text-fig. 2d) by original designation.

Moremanoceras straini Kennedy, Cobban and Hook, 1988

Plate 1, fig. 25; Plate 2, figs. 1–3, 9–23, 26–28, 31–33

?1955 *Desmoceras?* sp. Stephenson, p. 58, pl. 4, figs. 12 and 13.

1977a *Desmoceras (Pseudoulligella)* aff. *D. japonicum* Yabe; Cobban, p. 22, pl. 11, figs. 1–6, 9, 10.

1977b *Desmoceras (Pseudoulligella)* aff. *D. japonicum* Yabe; Cobban, fig. 4a–e.

1988 *Moremanoceras straini* Kennedy, Cobban and Hook, p. 36, fig. 1a–g, i, t.

Types. Holotype is USNM 416051 by original designation; paratypes USNM 416052–416060, from the base of the Boquillas Formation, *Acanthoceras amphibolum* zone, Cerro de Cristo Rey, New Mexico, the originals of Kennedy, Cobban and Hook, 1988, fig. 1c and d.

EXPLANATION OF PLATE I

Figs. 1–14. *Borissiakoceras orbiculatum* Stephenson, 1955, 1–3, USNM 420185; 4–6, USNM 420186; 7 and 8, USNM 420187; 9, USNM 420188; 10, USNM 420189; 11–13, USNM 420190, from USGS Mesozoic locality D12626, loose concretion at roadside 8.9 km (5.5 miles) north-east of Mansfield, Johnson County. 14, USNM 420192, from USGS Mesozoic locality D9502, concretion in field 0.5 km (0.3 mile) north-north-west of Lillian, Johnson County. All $\times 2$ from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone.

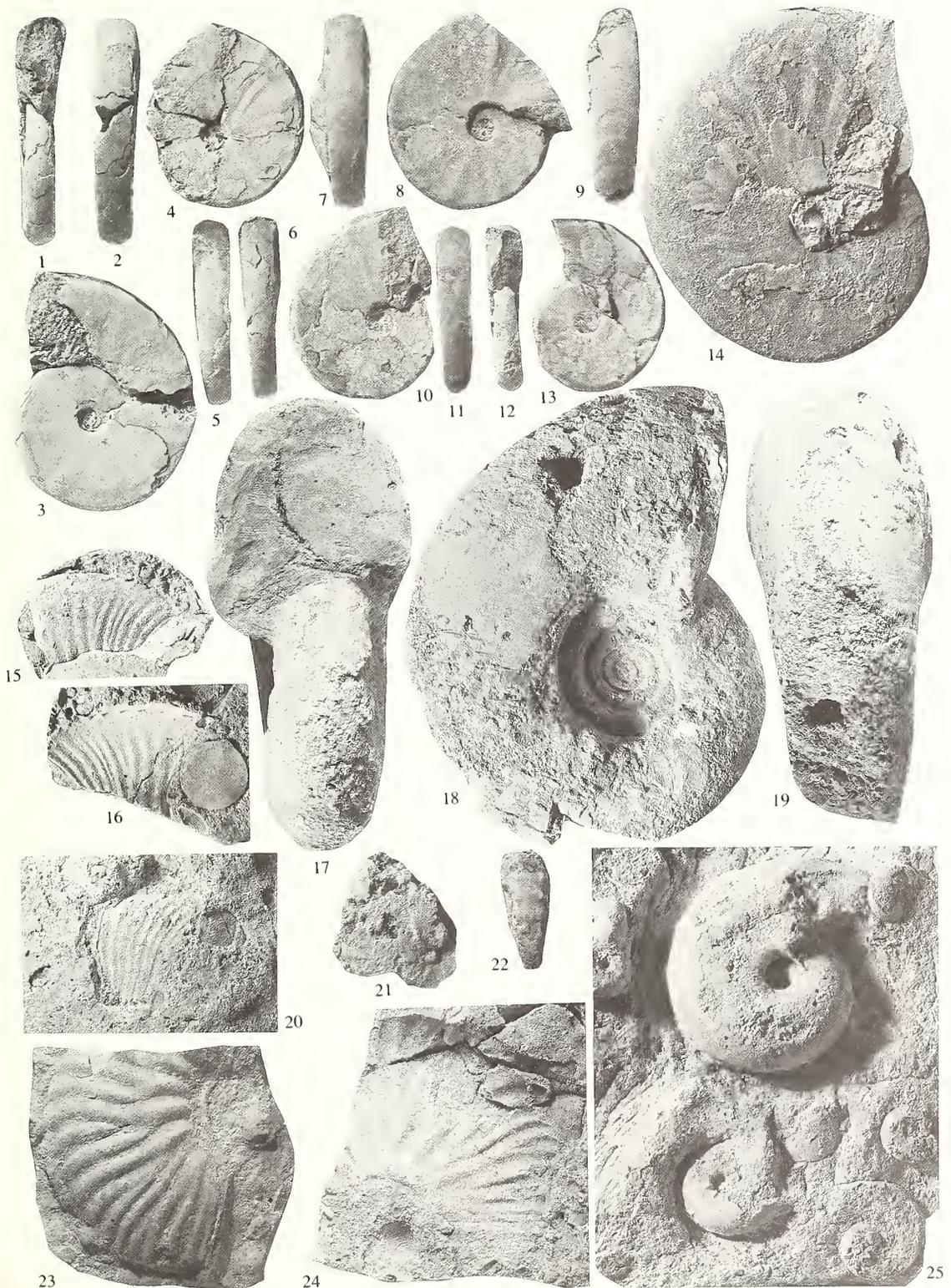
Figs. 15 and 16, 20, 23 and 24. *Forbesiceras brundrettei* (Young, 1958). 15 and 16, USNM 424120; 20, USNM 424121; 23 and 24, USNM 424122 all from USGS locality 14592, old brickpit on Cloice Branch, 1.3 km (0.8 mile) east of South Bosque, McLennan County. *F. brundrettei* zone, Pepper Shale (inferred).

Figs. 17–19. *Anagaudryceras involvulum* (Stoliczka, 1865). USNM 420184, from the basal shell bed of the Bluebonnet Member on Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.

Figs. 21 and 22. *Forbesiceras* cf. *chevillei* (Pictet and Renevier, 1866). USNM 420211, horizon and locality as for the originals of figs. 17–19.

Fig. 25. *Moremanoceras straini* Kennedy, Cobban and Hook, 1988. USNM 420210, from the Bluebonnet Member on Cloice Branch, east of South Bosque, McLennan County. *Acanthoceras amphibolum* zone.

Figures 1–14 are $\times 2$; the remainder are $\times 1$.



Material. Abundant specimens, including USNM 420195 to 420204 from USGS Mesozoic locality D 12626, 8.9 km (5.5 miles) north-east of Mansfield, Johnson County. Four specimens, USNM 420205 from USGS Mesozoic locality D9502, concretions in field 0.5 km (0.3 mile) north-north-west of Lillian, Johnson County. Four specimens, USNM 420206 to 420207 from 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) northeast of the town square in Alvarado, Johnson County. All basal Eagle Ford Group, middle Cenomanian *Acanthoceras amphibohum* zone.

Numerous specimens, USNM 420208 to 420209, from 7.2 km (4.5 miles) south of McGregor on western slope of eastern Moody Hills, opposite Bagett's Station, McLennan County; USNM 420210 from Cloice Branch east of South Bosque, McLennan County, all Bluebonnet Member of Lake Waco Formation, *Acanthoceras amphibohum* zone.

<i>Dimensions</i>	D	Wb	Wh	Wb:Wh	U
USNM 420203	17.2 (100)	8.7 (50.6)	7.5 (43.6)	1.16	2.3 (13.4)
USNM 420195	21.0 (100)	10.0 (47.6)	8.7 (41.4)	1.14	3.9 (18.6)
USNM 420202	29.8 (100)	13.4 (45.0)	12.6 (42.3)	1.06	7.3 (24.5)
USNM 420196	30.3 (100)	13.0 (42.9)	14.6 (48.1)	0.89	6.9 (22.7)

Description. Involute with small, deep umbilicus, umbilical ratio increasing with growth (see table of dimensions). Umbilical wall flattened, umbilical shoulder narrowly rounded. Whorl section initially depressed, becoming compressed in middle and later growth. Inner flanks flattened, subparallel, outer flanks convergent, venter arched, rounded. The internal mould is smooth but for traces of growth striae and constrictions, 5–6 per whorl, flanked by variability developed collar ribs. Constrictions are feebly concave over umbilical shoulder and inner flank, convex across mid-flank and concave on the outer flank where they strengthen markedly, projecting forwards over the ventrolateral shoulder, shallowing and narrowing, to cross the siphonal line in a narrow linguoid peak. The associated collar ribs are generally prominent only on the ventrolateral shoulder. At small diameters, the venter is evenly rounded. From approximately 25 mm onwards a blunt, rounded siphonal keel appears, flanked by shallow grooves, its crest marked by the linguoid peak of the growth lines.

Few well-preserved specimens have shell present. Those that do show little or no trace of constrictions or collars, and have a more conspicuous keel.

Sutures moderately incised, with symmetrically bifid E/L, trifold L and small, little-incised auxiliary lobes.

Discussion. *Moremanoceras elgini* (Young, 1958, p. 292, pl. 39, figs. 4–20, 24 and 25, 30 and 31; text-figs. 1a–e) is more compressed when young, develops thickened collar ribs from 15 mm diameter and strong, distant flank and ventrolateral ribs when mature. It never develops a keel. *Moremanoceras* sp. nov. of the *Calycoceras canitaurinum* zone of the Black Hills, New Mexico and

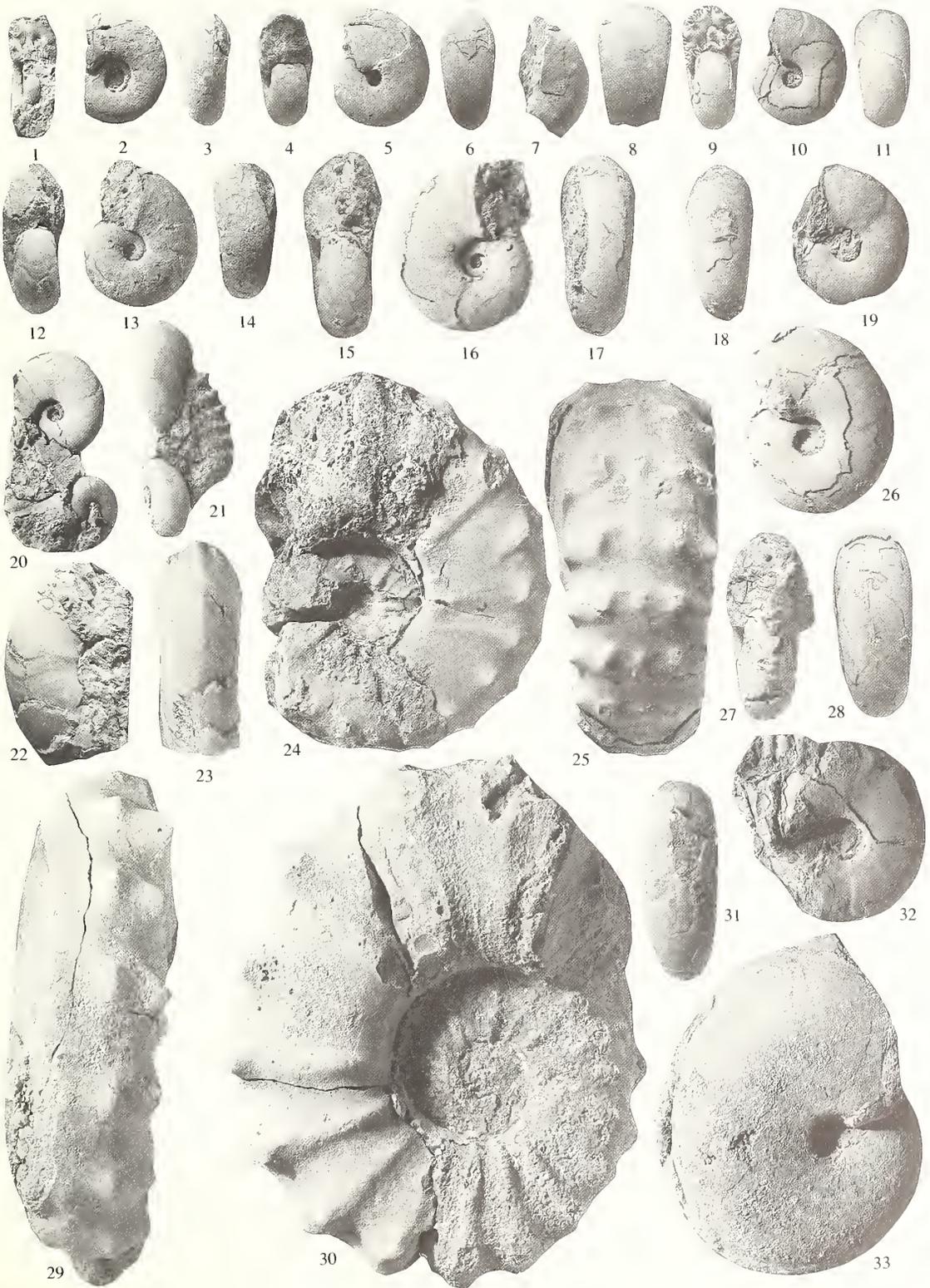
EXPLANATION OF PLATE 2

Figs. 1–3, 9–23, 26–28, 31–33. *Moremanoceras straini* Kennedy, Cobban and Hook, 1988. 1–3, USNM 108830, the original of Stephenson (1955, pl. 4, figs. 12 and 13) from USGS locality 11740 Walnut Creek, east-north-east of Mansfield, Tarrant County. 9–11, USNM 420195; 15–17, USNM 420196; 18 and 19, USNM 420197; 20 and 21, USNM 420198; 22 and 23, USNM 420199; 26–28, USNM 420200; 31 and 32, USNM 420201, all from USGS Mesozoic locality 12626, loose concretion, 8.9 km (5.5 miles) north-east of Mansfield, Johnson County. 12–14, USNM 420206, from USGS Mesozoic locality D9502, 0.5 km (0.3 miles) north-north-west of Lillian, Johnson County. All specimens are from the basal part of the Eagle Ford Group, *Acanthoceras amphibohum* zone. 33, USNM 420208, from the Bluebonnet Member, 7.2 km (4.5 miles) south of McGregor on western slope of eastern Moody Hills, McLennan County. *Acanthoceras amphibohum* zone. 4–6, USNM 105959 from USGS locality 14560, gullies south of old Sherman highway, 4.5 km (2.8 miles) east of Whitesboro, Grayson County. 7 and 8, USNM 105960, from USGS locality 13799, Golden Bluff, Red River, 4.8 km (3 miles) east of Arthur City, Lamar County. *Plesiocanthoceras wyomingense* zone.

Figs. 4–8. *Plesiocanthoceras bellsanum* (Stephenson, 1953a). 4–6, USNM 105959, from USGS locality 14560 on the old Sherman road, east of Whitesboro, Grayson County; 7 and 8, USNM 105960, from Golden Bluff, Lamar County. Both from the Templeton Member, *P. wyomingense* zone.

Figs. 24, 25, 29, 30. *Acanthoceras bellense* Adkins, 1928, 24 and 25, USNM 420212; 29 and 30 USNM 420214, both from the basal shell bed of the Bluebonnet Member on Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.

Figures 4–8 are $\times 2$; the remainder are $\times 1$.



Trans-Pecos Texas has a sharper keel, present from an earlier ontogenetic stage, strong concave ribs on the ventrolateral shoulder and is homoeomorphous with certain *Damesites* species. The type species, *M. scotti* (Moreman, 1942, p. 208, pl. 33, fig. 8; text-fig. 20) (see Cobban 1972, p. 6, pl. 2, figs. 1–23; text-figs. 3–5) of the *Sciponoceras gracile* zone lacks a siphonal ridge or keel and has a much smaller umbilicus and distant collar ribs that extend to the umbilical shoulder.

Occurrence. *Acanthoceras amphibolum* zone of central and Trans-Pecos Texas.

Subfamily PUZOSIINAE Spath, 1922a, p. 126

Genus and Subgenus PUZOSIA Bayle 1878, explanation of pls. 45 and 46

Type species. *Ammonites planulatus* J. de C. Sowerby, 1827 (p. 134, pl. 570, fig. 5), *non* Schlotheim 1820, p. 59; = *Ammonites mayorianus* d'Orbigny 1841, p. 267, pl. 79, figs. 1–3, by subsequent designation by H. Douvillé 1879, p. 91. See Wright and Kennedy (1984, p. 54) for discussion of the type species.

Puzosia (Puzosia) sp.

Material. OUM KT4986 from the base of the Bluebonnet Member, Pepper Creek, south-east of Interstate 35, 4.3 km (2.75 miles) north-east of Leon River Bridge, Bell County. *Acanthoceras bellense* zone.

Description. Specimen is a septate fragment only, with a maximum preserved whorl height of 69 mm. Only ventral ornament is preserved. It consists of coarse distant strong ribs with at least 15 much weaker ribs between.

Discussion. *Puzosia* has not been previously recognized in the mid-Cenomanian of the US Western Interior and Gulf Coast. The fragment is specifically indeterminate.

Occurrence. As for material.

Superfamily HOPLITACEAE H. Douvillé, 1890, p. 290

(*nom. correct.* Wright and Wright 1951, p. 21 (*pro* Hoplitida Spath, 1922b, p. 95, *nom. transl. ex* Hoplitidae Douvillé, 1890) (= Placenticerataceae Hyatt, 1900, p. 584, *nom. correct.* Casey, 1960, p. 208 *pro* Placenticeratida Hyatt, 1900; Engonocerataceae Hyatt, 1900, p. 585, *nom. transl.* Basse, 1952, p. 658, *ex* Engonoceratidae Hyatt, 1900)).

Genus METENGNOCERAS Hyatt, 1903, p. 179

(= *Epengonoceras* Spath, 1924, p. 308)

Type species. *Metengonoceras acutum* Hyatt, 1903 (p. 184, pl. 26, fig. 8; pl. 27, figs. 1 and 2).

Metengonoceras dumbli (Cragin, 1893)

- 1893 *Sphenodiscus dumbli* Cragin, p. 243, pl. 44, fig. 6.
- 1981 *Metengonoceras dumbli* (Cragin); Kennedy, Juignet and Hancock, p. 32, pl. 3, figs. 1–5; pl. 7, figs. 4–6; text-figs. 4A–G, 5B–F (with full synonymy).
- 1987a *Metengonoceras dumbli* (Cragin); Cobban, p. C2, pl. 1, figs. 3–6, 8; pl. 2, figs. 1–3, 9, 10; text-fig. 1 (with additional synonymy).
- 1988 *Metengonoceras dumbli* (Cragin, 1893); Kennedy, p. 37 (with additional synonymy).

Discussion. We have seen several hundred specimens from the *Conlinoceras tarrantense* zone of the Tarrant Formation and the *Plesiacanthoceras wyomingense* zone of the Templeton Member in central Texas, but none from the *Acanthoceras bellense* or *A. amphibolum* zones. This species is fully described by previous recent authors. Specimens from the *Dunveganoceras pondi* to *Metoicoceras*

mosbyense zones of Minnesota (Cobban 1983, p. 11, pl. 6; pl. 7, fig. 8; pl. 8, figs. 6 and 7) are better referred to *M. acutum* Hyatt, 1903 (p. 184, pl. 26, fig. 8; pl. 27, figs. 1 and 2), also known from the *Sciponoceras gracile* zone of north central Texas. Differences between the two are given by Cobban (1987*a*) and Kennedy (1988).

Occurrence. *C. tarrantense* and *P. wyomingense* zones in central Texas. *A. amphibolum* zone near Pueblo, Colorado. *Sciponoceras gracile* zone correlative in Sarthe and Loire-Atlantique, France; also recorded from Niger and Nigeria, the former probably better referred to *M. acutum*.

Superfamily ACANTHOCERATAE de Grossouvre, 1894, p. 22

(*nom. correct.* Wright and Wright 1951, p. 24, *pro* Acanthoceratida Hyatt, 1900, p. 585; *nom. transl.* ex Acanthoceratidae Hyatt, 1900, p. 585; *nom. correct.* ex Acanthoceratidés de Grossouvre, 1894).

Family FORBESICERATIDAE Wright, 1952, p. 220

(*nom. transl.* Wright 1955, p. 573; ex Forbesiceratinae Wright, 1952, p. 220)

Genus FORBESICERAS, Kossmat, 1897, p. 125

(*pro Discoceras* Kossmat, 1895, p. 179 (83) (*non* Barrande, 1867, p. 177); *Cenomanites* Haug, 1898, p. 78; *Neopulchellia* Collignon, 1929, p. 5)

Type species. *Ammonites largilliertianus* d'Orbigny, 1841 (p. 320, pl. 95), by subsequent designation of Diener (1925, p. 180).

Forbesiceras brundrettei (Young, 1958)

Plate 1, figs. 15 and 16, 20, 23, 24

- 1958 *Neopulchellia brundrettei* Young, p. 289, pl. 39, figs. 1–3; 26–28, 33, 35–38; pl. 40, figs. 6, 9, 11; text-figs. 1f, i, k, m.
 1959 *Neopulchellia brundrettei* Young; Young, pl. 1, figs. 4, 7 and 8; pl. 3, fig. 4.
 1978 *Forbesiceras brundrettei* (Young); Young and Powell, p. 15, pl. 3, figs. 1, 2, 6.
 1983 *Forbesiceras brundrettei* (Young); Hook and Cobban, p. 52.
 1984 *Forbesiceras brundrettei* (Young); Wright and Kennedy, p. 92.

Type. Holotype is TMM 10734, the original of Young 1958, pl. 39, figs. 35–37, from the base of the Boquillas Formation on the north-east flank of the Davis Mountains in Jeff Davis County, Trans-Pecos Texas.

Material. USNM 424120–424122 from USGS locality 14592, old brickpit on Cloice Branch 1.3 km (0.8 miles) east of South Bosque, McLennan County. One specimen from USGS locality 14598, 0.8 km (0.5 mile) east of South Bosque, near railroad, McLennan County. Probably from the Pepper Shale, *F. brundrettei* zone.

Discussion. *F. brundrettei* is a highly distinctive species, characterized by its crowded flexuous, sometimes bidichotomous ribs, terminating at ventral clavi on either side of a smooth venter, features that distinguish it from *Forbesiceras* species described by Wright and Kennedy (1984). The present specimens show the mature character of weakening and crowding of ribs at disparate sizes, which we take to indicate dimorphism.

Occurrence. *F. brundrettei* zone of central and Trans-Pecos Texas only.

Forbesiceras cf. *chevillei* (Pictet and Renevier, 1866)

Plate 1, figs. 21 and 22

compare:

- 1866 *Ammonites chevillei* Pictet and Renevier, p. 102, pl. 4, fig. 2.
 1984 *Forbesiceras chevillei* (Pictet and Renevier, 1866); Wright and Kennedy, p. 93, pl. 13, fig. 2; pl. 15, figs. 1 and 2; text-fig. 17.

Material. USNM 420211 from the basal shell bed of the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group on Bird Creek, 4.4 km (2.75 miles) north-east of the Leon River Bridge, south-east of Interstate 35, Bell County. *Acanthoceras bellense* zone.

Description. Specimen is a wholly septate fragment with a maximum preserved whorl height of 17.5 mm, the whorl section compressed with greatest breadth just outside the umbilical shoulder, the inner flanks broadly rounded, the outer flattened and convergent, the venter narrow and flat. There are very distant, narrow, prorsiradiate ribs on the inner to middle flank; broad, flat concave ribs on the outer flank are an estimated 4–5 times as numerous and terminate in pronounced ventral clavi, linked across the venter by a broad, rounded transverse rib.

Discussion. The distinctive ornament of this fragment matches that of the early stage of *F. chevillei*, with which it is compared (e.g. Wright and Kennedy 1984, pl. 15, fig. 1).

Occurrence. As for material *F. chevillei* is known from southern England, Spain, Switzerland, Turkmenian SSR, Nigeria, Madagascar and Zululand. It ranges from lower to lower middle Cenomanian *Mantelliceras mantelli* to *Acanthoceras rhotomagense* zones of the European standard.

Forbesiceras conlini Stephenson, 1953a

1953a *Forbesiceras conlini* Stephenson, p. 205, pl. 56, fig. 1; pl. 57, figs. 2–6.

Types. Holotype is USNM 105987, the original of Stephenson 1953a (pl. 57, figs. 5 and 6); there are two paratypes, all from the Tarrant Formation, branch of Big Bear Creek, 2.4 km (1.5 miles) east of Euless, Tarrant County. *Conlinoceras tarrantense* zone.

Discussion. We have nothing to add to Stephenson's careful account of this species. It most closely resembles *F. baylissi* Wright and Kennedy, 1984 (p. 22, pl. 13, figs 4 and 5) but has much larger and stronger lateral tubercles.

Occurrence. As for types.

Family ACANTHOCERATIDAE de Grossouvre, 1894, p. 22.

(*nom. correct.* Hyatt, 1900, p. 585; *ex* Acanthoceratidés de Grossouvre, 1894, p. 22).

Subfamily ACANTHOCERATINAE de Grossouvre, 1894, p. 22.

(*nom. correct.* Hyatt, 1900, p. 585; *ex* Acanthoceratidés de Grossouvre, 1894; *nom. transl.* Wright and Wright, 1951, p. 28 *ex* Acanthoceratidés de Grossouvre).

Genus ACANTHOCERAS Neumayr, 1875, p. 929

(= *Metacanthoplites* Hyatt, 1900, p. 589 (objective synonym); *Alternacanthoceras* Marciniowski, 1979, p. 61)

Type species. *Ammonites rhotomagensis* Brongniart, 1822, pp. 83, 391, pl. 6, fig. 2, by the subsequent designation of de Grossouvre, 1894, p. 27.

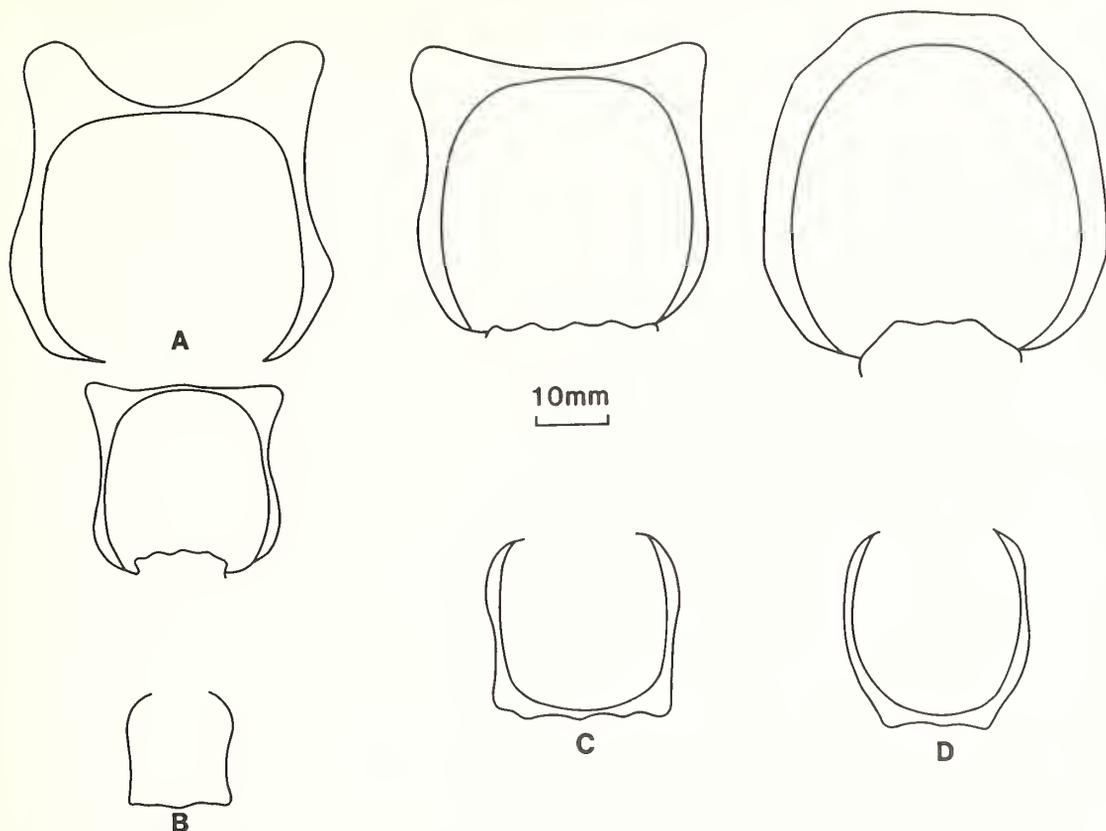
Acanthoceras bellense Adkins, 1928

Plate 2, figs. 24, 25, 29, 30; Plate 9, figs. 31 and 32; Plate 12, figs. 4, 7; text-figs. 5A, C, 6C, 7–10.

1928 *Acanthoceras bellense* Adkins, p. 245, pl. 30, figs. 1 and 2.

1928 *Acanthoceras stephensoni* Adkins, p. 246, pl. 31, figs. 1 and 2.

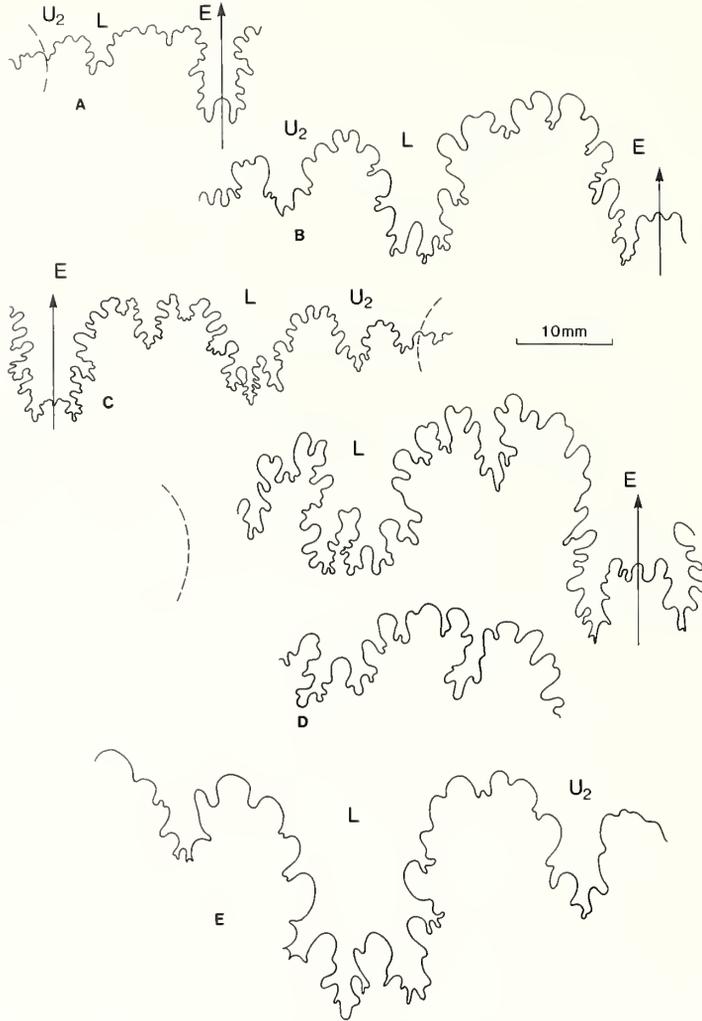
1928 *Acanthoceras* n. sp. 6 aff. *Cunningtoni* var. *cornutum* Kossmat, 1895; Adkins, p. 247, pl. 5, fig. 1.



TEXT-FIG. 5. Whorl sections of: A and C, *Acanthoceras bellense* Adkins, 1928, TMM 19803, 4211; B, *Acanthoceras amphibohum* Morrow, 1935, USNM 104971, D, *Confinoceras tarrantense* (Adkins, 1928), TMM 2424.

- ?1928 *Acanthoceras* n. sp. 7. Adkins, p. 247.
 1942 *Acanthoceras* aff. *rhotomagense* (Defrance); Moreman, p. 201.
 1942 *Acanthoceras* aff. *hunteri* Kossmat; Moreman, p. 203.
 1942 *Acanthoceras validum* Moreman, p. 203, pl. 32, fig. 1; text-fig. 2 j.
 1942 *Acanthoceras* aff. *sherborni* Spath; Moreman, p. 203, pl. 32, fig. 3; text-fig. 29.
 1942 *Acanthoceras bellense* Adkins; Moreman, p. 203.
 1942 *Acanthoceras stephensoni* Adkins; Moreman, p. 204.
 1942 *Acanthoceras* aff. *cunningtoni* (Sharpe); Moreman, p. 204.
 1942 *Acanthoceras* aff. *cunningtoni* var. *cornutum* Kossmat; Moreman, p. 204.
 1942 *Acanthoceras pepperense* Moreman, p. 204, pl. 32, fig. 5; text-fig. 2 m.
 1959 *Acanthoceras* n. sp. aff. *A. turneri* White, Adkins; Matsumoto, p. 84, text-fig. 37.
 1959 *Acanthoceras* sp. Matsumoto, p. 84 (?pars), ? text-fig. 38.
 1959 *Acanthoceras pepperense* Moreman; Matsumoto, p. 86, text-fig. 39.
 1959 *Acanthoceras* n. sp. Adkins; Matsumoto, p. 86.
 1978 *Euomphaloceras lonsdalei* Adkins; Young and Powell, pl. 5, fig. 7 only, non pl. 7, fig. 1.
 1987 *Acanthoceras bellense* Adkins, 1928; Wright and Kennedy, p. 190, text-fig. 66a.
 1987b *Acanthoceras bellense* Adkins; Cobban, p. 5, pl. 1, figs. 18, 19; pl. 2, figs. 1–29; text-fig. 5.

Types. The holotype of *Acanthoceras bellense* Adkins, 1928 (p. 245, pl. 30, figs. 1 and 2) is TMM 34034, by original designation. The holotype of *Acanthoceras stephensoni* Adkins, 1928 (p. 246, pl. 31, figs. 1 and 2) is TMM 34033, by original designation. The holotype of *Acanthoceras validum* Moreman, 1942 (p. 203, pl. 32, fig. 1; text-fig. 2j) is TMM 19802, by original designation. The holotype of *Acanthoceras pepperense* Moreman,



TEXT-FIG. 6. External sutures. A, *Tarrantoceras sellardsi* (Adkins, 1928), USNM 400771. B and E, *Acanthoceras amphibolum* Morrow, 1935, USNM 105971, 8629. C, *Acanthoceras bellense* Adkins, 1928, USNM 388109. D, *Conlinoceras tarrantense* (Adkins, 1928), USNM 105962.

1942 (p. 204, pl. 32, fig. 5; text-fig. 2 m) is TMM 19803, by original designation. All are from the basal shell bed of the Bluebonnet Member on Bird Creek at its intersection with the old Belton-Temple Highway, Bell County, *Acanthoceras bellense* zone.

Dimensions		D	Wb	Wh	Wb:Wh	U
USNM 420212	c	57.5 (100)	29.0 (50.4)	23.5 (40.8)	1.23	18.2 (31.7)
holotype	c	87.5 (100)	— (—)	38.2 (43.7)	—	24.5 (28.0)
USNM 420213	c	113 (100)	56.5 (50.0)	50.5 (44.7)	1.12	31.2 (27.6)
	ic		50.5 (—)	49.0 (—)	1.03	

Description. Coiling fairly evolute, umbilicus comprising around 30% of diameter, of moderate depth, with rounded wall. Whorls massive, slowly expanding. Intercostal whorl section depressed trapezoidal with greatest breadth just outside umbilical shoulder, inner flanks rounded, outer flanks flattened, convergent, ventrolateral



TEXT-FIG. 7. *Acanthoceras bellense* Adkins, 1928. TMM 19802, the holotype of *Acanthoceras validum* Moreman, 1942, a macroconch, from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Reduced $\times 0.6$.

shoulders broadly rounded, venter flattened. At the smallest diameters visible, in the umbilical region of larger specimens, flank ornament consists of bullate primary ribs alternating with shorter ribs or non-bullate primaries, the ribs totalling 8–9 per half whorl. In middle growth all the ribs are long, from a whorl height of 12 mm approximately. In middle growth ornament is highly variable. The holotype represents the feebly ornamented extreme, specimens like those referred to as *Acanthoceras* aff. *sherborni* by Moreman (1942, pl. 32, fig. 3) the robustly ornamented extreme. Most specimens have 17–20 primary ribs per whorl. These ribs arise at the umbilical seam, are broad and distant, and strengthen into weak (Pl. 2, fig. 24) to strong (Pl. 2, fig. 30) bullae, perched just outside the umbilical shoulder. The bullae give rise to straight, broad, prorsiradiate ribs, weak (Pl. 2, fig. 24) to strong (Pl. 2, fig. 30), which terminate in inner ventrolateral tubercles that are initially clavate but become conical and horn-like as size increases. A broad, low rib connects these to a clavate outer ventrolateral tubercle, corresponding to which is a clavate siphonal tubercle, borne on a low siphonal ridge. Occasional specimens may show a non-tuberculate ventral intercalatory. In the holotype the ribbing becomes progressively wider spaced as size increases, and the umbilical bulla weakens and moves out to an inner flank position, while growth lirae and striae are prominent on the well-preserved shell surface. This same outward migration is shown by robustly ornamented individuals (Pl. 2, fig. 30) and is a characteristic of middle growth. At the same time, the rib linking inner and outer ventrolateral tubercles strengthens, and the siphonal clavi decline. Ultimately, the mature phragmocone develops a highly characteristic section, with inflated inner flanks in costal section, concave mid- to outer flanks and a flat-topped horn produced by coalescence of inner and



TEXT-FIG. 8. *Acanthoceras bellense* Adkins, 1928. TMM 34033, the holotype of *Acanthoceras* n. sp. of Adkins, 1928, from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Natural size.

outer ventrolateral tubercles. The venter is depressed between these horns, with a low siphonal ridge persisting. On the adult body chamber, this ornament is progressively modified; umbilical bullae migrate out to mid-flank and decline, the rib flaring at their site, while the flat-topped horn changes into a pointed, outward-directed projection with an evenly concave ventral region between. The holotype of *Acanthoceras validum* Moreman, 1942 (text-fig. 7) seems to be an incomplete adult macroconch with a maximum preserved costal whorl height of 111 mm, the original of *Acanthoceras* n. sp. of Adkins (1928, pl. 27, fig. 2), an incomplete microconch with a costal whorl height of 72 mm at the base of the body chamber.

Suture line (text-fig. 6C) with broad bifid E/L, narrower L and broad L/U₂.



TEXT-FIG. 9. *Acanthoceras bellense* Adkins, 1928. TMM 34033, the holotype of *Acanthoceras stephensoni* Adkins, 1928, from the base of the Bluebonnet Member on Bird Creek in Bell County. Reduced $\times 0.75$.

Discussion. Numerous names have been applied to *Acanthoceras* from the base of the Bluebonnet Member in Bell County. Given the normal range of variation shown by acanthoceratines (Wright and Kennedy 1987) and the continuous variation shown by the present assemblage, it is apparent that the holotype of *A. bellense* (Pl. 9, figs. 31 and 32) is a feebly ornamented juvenile, the holotype of *A. stephensoni* (text-fig. 9) a robustly ornamented adult macroconch phragmocone, the holotype of *A. pepperense* (text-fig. 10) a near complete adult microconch and the holotype of *A. validum* (text-fig. 7) an adult macroconch with some body chamber. All these are linked by the same pattern of tubercles and rib development and siphonal ridge; apparent differences reflect variation and dimorphism alone.

Individuals of the *A. bellense* fauna from central Texas show superficial resemblances to the equally variable *Acanthoceras rhotomagense* faunas of western Europe and the *Acanthoceras flexuosum* (Crick, 1907) group from South Africa, but adults are easily distinguished and population structures are different, as discussed by Wright and Kennedy (1987, pp. 189–190).

The siphonal ridge and occasional intercalated ventral ribs, plus traces of looped riblets between ventral horns shown by some of the present specimens that are referred to *A. bellense* (e.g. USNM

420213) are features that develop consistently in *Cunningtoniceras* Collignon, 1937. Co-occurring *Cunningtoniceras lonsdalei* (Adkins, 1928, p. 244, pl. 26, fig. 5; pl. 27, fig. 3; see p. 121 herein) is probably derived from *A. bellense*, just as *C. inerme* (Pervinquier, 1907) is derived from *Acanthoceras rhotomagense* (Brongniart, 1822). Juvenile *C. lonsdalei* are easily separated from juvenile *A. bellense*: the former have 1 or 2 ventral clavi corresponding to 1 outer ventrolateral on the primary ribs and 2 ventral ribs intercalated between primaries, each with siphonal and, in some cases, outer ventrolateral tubercles.

Occurrence. *Acanthoceras bellense* zone, known only from central Texas and eastern Wyoming.

Acanthoceras amphibolum (Morrow, 1935)

Plate 3, figs. 1–5; Plate 4, figs. 1–17; text-figs. 5B, 6B and E, 11–14

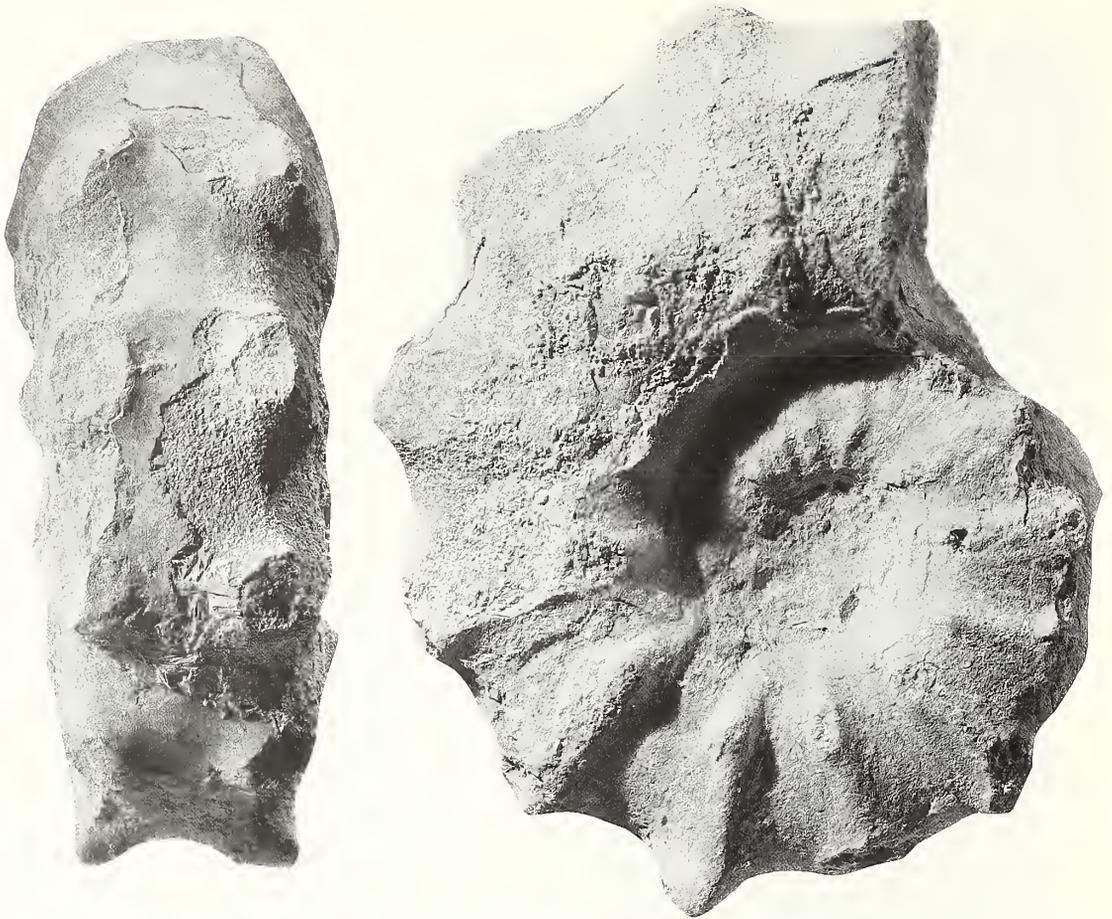
- 1877 *Ammonites loevianus* White, p. 201, pl. 19, fig. 1.
 1935 *Acanthoceras? amphibolum* Morrow, p. 470, pl. 49, figs. 1–4; 6; pl. 51, figs. 3 and 4; text-fig. 4.
 1942 *Acanthoceras alvaradoense* Moreman, p. 205, pl. 32, fig. 6; text-figs. 2o and t.
 1953a *Acanthoceras hazzardi* Stephenson, p. 201, pl. 48, figs. 1 and 2; pl. 49, fig. 4.
 1955 *Euomphaloceras alvaradoense* (Moreman); Stephenson, p. 63, pl. 7, figs. 1–9.
 1960 *Acanthoceras amphibolum* Morrow; Matsumoto, p. 41, text-fig. 5b–d.
 1960 *Acanthoceras hazzardi* Stephenson; Matsumoto, p. 41, text-fig. 5a.
 1960 *Acanthoceras alvaradoense* Moreman; Matsumoto, p. 41, text-fig. 6a–c.
 1963 *Paracanthoceras amphibolum* (Morrow); Haas, p. 18.
 1964 *Plesiakanthoceras [amphibolum]* (Morrow); Haas, p. 610.
 1965 *Plesiakanthoceras amphibolum* (Morrow); Hattin, pl. 4, figs. J and K; pl. 5, figs. C–F.
 1965 *Plesiakanthoceras amphibolum* (Morrow); Hattin, text-fig. 3 (8).
 1966 *Acanthoceras amphibolum* Morrow; Matsumoto and Obata, p. 45, text-figs. 4–6.
 1966 *Acanthoceras hazzardi* Stephenson; Matsumoto and Obata, p. 45, text-fig. 7.
 1968 *Plesiakanthoceras [amphibolum]* Morrow; Laporte, text-fig. 6–10H.
 1969 *Acanthoceras amphibolum* Morrow; Matsumoto, Muramoto and Takahashi, p. 226, pl. 31, fig. 1a and b.
 1973 *Acanthoceras amphibolum* Morrow; Cobban and Scott, p. 65 (*pars*).
 1977a *Acanthoceras alvaradoense* Moreman; Cobban, p. 24, pl. 6, figs. 1–7, 11–20; text-fig. 6.
 1977b *Acanthoceras alvaradoense* Moreman; Cobban, p. 219, figs. 3A–I.
 1977b *Acanthoceras amphibolum* Morrow; Cobban, p. 219, figs. 4N–Q.
 1977 *Acanthoceras amphibolum* Morrow; Hattin, p. 183, fig. 13.
 1978 *Acanthoceras amphibolum* Morrow; Hattin and Siemers, fig. 5 (14).
 1979 *Acanthoceras alvaradoense* Moreman; Merewether, Cobban, and Cavanaugh, pl. 1, figs. 3–7.
 1985 *Acanthoceras amphibolum* Morrow; Zaborski, p. 35, figs. 38–41.
 1987b *Cunningtoniceras amphibolum* (Morrow); Cobban, p. 9, pls. 4–8, pl. 9, figs. 48–63.
 1988 *Acanthoceras amphibolum* Morrow; Kennedy, Cobban and Hook, p. 38, figs. 1w–z, cc–ff, 2a and b.

EXPLANATION OF PLATE 3

Figs. 1–5. *Acanthoceras amphibolum* (Morrow, 1935). 1–3, USNM 420223, a topotype of *Acanthoceras hazzardi* Stephenson, 1953a, from USGS locality 18975, headwater branch of Walnut Creek, 0.5 km (0.3 mile) north of Gordonville, Grayson County, from the Lewisville Member, *Acanthoceras amphibolum* zone. 4 and 5, the holotype of *Ammonites loevianus* White, 1877 (p. 201, pl. 19, fig. 1), USNM 8629, from Ojo de los Cuervas, New Mexico. Specimen is inferred to be from the Paguate Tongue of the Dakota Sandstone.

All figures are $\times 1$.



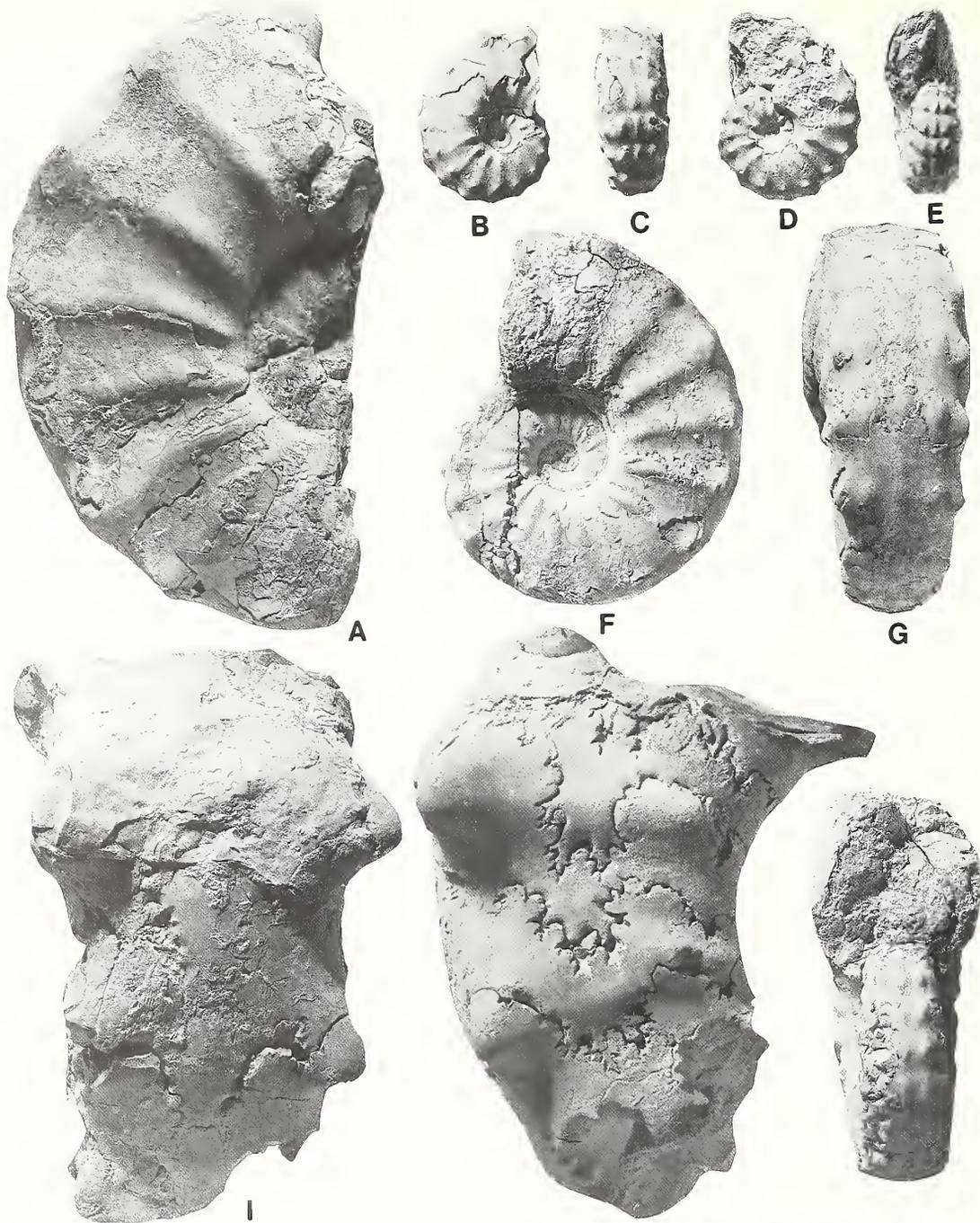


TEXT-FIG. 10. *Acanthoceras bellense* Adkins, 1928. TMM 19803, the holotype of *Acanthoceras pepperense* Moreman, 1942, from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Reduced $\times 0.65$.

EXPLANATION OF PLATE 4

Figs. 1–17. *Acanthoceras amphibolum* (Morrow, 1935). 1 is USNM 420224, from USGS locality 13577, branch south of Belton-Temple Road, 1.6 km (1 mile) east of Midway Church, Bell County. Note striking intercalated ventral ribs. Bluebonnet Member (inferred). 2 and 3, USNM 420217; 4–6, USNM 420216; 7, USNM 420225; 8, USNM 420227; 9–11, USNM 420226; 12–14, USNM 420230, concretions in gully in cotton field 1.6 km (1 mile) north of Lillian, west of Lillian–Retta road, Johnson County. 15, USNM 420228, from 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) north-east of town square in Alvarado, Johnson County. 16 and 17, USNM 420229, from USGS Mesozoic locality D12626, loose concretion, 8.9 km (5.5 mile) north-east of Mansfield, Tarrant County. All basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone. Figures 7–11 are $\times 2$; the remainder are $\times 1$.





TEXT-FIG. 11. *Acanthoceras amphibolum* Morrow, 1935. A, B-E, I, J, paratypes, F-H the holotype, all from the Graneros Shale on the south bank of the Smoky Hill River, south of Wilson, Kansas, all in the collections of the Geology Museum of the University of Kansas, and figured natural size.

Types. Lectotype, here designated, is the original of Morrow (1935, pl. 49, fig. 3) from the Graneros Shale near Wilson, Kansas, as are four figured syntypes (text-fig. 11). All middle Cenomanian *Acanthoceras amphibolum* zone. Specimens are in the University of Kansas and USNM Collections. The holotype of *Acanthoceras alvaradoense* Moreman, 1942 (p. 205, pl. 32, fig. 6; figs. 20 o and t) is TMM 19801, from the basal Eagle Ford Group (termed Tarrant by Moreman, 1942) 6.4 km (4 miles) south of Alvarado in Johnson County (text-fig. 12).

The holotype of *Acanthoceras hazzardi* Stephenson, 1953a is USNM 105971 from the Lewisville Member of the Woodbine Formation, headwater of Walnut Creek, 0.5 km (0.3 mile) north of Gordonville, Grayson County. All *Acanthoceras amphibolum* zone.

Material. Numerous specimens in the USGS, USNM and OUM Collections from concretions low in the Eagle Ford Group notably at USGS Mesozoic locality D12626, 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County; USGS D9502, concretions in field 0.3 miles north-north-west of Lillian, Johnson County; USGS 11740, 14580, 14582, Walnut Creek, Tarrant County; USGS 14583, field 4 km (2.5 miles) north-east of Alvarado, Johnson County; USGS 24510, 1.6 km (1 mile) north of Lillian, Johnson County; east of Old Highway, 6.4 km (4 miles) south of Alvarado, Johnson County. All middle Cenomanian *Acanthoceras amphibolum* zone. A topotype (USNM 420223) of *Acanthoceras hazzardi* is from USGS Locality 18975 (see above for details).

<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
USNM 420216	c	33.4 (100)	15.0 (44.9)	14.8 (44.3)	1.01	7.3 (21.9)
USNM 420217	c	35.6 (100)	17.0 (47.8)	16.8 (47.2)	1.01	7.4 (20.8)
USNM 420218	c	45.0 (100)	20.4 (45.3)	20.2 (44.9)	1.0	9.5 (21.1)
USNM 420219	c	93.2 (100)	40.0 (42.9)	41.3 (44.3)	0.97	28.3 (30.4)
	ic	91.0 (100)	35.5 (39.0)	37.3 (41.0)	0.95	28.3 (31.1)
USNM 420220	c	166 (100)	68.0 (41.0)	68.5 (41.3)	0.99	49.0 (29.5)
	ic	160 (100)	60.5 (37.8)	63.5 (39.7)	0.95	49.0 (30.6)
USNM 420221	c	133 (100)	56.0 (42.1)	54.0 (40.6)	1.04	45.5 (34.2)
(adult microconch)	ic	125 (100)	47.5 (38.0)	47.0 (37.6)	1.01	45.5 (36.4)

Description. Very small specimens match those illustrated by Cobban (1977a, 1987b). At a diameter of 12 mm they have 17–19 ribs per whorl, alternately long and short, the primaries feebly bullate or not, with conical inner ventrolateral and clavate outer ventrolateral and siphonal tubercles on all ribs; there are prominent constrictions. As size increases, the ribs are differentiated markedly, with 14–17 primary ribs per whorl. These arise at feeble umbilical bullae, are straight and prorsiradial, with a strong conical inner ventrolateral tubercle and clavate outer ventrolateral and siphonal tubercles on a broad transverse rib. Between are short intercalated ventral ribs, 1 or sometimes 2 in number, with outer ventrolateral and siphonal tubercles only, and sometimes with only siphonals. A pronounced siphonal ridge links tubercles at this stage. These secondary ribs disappear by 40–50 mm diameter, although there may be a trace of the siphonal clavi, and a marked siphonal ridge. Thereafter, the outer ventrolateral clavi decline, and the inner ventrolaterals strengthen into a clavate horn, sometimes linked across the venter to the corresponding horn by a pair of feeble riblets. The horns strengthen through late ontogeny, so that the outer whorls of adults have 12–14 distant primary ribs, effaced at mid-flank, with bullae that migrate from umbilical to inner lateral position, strong ventrolateral horns with a markedly concave venter in intercostal section, the venter smooth but for a low siphonal ridge and feeble riblets looping between horns or intercalating (text-figs. 13 and 14).

There are few adults in the present collections. A complete microconch USNM 420221 is 133 mm in diameter; the ornament described above extends onto the adult body chamber, with the final rib strengthened markedly to give a broad ventral flange instead of the concavity of the preceding ribs. A fragmentary macroconch (USNM 420222) shows exactly the same adult modification; with a whorl height of over 100 mm, its estimated diameter was 330 mm.

Suture line with broad bifid E/L narrower L and broad L/U₂ (text-fig. 6B and E).

Discussion. *Acanthoceras alvaradoense* and *hazzardi* are clear synonyms of *A. amphibolum*. Two subspecies of *A. amphibolum* can be recognized; all the present material belongs to the earlier form, *A. amphibolum amphibolum*. The late form, *A. amphibolum fallense* Cobban, 1987b, lacks multiplication of ventral ornament and has ventrolateral and siphonal tubercles that are clavate rather than nodate. The multiplication of ventral ribbing on juveniles of the older form of



TEXT-FIG. 12. *Acanthoceras amphibolum* Morrow, 1935. TMM 19801, the holotype of *Acanthoceras alvaradoense* Moreman, 1942, from the basal part of the Eagle Ford Group 6.4 km (4 miles) south of Alvarado, Johnson County. Natural size.

Acanthoceras amphibolum prompted Cobban (1987b) to assign the species to *Cunningtoniceras* Collignon, 1937 which has this type of ornament. The present authors now believe that there are separate lineages of *Cunningtoniceras* and *Acanthoceras*, and that *amphibolum*, although not typical, is best assigned to *Acanthoceras*. *A. amphibolum* evolved from *A. bellense*. They differ most obviously in the much earlier loss of differentiated inner and outer ventrolateral tubercles in *A. amphibolum*, where a massive horn develops, and the equally early loss of the siphonal tubercles.

Ammonites loevianus White, 1877 (p. 201, pl. 19, fig. 1) the original of which is shown as Pl. 3, figs. 4 and 5, is an *Acanthoceras amphibolum*, from Ojo de los Cuervas, New Mexico. The name has never been used since White's original account and should be suppressed under the plenary powers of the International Commission on Zoological Nomenclature to whom application has been made.

Occurrence. *Acanthoceras amphibolum* zone. Trans-Pecos and central Texas, New Mexico, Kansas, Colorado, Wyoming, South Dakota, Montana. Middle Cenomanian of Japan and Nigeria.



TEXT-FIG. 13. *Acanthoceras amphibolum* Morrow, 1935. USNM 420220, from the basal part of the Eagle Ford Group, 1.6 km (1 mile) north of Lillian and west of the Lillian-Retta road, Johnson County. Reduced $\times 0.8$.

Genus CALYCO CERAS Hyatt, 1903, p. 589

(= *Metacalycoceras* Spath, 1926a, p. 83; ICZN rejected name no. 1265)

Type species. ICZN Opinion 557, 1959, name no. 1633; *Ammonites navicularis* Mantell, 1822 (p. 198, pl. 22, fig. 5).

Subgenus NEWBOLDICERAS Thomel, 1972, p. 105.

Type species. *Acanthoceras newboldi* Kossmat, 1897, p. 5 (112), pl. 1(12), figs. 2, 3; pl. 3(14), fig. 2, by original designation.



TEXT-FIG. 14. *Acanthoceras amphibolum* Morrow, 1935. USNM 420231, from the basal part of the Eagle Ford Group, 1.6 km (1 mile) north of Lillian and west of the Lillian–Retta road, Johnson County. Reduced $\times 0.8$.

Calycoceras (Newboldiceras) sp.

Plate 11, figs. 3 and 4

- 1928 *Acanthoceras* n. sp. 2 (aff. *turneri* C. A. White); Adkins, p. 246, pl. 30, figs. 3 and 4.
 1942 *Acanthoceras* aff. *turneri* White, Adkins; Moreman, p. 202.
 1959 *Acanthoceras* n. sp. aff. *turneri* White, Adkins; Matsumoto, p. 84, text-fig. 37.

Material. TMM 34032, from the basal shell bed of the Bluebonnet Member, Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.

Discussion. What appears to be the only *Newboldiceras* known from the Gulf Coast region is a fragmentary specimen 110 mm in diameter. There are 12–13 ribs per half whorl, all of them long and extending from the umbilical shoulder, showing weak differentiation into feebly bullate and non-bullate, with blunt inner and clavate outer ventrolateral tubercles, the venter crossed by broad, bar-like ribs with a trace of a siphonal clavus. It most closely resembles *C. (N.) newboldi* (Kossmat, 1897, p. 5(112), pl. 1(12), figs. 2 and 3; pl. 3(14), fig. 2), but has a much lower rib density, 12–13

per half whorl versus 20 in the type material at comparable diameters. The Texas specimen is left in open nomenclature at this time.

Occurrence. As under material.

Genus *CONLINOCERAS* Cobban and Scott, 1973, p. 61

Type species. *Calycoceras (Conlinoceras) gilberti* Cobban and Scott, 1973 (p. 61, pl. 1; pl. 2, figs. 5–9, 13–18; pl. 3, figs. 5–7, 11; text-figs. 23 and 24).

Discussion. *Conlinoceras* was originally proposed as a subgenus of *Calycoceras*. The inner whorls of the type species are, however, quite distinct from those of the early subgenera of *Calycoceras*, rather being identical in style of ornament (notably the clavate ventral and ventrolateral tuberculation) and whorl section with *Acanthoceras rhotomagense* (e.g. Pl. 7, figs. 1–13, 23–25). Some middle growth stages of *Conlinoceras tarrantense* (Adkins, 1928) were actually placed in the synonymy of *A. rhotomagense* by Kennedy and Hancock (1970). In contrast, the outer whorls, with their rounded section, loss of tubercles and alternately long and short distant ribs (Pl. 5, figs. 1 and 2) are homoeomorphous with those of *Calycoceras (Proeucalycoceras)* Thomel, 1972. On the evidence of the inner whorls, we regard *Conlinoceras* as an independent genus allied to *Acanthoceras* and endemic to the US Western Interior and Gulf Coast Region.

Conlinoceras tarrantense (Adkins, 1928)

Plate 5, figs. 1–5; Plate 6, figs. 7–12; Plate 7, figs. 1–13, 15, 23–25; text-figs. 5D, 6D, 15–17.

- 1893 *Buchiceras inaequiplicatus* Shumard (probably in part); Cragin, p. 233.
 ?1927 *Acanthoceras rotomagense* (Defrance); Scott, p. 617, pl. 2, figs. 1 and 2.
 1927 *Acanthoceras* aff. *rhotomagense* (Defrance); Moreman, p. 92, pl. 13, fig. 1.
 1928 *Metacalycoceras (?) tarrantense* Adkins, p. 241, pl. 28, fig. 3; pl. 29, fig. 1.
 1928 *Acanthoceras wintoni* Adkins, p. 243, pl. 25, figs. 2 and 3.
 1942 *Acanthoceras wintoni* Adkins; Moreman, p. 202.
 1942 *Acanthoceras inaequiplicatum* (Adkins); Moreman, p. 201, pl. 32, fig. 2.
 1951 *Acanthoceras tarrantense* (Adkins); Adkins and Lozo, pl. 2, fig. 2.
 1953a *Acanthoceras tarrantense* (Adkins); Stephenson, p. 198, pl. 45, figs. 9 and 10; pl. 46, figs. 2–4.
 1953a *Acanthoceras tarrantense nitidum* Stephenson, p. 199, pl. 50, figs. 5 and 6.
 1953a *Acanthoceras wintoni* Adkins; Stephenson, p. 200, pl. 45, figs. 7 and 8; pl. 46, fig. 1; pl. 47, figs. 1 and 2.
 1970 *Acanthoceras wintoni* Adkins; Kennedy and Hancock, p. 487.
 1973 *Calycoceras (Conlinoceras) tarrantense* (Adkins); Cobban and Scott, p. 62.
 1973 *Acanthoceras adkinsi* Stephenson; Cobban and Scott, p. 62.
 1977a *Calycoceras (Conlinoceras) tarrantense* (Adkins); Cobban, p. 22, pl. 3, fig. 9; pl. 4, figs. 1–3, 6.
 1977b *Calycoceras (Conlinoceras) tarrantense* (Adkins); Cobban, p. 219, fig. 21.
 1978 *Conlinoceras tarrantense* (Adkins, 1928); Young and Powell, pl. 4, figs. 1, 5.

Types. Holotype of *C. tarrantense* is TMM 2424, from the Tarrant Formation '2 miles (not more than 1.5 miles) east of Tarrant Station, Tarrant County'. The holotype of *C. tarrantense nitidum* Stephenson, 1953a is USNM 105965, from the Tarrant Formation 14.5 km (9 miles) north of Arlington, Tarrant County. The holotype of *Acanthoceras adkinsi* Stephenson, 1953a is USNM 105968, from the Tarrant Formation, on a branch north of Chicago, Rock Island and Pacific Railroad, 1.6 km (1 mile) west of Dallas County Line, Tarrant County. The holotype of *Acanthoceras wintoni* Adkins, 1928 is TMM 2426, from the Tarrant Formation on Big Bear Creek, 4.8 km (3 miles) north-east of Tarrant Station, Tarrant County. All *Conlinoceras tarrantense* zone.

Name of species. Under the Rules of the International Commission on Zoological Nomenclature, *tarrantense* and *adkinsi* of Adkins are deemed to have been published simultaneously. As first revising authors Cobban and Scott (1973, p. 62) selected the name *tarrantense*.

<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
USNM 420232	c	13.2 (100)	7.5 (56.8)	6.1 (46.2)	1.23	2.1 (15.9)
USNM 420233	c	21.2 (100)	10.7 (50.5)	10.1 (47.6)	1.06	— (—)
USNM 420234	c	25.0 (100)	14.2 (56.8)	12.4 (49.6)	1.15	4.2 (16.8)
USNM 420235	c	27.2 (100)	16.8 (61.8)	13.0 (47.8)	1.29	5.3 (19.5)
USNM 420236	c	29.5 (100)	16.2 (54.9)	15.6 (52.9)	1.04	4.9 (16.6)
USNM 420237	c	29.7 (100)	17.0 (59.9)	15.0 (50.5)	1.13	— (—)
USNM 420238	c	32.0 (100)	16.5 (51.6)	16.5 (51.6)	1.0	5.9 (18.4)
USNM 420239	c	40.4 (100)	21.0 (50.7)	19.9 (49.3)	1.06	8.9 (22.0)
USNM 420240	c	47.2 (100)	— (—)	23.3 (49.4)	—	9.6 (20.3)
USNM 420241	c	49.8 (100)	26.0 (52.2)	23.6 (47.4)	1.13	10.7 (21.5)
USNM 420242	c	56.1 (100)	23.4 (41.7)	24.9 (44.4)	0.93	11.6 (20.7)
USNM 420243	c	60.8 (100)	33.2 (54.6)	26.4 (43.4)	1.26	14.2 (23.4)
USNM 420244	c	63.7 (100)	— (—)	28.5 (44.7)	—	14.7 (23.1)
USNM 420245	c	64.7 (100)	30.8 (47.6)	31.4 (48.5)	0.98	12.6 (19.5)
USNM 420246	c	66.2 (100)	30.9 (46.7)	28.9 (43.7)	1.07	13.4 (20.2)
USNM 420247	c	83.6 (100)	42.7 (51.5)	39.8 (47.6)	1.07	19.1 (22.8)
USNM 420248	c	101.2 (100)	49.7 (49.1)	45.4 (44.9)	1.09	27.4 (27.1)
USNM 420249	c	125.5 (100)	59.2 (47.2)	56.5 (45.0)	1.05	32.4 (25.8)
USNM 420250	c	146.0 (100)	60.0 (41.1)	62.0 (42.5)	0.97	41.2 (28.2)
USNM 420251	c	157.0 (100)	67.0 (42.7)	66.5 (42.4)	1.0	38.0 (24.2)
USNM 420252	c	205.0 (100)	80.5 (39.3)	90.0 (43.9)	0.89	61.0 (29.8)

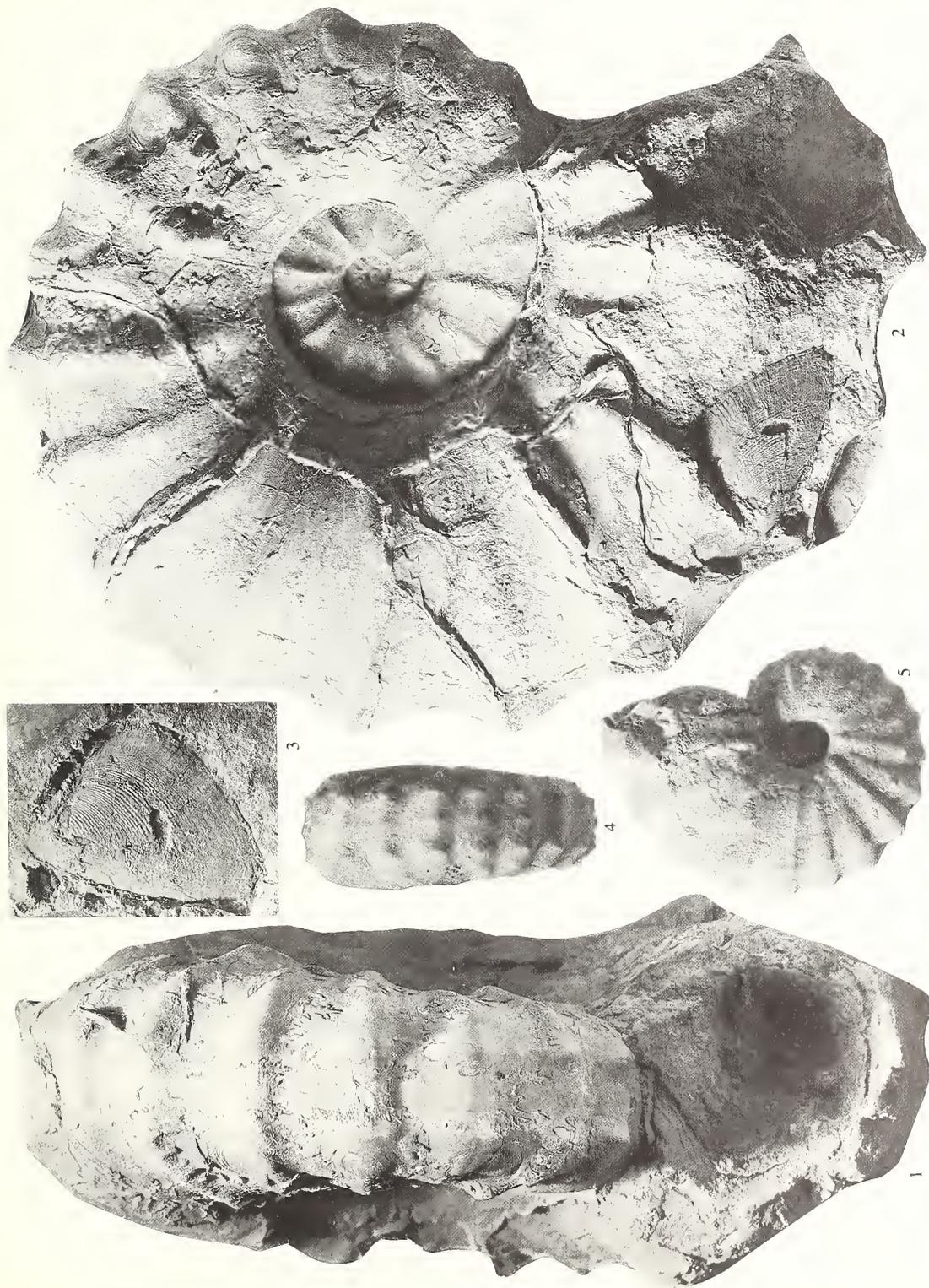
Material. More than 100 specimens from the Lewisville Member of the Woodbine Formation, in the Dallas-Fort Worth area and elsewhere in north-central Texas in the USNM, USGS, JPC and OUM Collections, not listed separately.

Description. The typical shell form and ornament of the middle growth stages are already present from 12 mm diameter and extend to approximately 100 mm diameter. Coiling is evolute, the umbilicus comprising 16–20% of diameter, the figure increasing through ontogeny. The whorl section varies from compressed to depressed (Wb:Wh varies from 1.23–0.98). The umbilicus is quite shallow, with a rounded umbilical wall on moulds, and a broadly rounded umbilical shoulder. The whorls are quadrate in intercostal section, with the greatest breadth below mid-flank, the sides and venter flattened, the ventrolateral shoulders broadly rounded. The costal section is trapezoidal in compressed forms, polygonal in depressed ones, with the greatest breadth at the umbilical bullae. Robust individuals have as few as 17 ribs per whorl, gracile ones up to 22. Primary and secondary ribs alternate very regularly. Primaries arise at the umbilical seam and strengthen into a weak to strong umbilical bulla which migrates outwards and declines in strength through ontogeny. In gracile specimens it may disappear at an early stage; in robust specimens it persists. Secondary ribs arise low on the flank. All ribs are straight and recti- to feebly prorsiradiate, and develop conical pointed inner ventrolateral tubercles. A low broad rib connects these to strong, long inner ventrolateral clavi, linked across the venter by a broad, low rib to significantly weaker siphonal clavi.

This ornament undergoes progressive modification in middle growth. The umbilical bullae decline at a variable rate, and migrate outwards to the inner flank. The ribs broaden and coarsen, the inner ventrolateral tubercles decline and ultimately disappear, the outer ventrolateral coarsening and persisting. The siphonal clavi also decline so that, by the beginning of the adult whorl there are none or only feeble umbilical bullae, strong ventrolateral clavi and none or only a trace of a weak siphonal clavus. The umbilical ratio increases progressively on the outer whorl, and the umbilical wall flattens markedly, so that the ribs appear to arise on the inner flank. They change from straight to feebly convex in many specimens, while the ventral ribbing

EXPLANATION OF PLATE 5

Figs. 1–5. *Conlinoceras tarrantense* (Adkins, 1928). 1–3, USNM 420253, from 2.4 km (1.5 miles) east of Euless, south bank of tributary to Big Bear Creek, Tarrant County. Note anaptychus in 2 and 3. 4 and 5, USNM 420240, from USGS locality 22614, 6.4 km (4 miles) south-east of Euless, Tarrant County. Both specimens are from the Tarrant Formation, *Conlinoceras tarrantense* zone. Figs. 3–5 are $\times 1$; figures 1 and 2 are reduced $\times 0.75$.





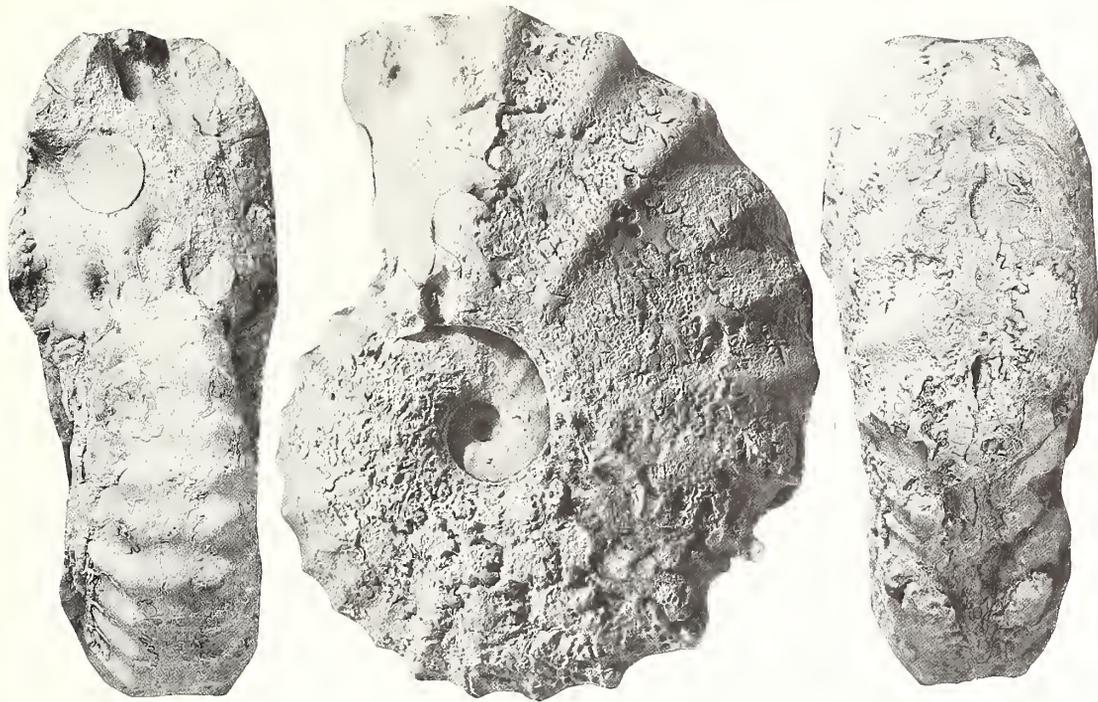
TEXT-FIG. 15. *Conlinoceras tarrantense* (Adkins, 1928). TMM 2426, the holotype of *Acanthoceras wintoni* Adkins, 1928, from the Tarrant Formation, Big Bear Creek, near Dallas County line, Tarrant County. Natural size.

strengthens on the body chamber so that the costal ventral profile changes from concave to tabulate with a strong bar-like rib crossing the venter, into which the ribs are progressively assimilated. The last few ribs of the adult body chamber weaken somewhat and crowd, and the venter becomes rounded. Specimens regarded as macroconchs (USNM 420252) are adult at up to 200 mm diameter. Adult microconchs are 150 mm diameter or less.

Suture line with broad, bifid E/L narrower L and broad L/U₂.

One adult, USNM 420253, preserves part of the jaw apparatus in the body chamber (Pl. 5, figs. 1 and 2). The shell is 185 mm in diameter, the lower jaw 40 mm long at the symphysis, with fine concentric growth lines as well as radial striations, most conspicuous on the lateral and outer edges. It is preserved as a blackened film and is unmineralized.

Discussion. The abundant material before us is highly variable, demonstrating the holotype of *Metacalycoceras? tarrantense* Adkins, 1928 (p. 241, pl. 28, fig. 3; pl. 29, fig. 1; see Stephenson 1953a, pl. 45, figs. 9 and 10; pl. 46, fig. 2 for better photographs) to be an incomplete macroconch of a rather average morphology, while the holotype of *Acanthoceras wintoni* Adkins, 1928 (p. 243, pl. 25, figs. 2 and 3) is merely more compressed and feebly, if as distantly ribbed (text-fig. 15). *Acanthoceras adkinsi* Stephenson, 1953a (p. 200, pl. 47, figs. 3 and 4) is no more than a juvenile of the gracile form



TEXT-FIG. 16. *Conlinoceras tarrantense* (Adkins, 1928). USNM 105968, the holotype of *Acanthoceras adkinsi* Stephenson, 1953a, from the Tarrant Formation, branch north of Chicago, Rock Island and Pacific railroad near Dorothy Siding, Tarrant County. Natural size.

with dense ribbing (text-fig. 16). *Acanthoceras tarrantense nitidum* Stephenson, 1953a (p. 199, pl. 50, figs. 5 and 6) is another variant with well-differentiated tubercles on the inner whorls which link to the robust individuals shown here as Pl. 6, figs. 7–12; Pl. 7, figs. 23–25.

Conlinoceras tarrantense and *C. gilberti* are closely allied. They differ chiefly in that *C. gilberti* has much higher, stronger ribs. '*Acanthoceras*' *barcusi* Jones, 1938 (p. 117, pl. 6, figs. 2, 3, 8, 9) is a much smaller species that also comes from the Tarrant Formation of north central Texas. The two differ in the much more spinose inner whorls of '*A.*' *barcusi* which have a rounded rather than flattened venter, persistence of all tubercles to the middle of the adult body chamber and rounded venter at maturity.

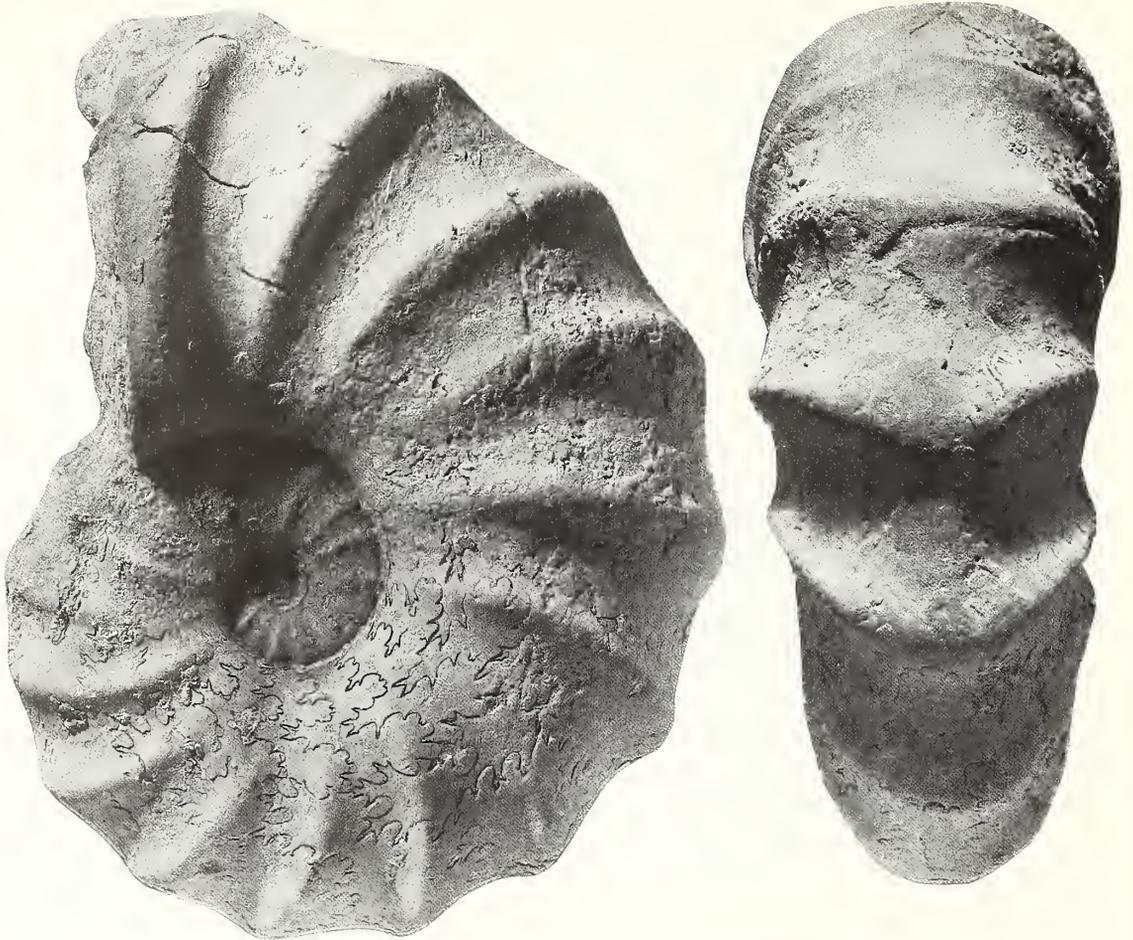
Text-fig. 17 shows a remarkable pathological specimen of *C. tarrantense* with rursiradiate ribbing and no tubercles on the outer whorl. This specimen is the basis for the occurrence of *Paracalycoceras* in Texas cited in the *Treatise* (Wright 1957).

Occurrence. *Conlinoceras tarrantense* zone, Tarrant Formation of central Texas; Oak Canyon Member and Cubero Tongue of Dakota Sandstone in west-central New Mexico.

Conlinoceras sp.

Text-fig. 18

Discussion. A species of *Conlinoceras* is represented by a fragment from the *Acanthoceras bellense* zone on Bird Creek in Bell County. USNM 420255 corresponds to the coarse ribbed variants of *C. tarrantense*, with striking differentiation into primary and secondary ribs.



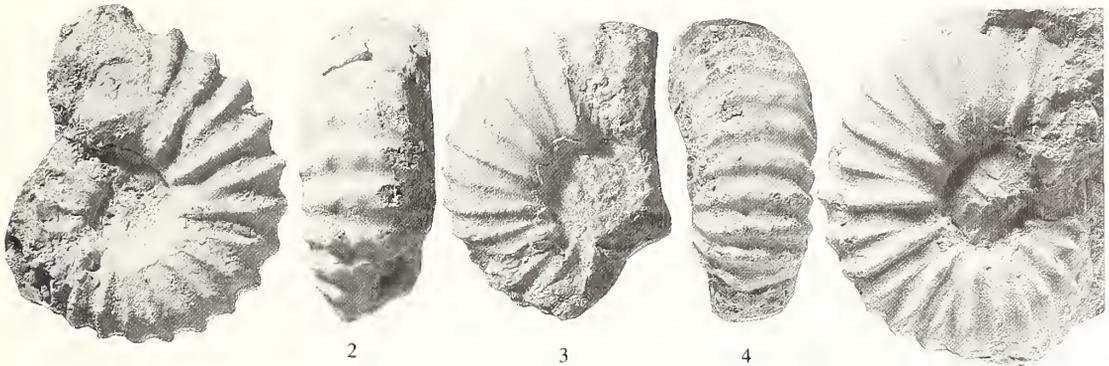
TEXT-FIG. 17. *Conlinoceras tarrantense* (Adkins, 1928). USNM 420254, from the Tarrant Formation, tributary to Big Bear Creek, 2.4 km (1.5 miles) east of Euless, Tarrant County. This pathological specimen is the basis for the *Treatise* record of *Paracalyoceras* in Texas. Reduced $\times 0.9$.

EXPLANATION OF PLATE 6

Figs. 1-6. *Paraconlinoceras leonense* (Adkins, 1928). 1 and 2, USNM 420260; 3 and 4, USNM 420261, both from USGS locality 13577, branch south of Belton-Temple road, 1.6 km (1 mile) east of Midway Church, Bell County. 5 and 6, the holotype, TMM 34051, from near the Belton-Temple Highway, Bell County. All specimens are from the basal shell bed of the Bluebonnet Member, *Acanthoceras bellense* zone.

Figs. 7-12. *Conlinoceras tarrantense* (Adkins, 1928). 7 and 8, USNM 420244; 9 and 10, USNM 420241; 11 and 12, USNM 420248, all from USGS locality 22614, 6.4 km (4 miles) south-east of Euless, Tarrant County; all from the Tarrant Formation, *Conlinoceras tarrantense* zone.

All figures are $\times 1$.



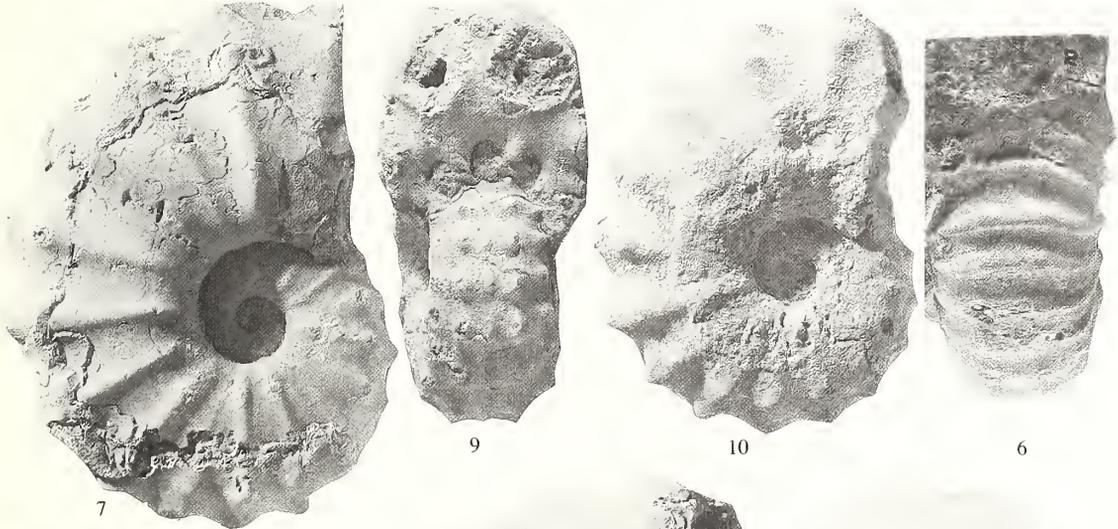
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Genus *PARACONLINOCERAS* nov.

Type species. Eucalycoceras leonense Adkins, 1928, p. 240, pl. 28, fig. 1; pl. 29, fig. 3.

Diagnosis. Moderately small ammonites with narrow, high ribs that cross the venter; acanthoceratine nuclei bearing long and short ribs with umbilical bullae, conical inner ventrolateral and nodate to clavate outer ventrolateral and siphonal tubercles; inner ventrolaterals decline in middle growth, all tubercles except umbilical ones lost on later parts of body chamber where venter rounds; umbilical bullae decline and disappear at adult aperture.

Discussion. *Paraconlinoceras* microconchs are adult at 50–60 mm, macroconchs at 90 mm. Nuclei of *P. leonense* are identical in style and shape of ornament to slightly older *Conlinoceras tarrantense* (text-fig. 19) while sutures are identical in style (compare text-figs. 6D and 20F). *Conlinoceras tarrantense* reach maturity at 150 mm or less in microconchs, 200 mm in macroconchs. The acanthoceratine stage persists in *Conlinoceras tarrantense* to a size where *Paraconlinoceras leonense* are adult (Pl. 9, figs. 26, 27, 29, 30). If adult phragmocones are compared, *Conlinoceras tarrantense* has passed from a stage of alternately long and short ribs to one in which all ribs are long and variably bullate, have lost their inner ventrolateral and, commonly, siphonal tubercles. Ribs are broad and blunt, rather than sharp and narrow. Adult body chambers are utterly distinct.

On the basis of comparable nuclei and stratigraphic occurrence, *Paraconlinoceras leonense* is regarded as a possible derivative of *Conlinoceras*, via '*Acanthoceras*' *barcusi* Jones, 1938, which is also referred to the new genus. *Paraconlinoceras* is a homoeomorph of *Gentoniceras* Thomel, 1972. They differ in the acanthoceratine nuclei of the former which have markedly clavate outer ventrolateral and siphonal tubercles, not seen in *Gentoniceras*.

Occurrence. Middle Cenomanian *Conlinoceras tarrantense* zone of Texas, *Acanthoceras bellense* zone of Texas and Wyoming, *Conlinoceras gilbertii* zone of Colorado.

Paraconlinoceras barcusi (Jones, 1938)

Pl. 8, figs. 1–7

- 1938 *Acanthoceras barcusi* Jones, p. 117, pl. 6, figs. 2, 3, 8, 9.
 1951 *Acanthoceras barcusi* Jones; Adkins and Lozo, pl. 2, fig. 4.
 1953a *Acanthoceras barcusi* Jones; Stephenson, p. 203, pl. 44, figs. 9–11.

Type. Holotype is UMM 16543, the original of Jones (1938, pl. 6, fig. 2) from the 'basal Eagle Ford' of Tarrant County, Texas.

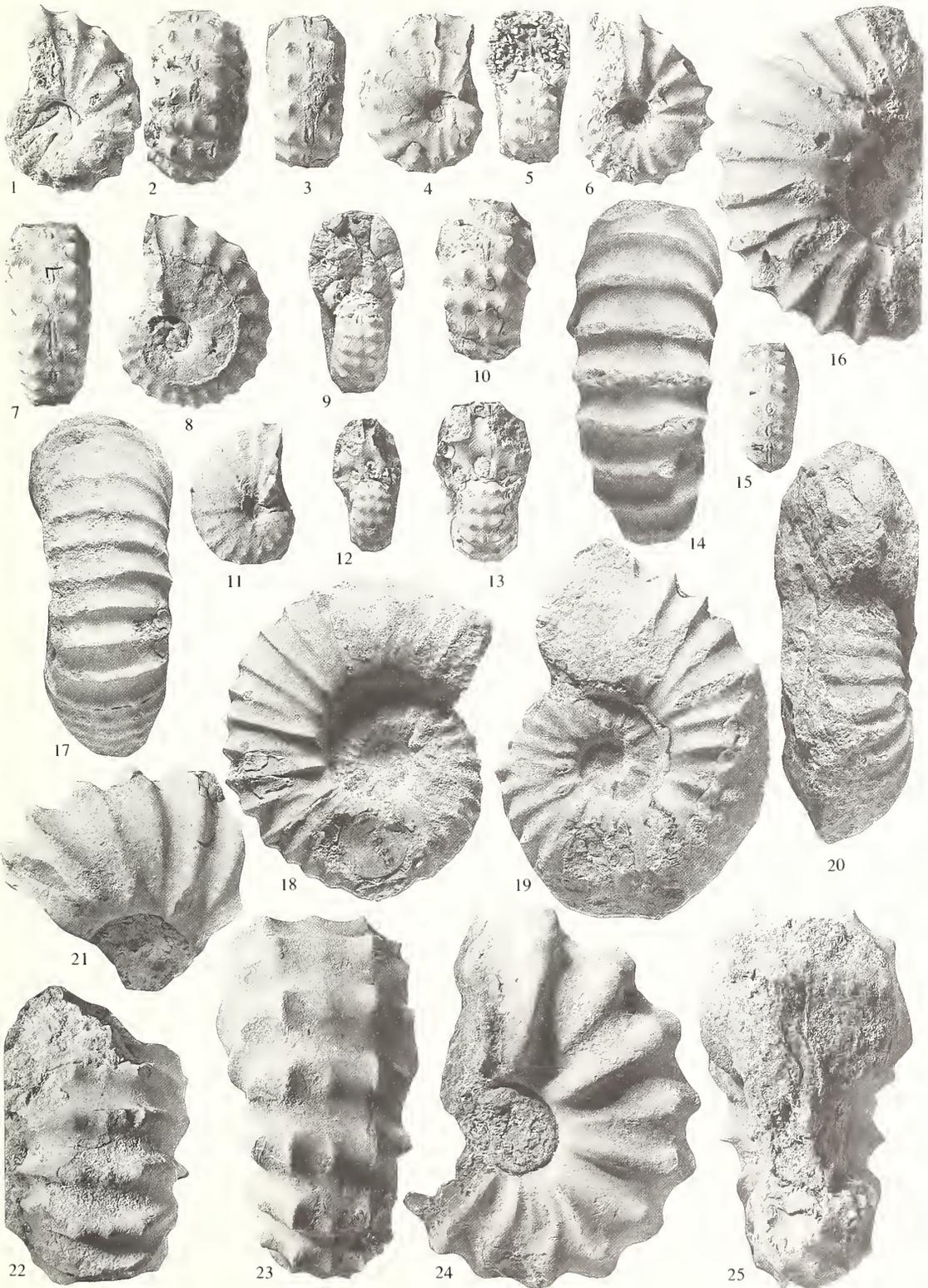
Material. USNM 420264–420267 without precise locality data; USNM 105977 from Big Bear Creek, Dallas County, all from the Tarrant Formation, middle Cenomanian *Conlinoceras tarrantense* zone.

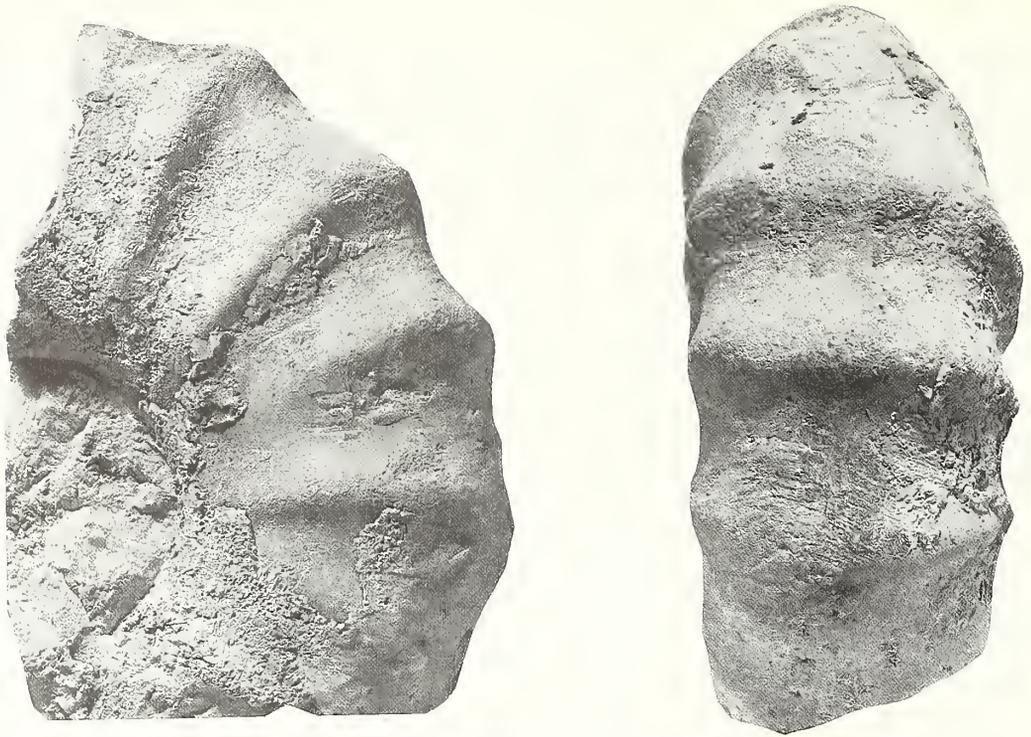
EXPLANATION OF PLATE 7

Figs. 1–13, 15, 23–25. *Conlinoceras tarrantense* (Adkins, 1928). 1 and 2, USNM 420237; 3–5, USNM 420234; 6, 10, 13, USNM 420235; 7–9, USNM 420238; 11 and 12, 15, USNM 420233; 23–25, USNM 420243, all from 2.4 km (1.5 miles) east of Euless, south bank of tributary to Big Bear Creek, Tarrant County; Tarrant Formation, *Conlinoceras tarrantense* zone.

Figs. 14, 16, 17–22. *Paraconlinoceras leonense* (Adkins, 1928). 14, 16, USNM 420257; 17 and 18, USNM 420256; 19 and 20, USNM 420262, from USGS Locality 11845; 21 and 22, USNM 420263, all from the basal shell bed of the Bluebonnet Member, Bird Creek, 6.4 (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.

All figures are $\times 1$.





TEXT-FIG. 18. *Conlinoceras* sp. USNM 420255, from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Natural size.

Dimensions		D	Wb	Wh	Wb:Wh	U
USNM 420264	c	52.0 (100)	28.9 (55.6)	21.7 (41.7)	1.33	— (—)
	ic	48.5 (100)	22.9 (47.2)	19.0 (39.2)	1.21	— (—)
USNM 105977	c	58.7 (100)	— (—)	22.0 (37.5)	—	19.7 (33.6)
	ic	55.5 (100)	— (—)	20.0 (36.0)	—	— (—)
USNM 420265	c	64.2 (100)	30.4 (47.4)	25.0 (38.9)	1.2	23.2 (36.1)
	ic	60.2 (100)	26.5 (44.0)	22.3 (37.0)	1.19	— (—)

Description. Coiling evolute with $U = 33-36\%$ of diameter, quite deep with subvertical wall in early growth becoming rounded at maturity. Umbilical shoulder broadly rounded. Costal whorl section depressed (Wb:Wh ratio 1.2-1.33), polygonal, with greatest breadth at umbilical bullae. Intercoastal section depressed trapezoidal (Wb:Wh ratio 1.19-1.21) with broadly rounded inner flanks, flattened convergent outer, broadly rounded ventrolateral shoulders and somewhat flattened venter. There are 12-13 primary ribs per whorl in middle growth. These arise at the umbilical seam and develop into strong, distant coarse ribs with a strong, pointed bulla perched on the umbilical shoulder. These give rise to strong rursiradiate ribs which alternate regularly with secondary ribs that arise low on the flank. These strengthen to match the development of the primaries.

EXPLANATION OF PLATE 8

Figs. 1-7. *Paraconlinoceras barcusi* (Jones, 1938). 1, 5, 6, the holotype, UMM 16543, from the 'Basal Eagle Ford' (e.g. Tarrant Formation) of Tarrant County. 2, 7, USNM 105977, from 2.4 km (1.5 miles) east of Euless, on south bank of Big Bear Creek, Tarrant County. 3 and 4, USNM 420265, without precise locality data but from the Tarrant Formation of Tarrant County. All *Conlinoceras tarrantense* zone. All figures are $\times 1$.



KENNEDY and COBBAN, *Paraconlinoceras*

and all ribs bear a sharp inner ventrolateral tubercle linked by a strong rib to clavate outer ventrolateral and siphonal tubercles. This ornament persists to the beginning of the adult body chamber, where there is a progressive outward migration and decline in strength of the umbilical bullae, weakening of the ventrolateral and siphonal tubercles. Specimens that we take to be adult microconchs are 59–63 mm in diameter, and show marked egression of the umbilical seam with the last few ribs before the aperture weakened and crowded, with no or very weak tubercles and an evenly rounded costal whorl section. The holotype and USNM 420265 are over 80 mm in diameter and appear to be incomplete macroconchs.

Suture (Jones 1938, pl. 6, fig. 3) with broad, bifid E/L and narrow L.

Occurrence. *Conlinoceras tarrantense* zone. Tarrant Formation of north central Texas only.

Paraconlinoceras leonense (Adkins, 1928)

Plate 6, figs. 1–6; Plate 7, figs. 14, 16–22; Plate 9, figs. 26, 27, 29, 30; text-figs. 19A–H.

- 1928 *Eucalycoceras leonense* Adkins, p. 240, pl. 28, fig. 1; pl. 29, fig. 3.
 1928 *Metacalycoceras* ? sp. 2; Adkins, p. 242, pl. 28, fig. 2; pl. 29, fig. 2.
 1942 *Eucalycoceras leonense* Adkins; Moreman, p. 207.
 1969 *Eucalycoceras (Proeucalycoceras) leonense* Adkins, Thomel, p. 650.
 1972 *Eucalycoceras (Proeucalycoceras) leonense* Adkins; Thomel, p. 81.
 1973 *Calycoceras leonense* (Adkins); Cobban and Scott, p. 60, pl. 3, figs. 1–4.
 1987b *Calycoceras (Gentoniceras) leonense* (Adkins); Cobban, p. 4, pl. 1, figs. 1–17, text-fig. 2.

Holotype. TMM 34051, the original of Adkins (1928, p. 240, pl. 28, fig. 1; pl. 29, fig. 1), from the basal shell bed of the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group near the old Belton-Temple Highway, Bell County, *Acanthoceras bellense* zone.

Material. More than 100 specimens and fragments from the same horizon as the holotype: USGS localities 11845, 13577 and 19554, J. P. Conlin and OUM collections, on Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County. Middle Cenomanian *Acanthoceras bellense* zone.

<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
USNM 420256 (microconch)	c	49.7 (100)	21.5 (43.3)	18.0 (36.2)	1.2	17.5 (35.2)
USNM 420257 (juvenile)	c	53.0 (100)	22.5 (42.4)	20.8 (39.2)	1.08	15.5 (29.2)
USNM 420258 (microconch)	c	61.0 (100)	27.5 (45.1)	26.5 (43.4)	1.04	20.5 (33.6)
USNM 420259 (macroconch)	c	90.0 (100)	— (—)	30.5 (—)	—	32.8 (36.4)
	c	80.5 (100)	31.2 (38.8)	28.0 (34.8)	1.14	27.2 (33.8)

EXPLANATION OF PLATE 9

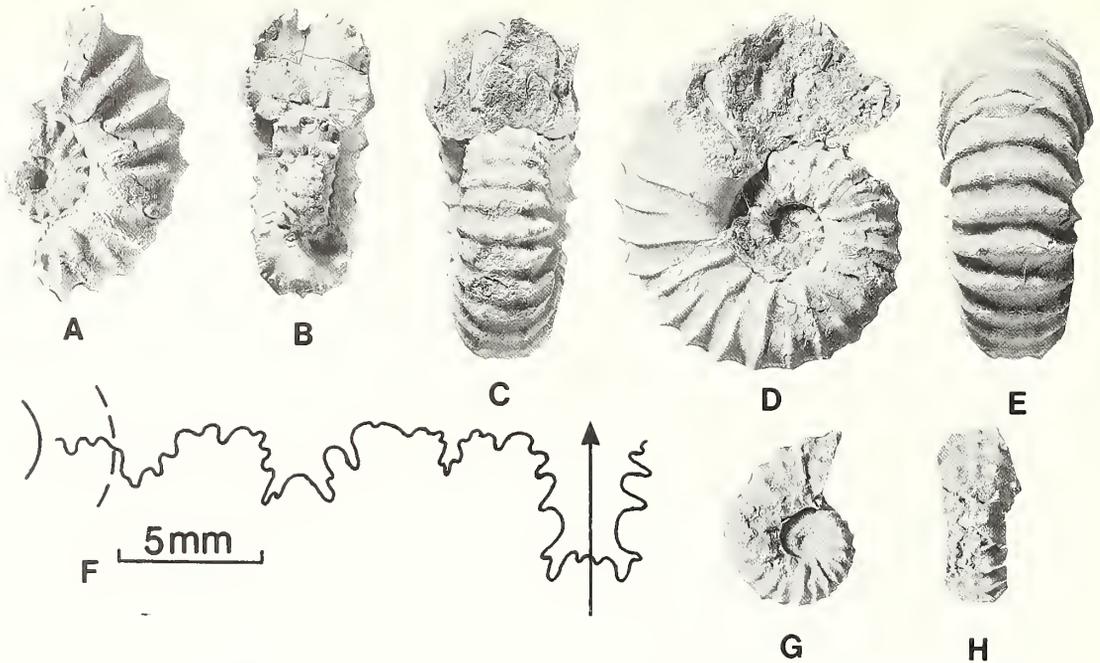
Figs. 1–25, 28. *Plesiacanthoceratoides vetula* (Cobban, 1987b). 1–4, USNM 420291; 5–8, USNM 420292; 10–12, USNM 420290; 13–16, USNM 420287; 17–20, USNM 420289, all from a loose concretion at USGS Mesozoic locality D12626, basal part of the Eagle Ford Group, 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County. 21 and 22, paratype USNM 388194; 23–25, paratype USNM 388195; 28, paratype USNM 388197, all from USGS Mesozoic locality D5900, Belle Fourche Shale, Old Woman anticline (south-west of the Black Hills, head of Elm Creek, in W $\frac{1}{2}$ sec. 14, T.36N, R.62W, Niobrara County, Wyoming. All *Acanthoceras amphibolum* zone.

Figs. 26 and 27, 29 and 30. *Paraconlinoceras leonense* (Adkins, 1928). 26 and 27, USNM 420258; 29 and 30, USNM 420259, from USGS locality 13577, basal shell bed of Bluebonnet Member, Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County.

Figs. 31 and 32. *Acanthoceras bellense* Adkins, 1928. The holotype, TMM 3034, from the same horizon and locality as the originals of figs. 26 and 27.

Figures 21–25, 28 are $\times 2$; the remainder are $\times 1$.





TEXT-FIG. 19. *Paraconlinoceras leonense* (Adkins, 1928). A and B, USNM 388089; C-E, USNM 388087; F, external suture of USNM 388087; G and H, USNM 388088. All are from the Belle Fourche Shale at USGS Mesozoic locality D8841, west of Osage in the SW1/4 sec. 8, T. 46 N., R. 63 W., Weston County, Wyoming. A-E, G and H are natural size.

Description. The species appears to be markedly dimorphic; 2 complete microconchs are 50 and 61 mm diameter, two macroconchs 90 and 92 mm diameter. The early growth stages are not shown by the Texas material. In middle growth as far as the beginning of the adult body chamber, the coiling is evolute, with $U = 27-33\%$ of diameter, shallow, with a rounded wall. Intercostal whorl section depressed, reniform, the greatest breadth well below mid-flank. Costal section trapezoidal-polygonal. There are generally 12-14 primary ribs per whorl. They arise at the umbilical seam, strengthen into sharp bullae on the umbilical shoulder and give rise to sharp, distant, prorsiradiate primary ribs. At the smallest diameters visible these bear small inner ventrolateral tubercles that are no wider than the rib, linked by a strong rib to a clavate outer ventrolateral and a somewhat weaker siphonal tubercle. At small sizes ribs may arise in pairs from the umbilical bullae, but in general the primaries alternate regularly with secondaries inserted at or below mid-flank. The latter strengthen to equal the primaries at the ventrolateral shoulder, where they develop a full complement of tubercles. The inner ventrolateral tubercles decline around the outer whorl of the phragmocone, and the beginning of the body chamber bears outer ventrolateral and siphonal tubercles only. The umbilical seam of the mature body chamber egresses markedly, to give $U =$ up to 37%. Umbilical bullae migrate out to the inner flank, before declining and disappearing just before the adult aperture. The outer ventrolateral and siphonals persist to the last quarter whorl before the adult aperture, thereafter they decline. The last few ribs before the aperture are weakened, and extend to the umbilical shoulder without bullae.

Suture with broad, symmetrically bifid E/L, narrow bifid L and broad L/U₂.

Discussion. The Texas material does not show the inner whorls. Study of well-preserved material from the Belle Fourche Shale at USGS Mesozoic locality D8841 in Weston County, Wyoming (text-fig. 19) shows juveniles to have strikingly *Acanthoceras*-like nuclei, with a polygonal whorl section in costal section and markedly clavate outer ventrolateral clavi. This is quite different from inner whorls of *Gentoniceras* Thomel, 1972, which the species resembles at maturity. We conclude that *P. leonense* is a homoeomorph of *Gentoniceras*, its inner whorls pointing to an origin in slightly older *Paraconlinoceras barcusi* which has comparable inner whorls (Pl. 8, figs. 1-7) and outer whorls with high, narrow ribs.

Occurrence. Middle Cenomanian *Acanthoceras bellense* zone of central Texas and eastern Wyoming. *Conlinoceras gilberti* zone of southeastern Colorado.

Genus CUNNINGTONICERAS Collignon, 1937, p. 64 (40)

(? = *Guerangericeras* Thomel, 1972)

Type species. *Anmonites cunningtoni* Sharpe, 1855 (p. 35, pl. 15, fig. 2).

Discussion. See Wright and Kennedy (1987, p. 193).

Cunningtoniceras lonsdalei (Adkins, 1928)

Plate 12, figs. 1–3, 8; text-figs. 20–22

- 1928 *Acanthoceras lonsdalei* Adkins, p. 244, pl. 26, fig. 5; pl. 27, fig. 3.
 1942 *Acanthoceras lonsdalei* Adkins; Moreman, p. 204.
 1955 *Euomphaloceras lonsdalei* (Adkins); Stephenson, p. 62 (*pars*), pl. 6, figs. 6–8, *non* 9–20.
 1963 *Euomphaloceras lonsdalei* (Adkins); Wright, p. 609, pl. 87, fig. 2; pl. 88, fig. 1; pl. 89, fig. 2.
 ?1973 *Euomphaloceras cf. lonsdalei* (Adkins); Cobban and Scott, p. 71, pl. 5, figs. 1, 2, 4.
 1978 *Euomphaloceras lonsdalei* (Adkins); Young and Powell, pl. 5, fig. 1 only (*non* 7, = *Acanthoceras bellense*).
 1987 *Cunningtoniceras lonsdalei* (Adkins); Wright and Kennedy, p. 194, text-fig. 80.

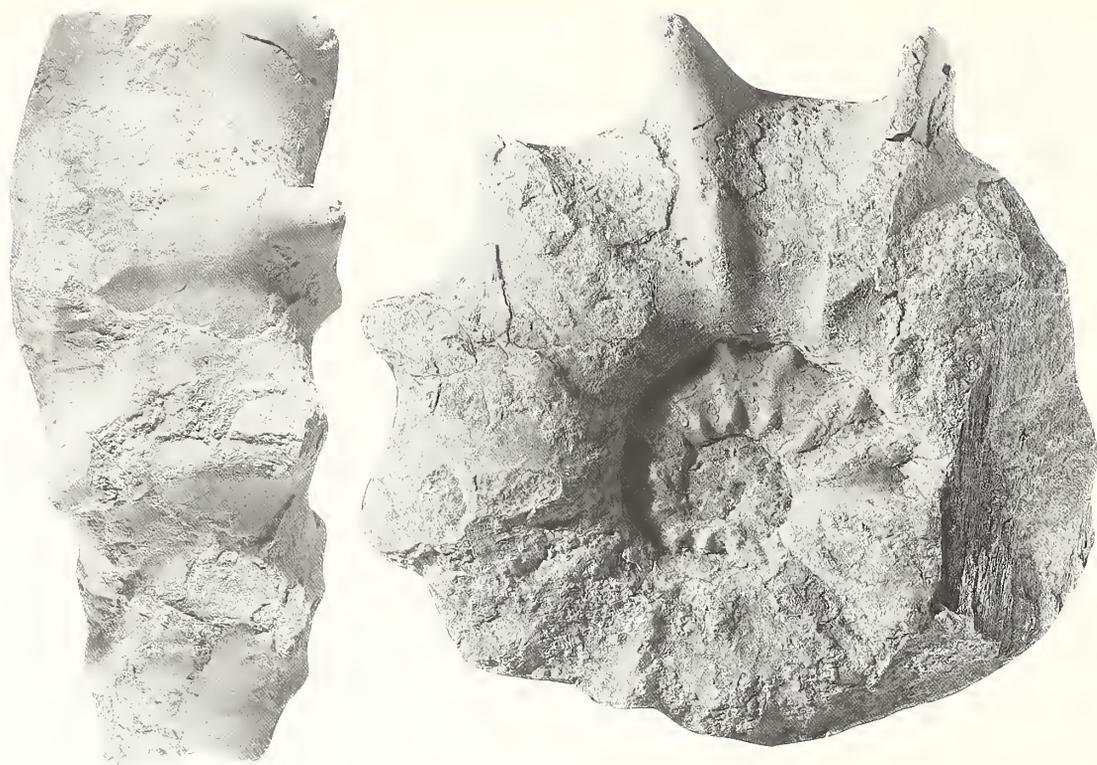
Holotype. TMM 2410, the original of Adkins (1928, p. 244, pl. 26, fig. 5, pl. 27, fig. 3) by original designation. From the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group on the Belton-Temple road, Bell County. Middle Cenomanian *Acanthoceras bellense* zone.

Material. USNM 108831a–b (originals of Stephenson 1955, pl. 6, figs. 6–8), USNM 420268–420272, TMM 1069, WSA 12830, all from the same horizon as the holotype on Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County.

<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
USNM 108831b	c	51.5 (100)	32.1 (62.3)	24.0 (46.6)	1.34	12.3 (23.9)
USNM 420269	c	52.3 (100)	28.9 (55.3)	24.0 (45.9)	1.20	12.9 (24.7)
TMM 2410	c	79.2 (100)	43.5 (54.9)	35.5 (44.8)	1.23	22.0 (27.7)
			41.0 (—)	36.1 (—)	1.14	

Description. Up to 100 mm: coiling very evolute, umbilicus comprises up to 28% of diameter. Whorl section depressed, rounded-trapezoidal in intercostal section (Wb:Wh 1.14), with greatest breadth outside umbilical shoulder. Inner flanks rounded, outer flanks flattened, convergent, ventrolateral shoulders broadly rounded, venter somewhat flattened. Costal section very depressed, polygonal, with greatest breadth at umbilical bullae. Distant primary ribs, 10 per half whorl, arise at the umbilical seam. They strengthen across the umbilical wall and develop into strong umbilical bullae perched just outside the umbilical shoulder. These give rise to broad, straight, prorsiradiate ribs, somewhat effaced on the outer flank, where they connect to a strong conical inner ventrolateral horn. A low broad rib connects to a clavate inner ventrolateral tubercle, accompanied by one or two weaker ribs connecting to generally weaker inner ventrolaterals, all ribs extending to evenly developed siphonal tubercles. There are occasional intercalated ribs with outer ventrolateral and siphonal tubercles so that the 10 or so primary ribs per half whorl correspond to 20 or more ventral ribs. An adult specimen, USNM 420271 (text-fig. 20), has inner whorls identical to those of the holotype and is mature at an estimated intercostal diameter of just over 200 mm. On the early body chamber there are distant ribs with flared umbilical bullae and a strong conical ventrolateral horn without a trace of an outer ventrolateral clavus, the horns linked across the venter by a pair of looped riblets on a broad low rib, the costal section being markedly concave. The ventral rib strengthens markedly at the end of the body chamber and is strong and bar-like, the costal profile losing the deep ventral concavity.

Discussion. There is some variation in the ventral ribbing, as in other *Cunningtoniceras* species (Wright and Kennedy 1987). *Cunningtoniceras lonsdalei* was derived from *Acanthoceras bellense* by stabilization of multiple ventral ribbing; it is linked to *A. bellense* by a common style of flank ornament, whorl proportions, the presence of a marked siphonal ridge and distinctive bar-like rib



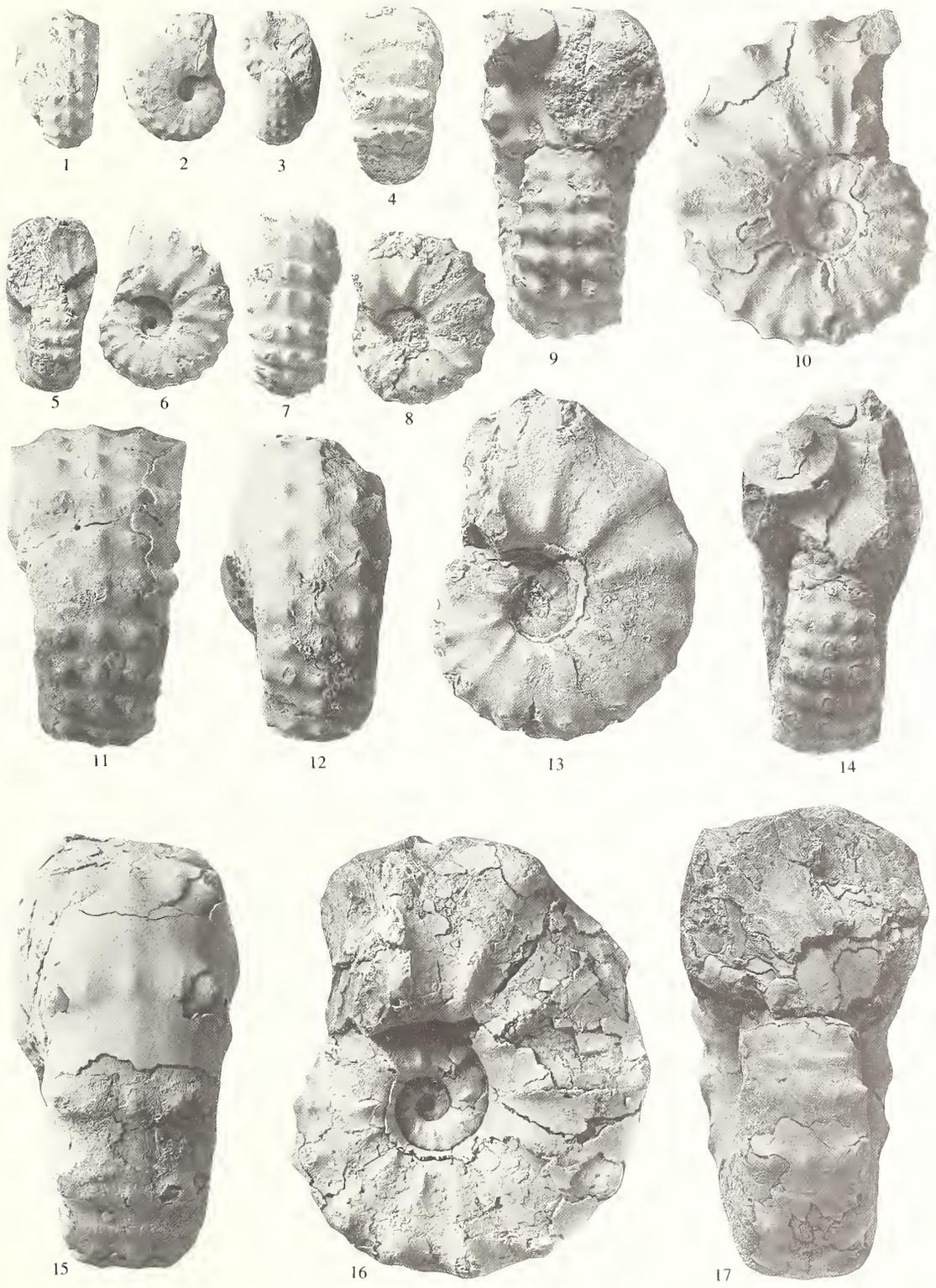
TEXT-FIG. 20. *Cunningtonicerias lonsdalei* (Adkins, 1928). USNM 420271, an adult specimen from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Reduced $\times 0.5$.

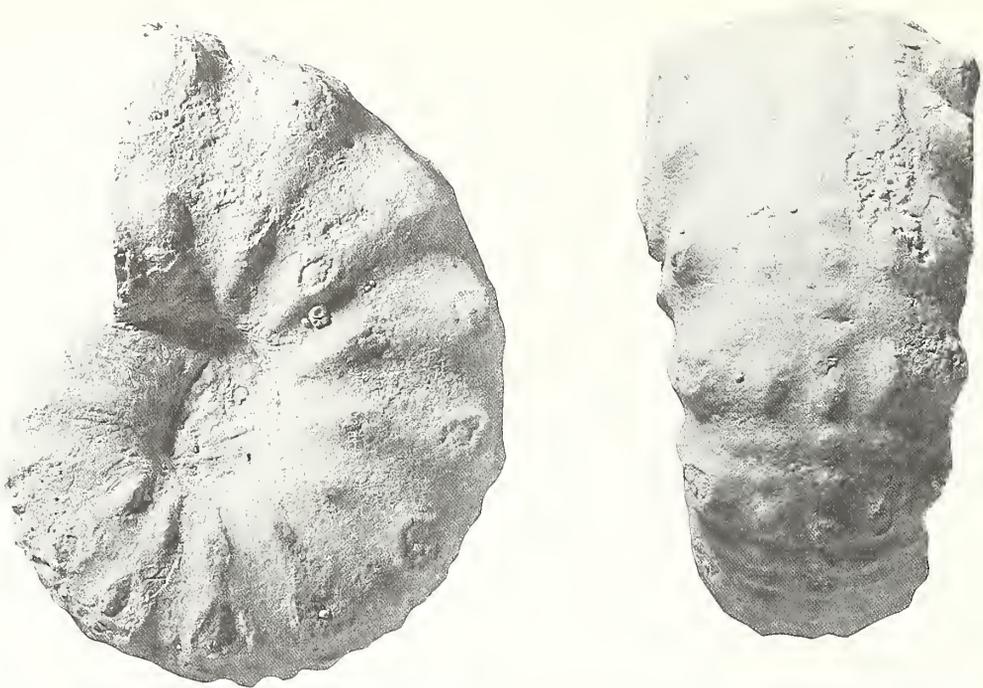
at the adult aperture. Zaborski (1985) regarded *C. lonsdalei* as a subspecies of *C. cunningtoni*, but the latter is a derivative of *Acanthoceras rhotomagense*. The two species differ in that *C. cunningtoni* is much more depressed, has far fewer ribs, massive inner ventrolateral horns, obvious looping of ventral ribs and utterly different adult ornament. Stephenson (1955) confused *C. lonsdalei* and *C. johnsonanum* (Stephenson, 1955); differences are outlined below; features of other *Cunningtonicerias* species are reviewed by Wright and Kennedy (1987) and are not repeated here.

Occurrence. *Acanthoceras bellense* zone, central Texas. Middle Cenomanian of Bathurst Island, northern Australia. There is a doubtful record from the *Acanthoceras muldoonense* zone of SE Colorado.

EXPLANATION OF PLATE 10

Figs. 1–17. *Cunningtonicerias johnsonanum* (Stephenson, 1955). 1–3, USNM 420275, from east of old Alvarado–Grandview highway, 6.4 km (4 miles) south of Alvarado, Johnson County; 4, 8, USNM 420276; 5–7, USNM 420273; 15–17, USNM 420278, from concretions in cotton field 1.6 km (1 mile) north of Lillian, Johnson County; 9–11, USNM 420274; 12–14, USNM 420277, from 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) north-east of the town square in Alvarado, Johnson County. All specimens from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone. All figures are $\times 1$.





TEXT-FIG. 21. *Cunningtoniceras lonsdalei* (Adkins, 1928). The holotype, TMM 2410, from the basal shell bed of the Bluebonnet Member on the Belton-Temple road, Bell County. Natural size.

Cunningtoniceras johnsonanum (Stephenson, 1955)

Plate 10, figs. 1–17; Plate 11, figs. 1 and 2.

1955 *Acanthoceras johnsonanum* Stephenson, p. 58, pl. 4, figs. 14–17.

1955 *Euomphaloceras lonsdalei* (Adkins); Stephenson, p. 62 (*pars*), pl. 6, figs. 9–20 only.

Type. The holotype is USNM 108846, from USGS locality 14583, north facing slope of Mountain Creek Valley, 4 km (2.5 miles) north-north-east of Alvarado, Johnson County. Basal part of the Eagle Ford Group, *Acanthoceras amphibohum* zone.

Material. Numerous specimens from the same horizon as the holotype at the following localities: gully in field 1.6 km (1 mile) north of Lillian, west of Lillian–Retta road; scattered concretions east of the old Alvarado–Grandview highway, 6.4 km (4 miles) south of Alvarado; hillside 0.3 km (0.2 mile) south of Mountain Creek and west of secondary road 6.1 km (3.8 miles) airline north-east of the town square in Alvarado, all in Johnson County and all *ex* Conlin Collection. USGS Mesozoic locality D12626, 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County. All of the above are from concretions in the basal part of the Eagle Ford Group, *Acanthoceras amphibohum* zone.

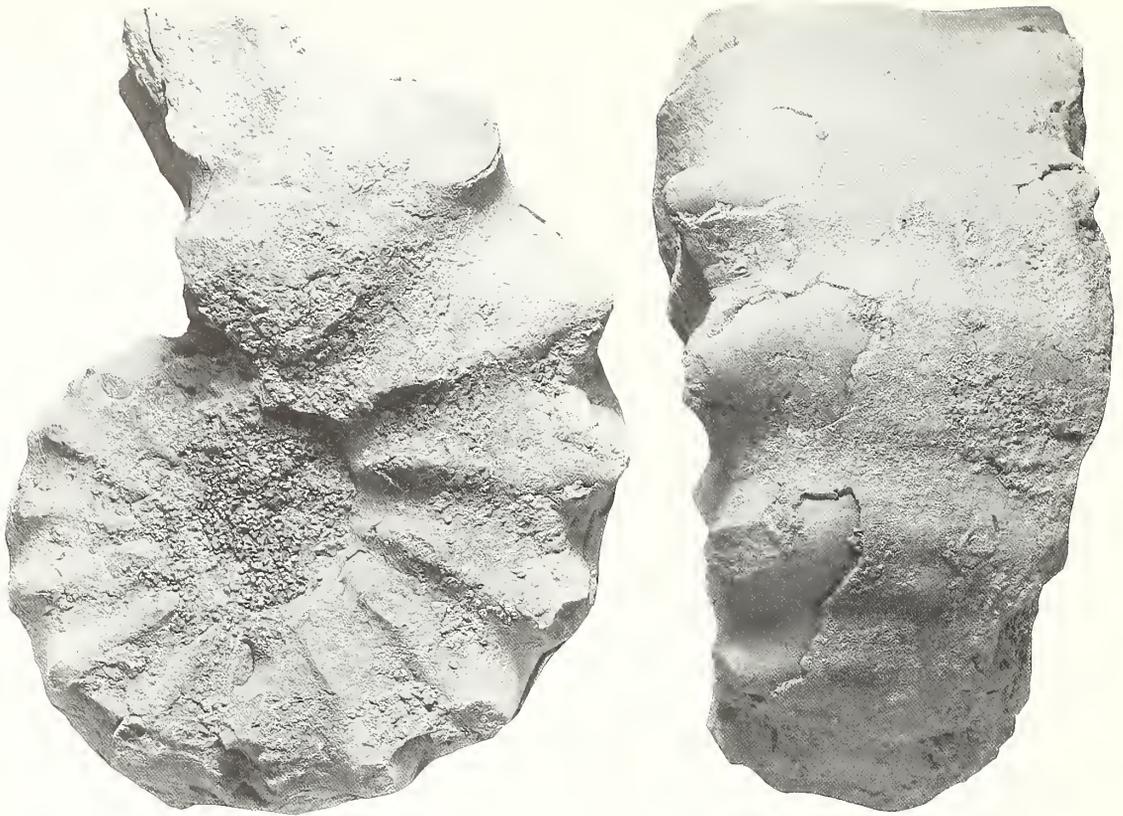
EXPLANATION OF PLATE 11

Figs. 1 and 2. *Cunningtoniceras johnsonanum* (Stephenson, 1955). The holotype, USNM 108846, from USGS locality 14583, north-facing slope on Mountain Creek Valley, 4 km (2.5 miles) north-north-east of Alvarado, Johnson County, *Acanthoceras amphibohum* zone.

Figs. 3 and 4. *Calycoceras* (*Newboldiceras*) sp. TMM 34032, from the basal shell bed of the Bluebonnet Member, Belton-Temple Highway, Bell County. *Acanthoceras bellense* zone.

All figures are $\times 1$.





TEXT-FIG. 22. *Cumingtoniceras lonsdalei* (Adkins, 1928). TMM W. S. Adkins Collection 12830, from the basal shell bed of the Bluebonnet Member on Bird Creek, Bell County. Reduced $\times 0.95$.

EXPLANATION OF PLATE 12

- Figs. 1–3, 8. *Cumingtoniceras lonsdalei* (Adkins, 1928). 1 and 2, USNM 420268; 3, 8, USNM 420269, from the basal shell bed of the Bluebonnet Member, Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.
- Figs. 4, 7. *Acanthoceras bellense* Adkins, 1928. USNM 420215, horizon and locality as for the originals of figs. 1–3, 8.
- Figs. 5, 6, 11. *Turrilites (Turrilites) dearingi* Stephenson, 1953a. 5, USNM 420314; 6, USNM 420315, casts of specimens in the Gerry Kienzlen Collection (Dallas, Texas), from roadcut on east side of Texas Highway 360, 1.9 km (1.2 miles) south of bridge over Trinity River. 11, paratype USNM 105957, from a branch of Big Bear Creek, 2.4 km (1.5 miles) east of Euless, both in Tarrant County, Tarrant Formation, *Conlinoceras tarrantense* zone.
- Fig. 9. *Plesiachanthoceras bellsanum* (Stephenson, 1953a). USNM 105984, from the Templeton Member of the Woodbine Formation 4.3 km (2.7 miles) north of Bells, Grayson County.
- Fig. 10. *Turrilites (Turrilites) acutus* Passy, 1832. USNM 420301, from the same horizon and locality as the originals of figs. 1–3, 8.
- Figs. 12–14. *Sciponoceras?* sp. TMM 2425, from the base of the Bluebonnet Member, 0.8 km (0.5 mile) south-east of Round Rock, Williamson County. *Acanthoceras bellense* zone.
- Figure 9 is $\times 2$; the remainder $\times 1$.



<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
USNM 420273	c	26.8 (100)	15.0 (56.0)	12.2 (45.5)	1.23	6.5 (24.3)
USNM 420274	c	31.0 (100)	16.5 (53.2)	13.2 (42.6)	1.25	8.0 (25.8)
USNM 420275	c	50.3 (100)	28.5 (56.7)	20.6 (40.9)	1.38	13.2 (26.2)
	ic	46.5 (100)	24.5 (52.7)	19.3 (41.5)	1.27	

Description. Coiling is moderately evolute with approximately 30% of the previous whorl covered. Umbilicus of moderate depth, comprising 24–26% of diameter, with subvertical wall. Whorls vary from very depressed (intercostal Wb:Wh ratio 1:27) to equidimensional. The intercostal whorl section is trapezoidal, the costal section polygonal, with the greatest breadth at the umbilical bulla. There are generally 12–14 primary ribs per whorl. They arise at the umbilical seam, strengthen across the umbilical wall and shoulder and develop weak to strong umbilical bullae, strength of ornament varying from weak to coarse between individuals. In robust individuals (USNM 420270, 420272, 420274) straight prorsiradiate ribs broaden and weaken somewhat as they pass across the flanks only to strengthen into a pronounced inner ventrolateral horn. A broad rib leads to strong outer ventrolateral and siphonal clavi. At small diameters, shorter ribs intercalate low on the flank and bear a full complement of tubercles, with the inner ventrolateral weaker than on the primary ribs. With increasing diameter this tubercle effaces to leave short ventral ribs with inner ventrolateral and siphonal clavi only, the short ribs sometimes linking to the inner ventrolateral horns of the primary ribs, there being twice as many ventral as flank ribs. In gracile individuals (USNM 420279), there may be up to 2 intercalated ribs with outer ventrolateral and siphonal clavi between primaries, so that there are 3 times as many ventral as flank ribs.

Most specimens are less than 70 mm in diameter, and closely resemble the holotype (Pl. 11, figs. 1 and 2). This appears to be a microconch, showing effacement of tuberculation and rounding of venter not seen in our material. The latter includes larger fragments in which inner and outer ventrolateral tubercles are differentiated to whorl heights of up to 35 mm, with multiple ventral ribs and tubercles (USNM 420274). We presume these differences to be within the limits of intraspecific variation.

Suture not seen.

Discussion. Stephenson (1955 p. 62) confused this species with the older *Cunningtoniceras lonsdalei*. Adkin's species has a rounded, rather than polygonal section, more intercalated ribs, with tubercles often much weaker than on the primaries. *C. johnsonanum* may well be descended from *C. lonsdalei*.

Co-occurring *Acanthoceras amphibolum amphibolum* variants may be superficially similar to *C. johnsonanum*. They have constricted innermost whorls, however, are compressed with distant ribs and show early loss of inner ventrolateral clavi leaving a single ventrolateral horn, with a siphonal ridge and weak siphonal clavi (Pl. 4, figs. 1–14). Adults, with striking umbilical bullae and ventrolateral horns as the only strong tuberculation are immediately distinct (text-figs. 13 and 14).

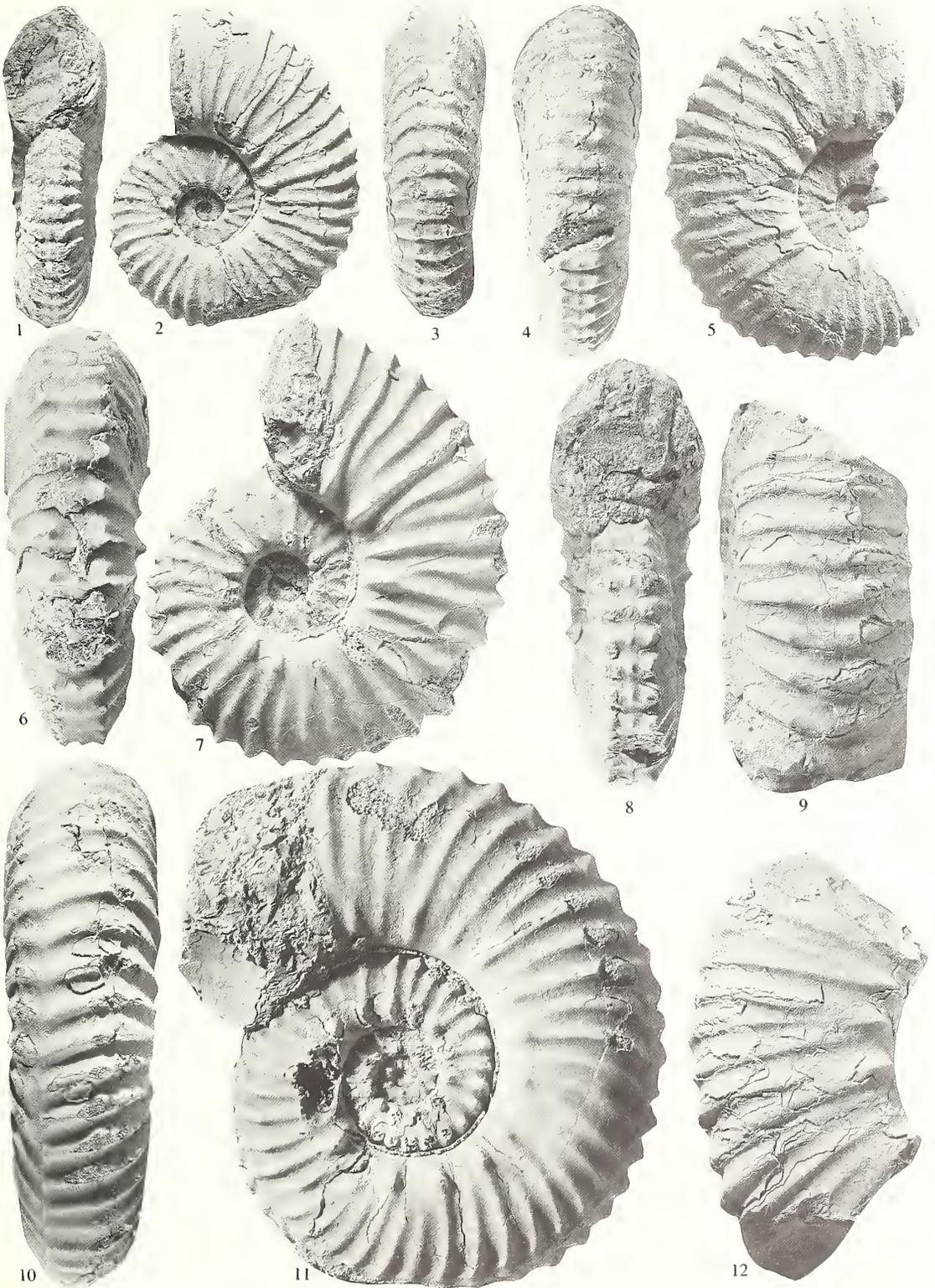
Occurrence. *Acanthoceras amphibolum* zone of central Texas only.

Cunningtoniceras inerme (Pervinquierè, 1907)

- 1855 *Ammonites sussexiensis* Mantell; Sharpe, p. 34, pl. 15, fig. 1.
 1907 *Acanthoceras cunningtoni* var. *inermis* Pervinquierè, p. 277.
 1953a *Acanthoceras? eulssanum* Stephenson, p. 201, pl. 47, fig. 5; pl. 48, figs. 3 and 4.
 1987 *Cunningtoniceras inerme* (Pervinquierè, 1907); Wright and Kennedy, p. 194, pl. 52, fig. 1; pl. 53, fig. 6; text-figs. 74 and 75, 79 (with full synonymy).

EXPLANATION OF PLATE 13

Figs. 1–12. *Tarrantoceras sellardsi* (Adkins, 1928). 1–3, USNM 400759; 4 and 5, USNM 400769; 10 and 11, USNM 400770, from concretions in cotton field 1.6 km (1 mile) north of Lillian, west of the Lillian–Retta Road, Johnson County. 6–8, USNM 400760; 9, 12, USNM 420284, from USGS Mesozoic locality D12626, 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County. All specimens are from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone. All figures are $\times 1$.



Discussion. Wright (1963) and Kennedy (1971) both regarded *Acanthoceras* ? *eulesanum* Stephenson, 1953a as a synonym of *Cunningtoniceras cunningtoni*. Wright and Kennedy (1987, p. 204) pointed out that it had strong flank ribs and compared it to *C. inerme*. It differs from specimens of the latter species (from the English Chalk) only in its lower rib density (13–14 per whorl vs. 17–20), and it is in this respect transitional to *C. cunningtoni*. We regard it as no more than a variant of *C. inerme*.

Occurrence. *Conlinoceras tarrantense* zone, Tarrant Formation of north central Texas. Where precisely dated in western Europe, it occurs at the top of the lower, *Turrilites costatus* subzone of the *Acanthoceras rhotomagense* zone in England and the German Federal Republic. It also occurs in the middle Cenomanian of France and Japan.

Genus TARRANTOCERAS Stephenson, 1955

Type species. *Tarrantoceras rotatile* Stephenson, 1955 (p. 59, pl. 5, figs. 1–10) by original designation (= *Mantelliceras sellardsi* Adkins, 1928, p. 239, pl. 25, fig. 1; pl. 26, fig. 1).

Diagnosis. Small, macroconchs adult at 90–100 mm, microconchs adult at 60 mm or less. Evolute, compressed, early whorls with umbilical bullae, inner and outer ventrolateral and siphonal clavi on flexuous primary ribs separated by several secondaries; all but umbilical bullae decline or disappear at maturity. Suture simple, with broad bifid E/L and shallow bifid L.

Discussion. *Tarrantoceras* is a homoeomorph of certain *Eucalycoceras* species. The types of the two genera are distinct enough, while species such as *Eucalycoceras rowei* (Spath, 1926b) (see Kennedy 1971, p. 83, pl. 49, figs. 2–7; pl. 50, figs. 3–7) can be distinguished by the greater complexity of the suture with a long, narrow L, and umbilical bullae that project into the umbilicus. The inner whorls of *Tarrantoceras* have far more pronounced ventral clavi.

Cooper (1978) believed *Sumitomoceras* to be a synonym of *Tarrantoceras*; Wright and Kennedy (1981) and Kennedy (1988) regarded *Sumitomoceras* as a subgenus of *Tarrantoceras*. Subsequent work supports separation; the very early loss of siphonal tubercles in *Sumitomoceras*, presence of constrictions and suture with deep L are distinctive; the last feature suggests *Sumitomoceras* is allied to the Old World acanthoceratines, not those of the New World.

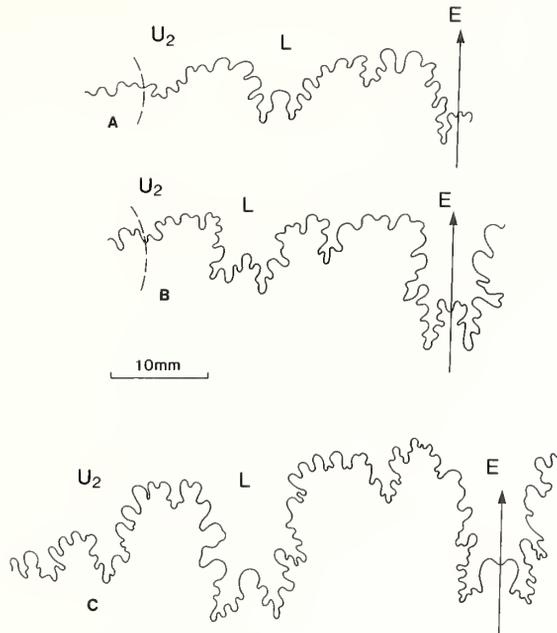
Occurrence. Middle and low upper Cenomanian of the US Western Interior and Angola.

Tarrantoceras sellardsi (Adkins, 1928)

Plate 13, figs. 1–12; Plate 14, figs. 1–16, 19, 20, 25, 29, 30; text-figs. 6A, 23A and B.

- 1928 *Mantelliceras sellardsi* Adkins, p. 239, pl. 25, fig. 1; pl. 26, fig. 4.
- 1942 *Mantelliceras sellardsi* Adkins; Moreman, p. 207.
- 1955 *Tarrantoceras rotatile* Stephenson, p. 59, pl. 5, figs. 1–10.
- 1955 *Tarrantoceras stantoni* Stephenson, p. 60, pl. 5, figs. 11–21.
- 1955 *Tarrantoceras lillianense* Stephenson, p. 60, pl. 5, figs. 22–27.
- 1971 *Eucalycoceras sellardsi* (Adkins); Kennedy, p. 84.
- 1973 *Tarrantoceras rotatile* Stephenson; Cobban and Scott, p. 64, pl. 10, figs. 1–11; text-fig. 25.
- 1977a *Tarrantoceras rotatile* Stephenson; Cobban, p. 23, pl. 6, figs. 8–10, 28 and 29; pl. 11, figs. 7 and 8, 11–16; pl. 12, figs. 13 and 14; text-fig. 4.
- 1977b *Tarrantoceras rotatile* Stephenson; Cobban, p. 219, figs. 3N and O, 4G.
- 1978 *Utaturiceras* ? *sellardsi* (Adkins); Young and Powell, p. xxv, 18.
- 1978 *Tarrantoceras rotatile* Stephenson; Cooper, p. 92, text-fig. 20.
- 1984 *Tarrantoceras sellardsi* (Adkins); Cobban, p. 78.
- 1986 *Tarrantoceras sellardsi* (Adkins); Cobban, p. 78, figs. 3C and D.

Types. The holotype is TMM 34048, the original of Adkins (1928, pl. 25, fig. 1; pl. 26, fig. 1) from the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group, 2.4 km (1.5 miles) south-east of



TEXT-FIG. 23. External sutures. A and B, *Tarrantoceras sellardsi* (Adkins, 1928), USNM 400772, 400760. C, *Plesiacanthoceras bellsanum* (Stephenson, 1953a), USNM 105983.

Round Rock, Williamson County, by original designation. The holotype of *T. rotatile* is USNM 11740, the original of Stephenson (1955, pl. 5, figs. 1–4) from Walnut Creek, 7.6 km (4.75 miles) east-north-east of Mansfield, Tarrant County. The holotype of *T. stantoni* is the original of Stephenson (1955, pl. 5, figs. 11–13); the holotype of *T. lillianense* is USNM 108841, the original of Stephenson (1955, pl. 5, figs. 22 and 23), both specimens from gully in field 1.6 km (1 mile) north of Lillian, Johnson County, both basal Eagle Ford Group. All of the above are from the *Acanthoceras amphibolum* zone.

Material. Numerous specimens from USGS Mesozoic locality 12626, roadside 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County, in a loose concretion; from USGS locality 24510 from a concretion in a crop field 1.6 km (1 mile) north of Lillian, Burlestone, Johnson County; from a concretion on hillside 0.3 km (0.2 miles) south of Mountain Creek, 6.1 km (3.8 miles) north-east of town square in Alvarado; from USGS locality 14591, 2.3 m (7.5 feet) above base of Cloice Member of the Lake Waco Formation, abandoned brickpit on Cloice Branch, 1.3 km (0.8 mile) east of South Bosque, McLennan County. Also numerous specimens as OUM KT40008–9, concretions from Walnut Creek, 7.6 km (4.75 miles) east of Mansfield, Tarrant County; from USGS Mesozoic locality D9502, concretions in field just east of gravel road, 0.5 km (0.3 mile) north-north-west of Lillian; from USGS Mesozoic locality D96 ‘Eagle Ford Shale’ 6.1 m (20 feet) above base, concretion 6.7 km (4.15 miles) northeast of centre of Alvarado, Johnson County. All lower part of Eagle Ford Group, *Acanthoceras amphibolum* zone.

Dimensions		D	Wb	Wh	Wb:Wh	U
USNM 420280	c	23.0 (100)	9.0 (39.1)	9.0 (39.1)	1.0	7.6 (33.0)
USNM 420281	c	23.0 (100)	9.5 (41.3)	8.4 (36.5)	1.13	8.7 (37.8)
USNM 420282	c	29.0 (100)	11.3 (38.9)	11.1 (39.0)	1.02	11.1 (38.3)
USNM 400759	c	51.7 (100)	17.8 (34.4)	18.0 (34.8)	0.98	18.2 (35.2)
USNM 400760	c	71.0 (100)	25.0 (35.2)	26.7 (37.6)	0.94	23.3 (32.8)
USNM 400770	c	89.0 (100)	26.5 (29.8)	32.0 (36.0)	0.83	32.9 (37.0)

Description. The species is markedly dimorphic. A near-complete microconch is 57.5 mm in diameter (Pl. 13, figs. 4 and 5), complete macroconchs are 90 mm in diameter (Pl. 13, figs. 10 and 11), and a fragment (Pl. 13, figs. 9, 12) with a whorl height of 33.5 mm suggests a macroconch diameter of nearly 100 mm.

Juveniles are variable. Coiling is very evolute, with $U = 33\text{--}38\%$, the umbilicus shallow, with a flattened umbilical wall and broadly rounded shoulder. The intercostal whorl section is compressed trapezoidal, with flattened convergent flanks, broadly rounded ventrolateral shoulders and flattened venter. The costal section varies from slightly compressed to slightly depressed, with greatest breadth at the umbilical bullae, and polygonal. There are generally 10–13 strong umbilical bullae per whorl, perched on the umbilical shoulder, and connected to the umbilical seam by a low broad rib. Additional non-bullate ribs extend to the umbilical shoulder. The ribs are strong, straight, narrow, prorsiradial and wider than the interspaces. Single intercalated ribs arise around the middle of the flank and strengthen to match the primaries by the ventrolateral shoulder, where all bear a small, sharp inner ventrolateral tubercle that is the same width as the rib. A somewhat broadened rib extends forwards across the ventrolateral shoulder to spinose to feebly clavate inner ventrolateral clavi; a low broad transverse rib extends across the venter and bears a siphonal clavus, weaker than the outer ventrolateral. As size increases the whorls generally become more compressed and denser-ribbed, with coarsely ornamented variants with persistent tubercles having as few as 30 ribs and weakly ornamented variants having as many as 48 ribs per whorl, the inner ventrolateral tubercles weakening markedly.

On the adult body chamber of both macro- and microconchs the umbilical seam egresses and the coiling becomes progressively more evolute. The ribs flex back, becoming coarser and rectiradial, sometimes bunching at bullae. The inner ventrolateral tubercles efface at the beginning of the body chamber, the umbilical bullae efface towards the aperture. The siphonal tubercle declines to give a flattened venter while at the adult aperture ribbing weakens and the venter rounds.

Suture simple, with broad, asymmetrically bifid E/L, narrow, little-incised L and broad L/U₂ (text-figs. 6A, 23A and B).

Discussion. Juveniles are highly variable, from hypernodose to feebly tuberculate (Pl. 14, figs. 1–11, 25, 29). This variation persists into middle growth, with the holotype of *T. stantoni* a coarsely ribbed and tuberculate individual, the holotypes of *T. sellardsi* and *T. rotatile* with subdued tuberculation and the holotype of *T. lillianense* intermediate between the two. *Tarrantoceras multicostatum* Stephenson, 1955 (p. 61, pl. 6, figs. 21–23) comes from a different locality than the types of *T. sellardsi* (and its synonyms), and is kept separate here, with no great confidence. It has an estimated 60 ribs per whorl, a rounded whorl section and early loss of tubercles. An as yet undescribed *Tarrantoceras* species is present in the *Calycoceras canitaurinum* zone in Trans-Pecos Texas,

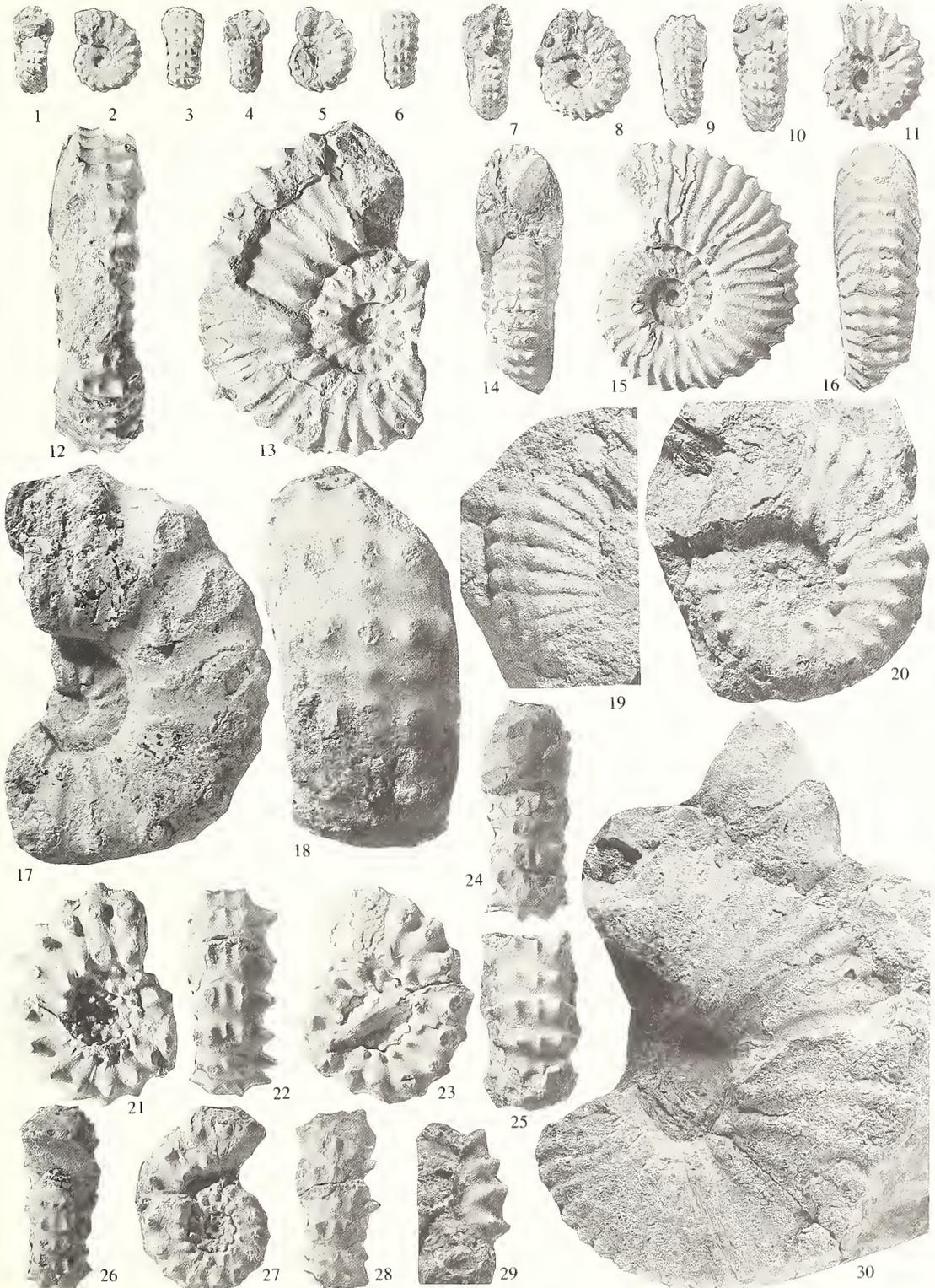
EXPLANATION OF PLATE 14

Figs. 1–16, 19, 20, 25, 29, 30. *Tarrantoceras sellardsi* (Adkins, 1928). 1–3, USNM 400762; 4–6, USNM 400767; 10 and 11, USNM 400766, from USGS Mesozoic locality D12626, 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County. 7 and 8, USNM 400763, from hillside 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) north-east of the town square in Alvarado, Johnson County. 12 and 13, USNM 400764, from USGS locality 11740, left bank of Walnut Creek, 7.6 km (4.75 miles) east-north-east of Mansfield, Tarrant County. 14–16, USNM 400765, from USGS locality D10113, 1.6 km (1 mile) north of Lillian, west of Lillian–Retta road, Johnson county. 25, 29, USNM 420283, from 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) north-east of the town square in Alvarado, Johnson County. All specimens from the basal part of the Eagle Ford Group. 30, the holotype, TMM 34048, from the Bluebonnet Member, 2.25 km (1.5 miles) south-east of Round Rock, Williamson County. 19 is USNM 420285; 20 is USNM 420286, both from USGS Mesozoic locality 14591 at brick pit on Cloice Branch, 1.3 km (0.8 mile) east of South Bosque, McLennan County. All specimens are from the *Acanthoceras amphibolum* zone.

Figs. 21–24, 26–28. *Tarrantoceras cuspidum* (Stephenson, 1953a). 21–24, holotype, USNM 105974; 26–28 paratype, USNM 105975, both from USGS locality 18971, gullies south of old Sherman highway, 4.5 km (2.8 miles) east of Whitesboro, Grayson County, Templeton Member, *Plesiacanthoceras wyomingense* zone.

Figs. 17 and 18. *Cunningtoniceras lonsdalei* (Adkins, 1928). USNM 420270, from the basal shell bed of the Bluebonnet Member, 6.4 km (4 miles) east-north-east of Belton, Bell County. *Acanthoceras bellense* zone.

All figures are $\times 1$.



Wyoming and western South Dakota. It differs from *T. sellardsi* in the persistent strong ventrolateral and siphonal clavi.

Tarrantoceras cuspidum (Stephenson, 1953a) (p. 202, pl. 50, figs. 1–4) from the *P. wyomingense* zone fauna of the Templeton Member of the Woodbine Formation is discussed further below; it is much more coarsely ribbed and tuberculate than any *T. sellardsi* seen. Of the four species of *Tarrantoceras* described (Collignon 1967) from the mid-Cenomanian of the Tarfaya Basin in Morocco, three co-occur, and represent no more than a single variable species, for which we here select the name *T. wrighti*. They are stouter than *T. sellardsi*, with coarser, blunter ribbing and tuberculation; persistent ventrolateral and siphonal tuberculation plus ribs that arise in pairs from bullae suggest they belong to some other genus. The *Tarrantoceras* cf. *rotatile* of Collignon (1967, p. 30, pl. 16, fig. 2) is generically indeterminate from the figure and does not belong to *T. sellardsi*.

Occurrence. *Acanthoceras amphibohum* zone. Central and Trans-Pecos Texas, many localities in New Mexico, Colorado and, rarely, eastern Wyoming.

Tarrantoceras multicoatum Stephenson, 1955

1955 *Tarrantoceras multicoatum* Stephenson, p. 61, pl. 6, figs. 21–23.

Discussion. This species is carefully described and well illustrated by Stephenson (1955). None of the more than 100 specimens of *T. sellardsi* seen matches the holotype and paratype of *T. multicoatum* and they are in consequence kept separate here.

Occurrence. Basal part of the Eagle Ford Group, *Acanthoceras amphibohum* zone, 3.6 km (2.25) miles north-east of Mansfield, Tarrant County only.

Tarrantoceras cuspidum (Stephenson, 1953a)

Plate 14, figs. 21–24, 26–28

1953a *Acanthoceras cuspidum* Stephenson, p. 202, pl. 50, figs. 1–4.

1971 *Protacanthoceras cuspidum* (Stephenson); Kennedy, p. 122.

1980 '*Acanthoceras*' *cuspidum* Stephenson; Wright and Kennedy, p. 99, figs. 56, 59C.

non 1980 '*Acanthoceras*' aff. *cuspidum* Stephenson; Wright and Kennedy, p. 100, figs. 55, 59a and b.

Types. Holotype is USNM 105947, by original designation; a paratype is USNM 18971, both from gullies south of the old Sherman road, 4.5 km (2.8 miles) east of Whitesboro, Grayson County. Paratype USNM 14902 is from a bluff south of the Missouri–Kansas–Texas Railroad, 1.6 km (1 mile) north and 2.9 km (1.85 miles) east of Sadler, Grayson County. All are from the Templeton Member of the Woodbine Formation, *Plesiocanthoceras wyomingense* zone.

Discussion. This species is carefully described and well figured by Stephenson (1955). Of interest are the affinities of the species. Wright and Kennedy (1980) drew attention to the distinctive asymmetry of the ventrolateral clavi, a feature common to several North American acanthoceratines such as *Plesiocanthoceras* and *Dunveganoceras*. We have since noted remarkable similarities in this feature, as well as style of ribbing, to the most ornate variants of *T. sellardsi* (compare Pl. 14, figs. 21–24, 26–28 and Pl. 14, figs. 25, 29) such that we place *cuspidum* in *Tarrantoceras*.

Occurrence. As for types.

Genus PLESIACANTHOCERAS Haas, 1964

(= *Paracanthoceras* Haas, 1963, p. 2; non Furon, 1935, p. 59)

Type species. By original designation: *Metoicoceras wyomingensis* Reagan, 1924 (p. 181, pl. 19, figs. 1 and 2).

Diagnosis. Large, markedly dimorphic. Inner whorls with polygonal whorl section; bullate primaries alternate with secondaries, all ribs bearing strong conical inner and clavate outer ventrolateral and siphonal tubercles with markedly asymmetric profile; intercalated ventral ribs transiently present in some. Secondary ribs disappear after an early stage, siphonal clavi disappear at a progressively earlier ontogenetic stage in stratigraphically younger species. Inner and outer ventrolateral tubercles fuse into prominent horns in middle and late growth stages. Final rib flattened and bar-like over venter.

Suture with broad E/L and L.

Discussion. The type species, *P. wyomingense* is the last member of a Western Interior lineage that can be traced back to *Conlinoceras tarrantense* via *Plesiacanthoceras muldoonense* (Cobban and Scott, 1973). We also refer *Mammites bellsanus* Stephenson, 1953a to *Plesiacanthoceras*. All show variable ontogenetic development in early stages, but are linked by progressively earlier loss of siphonal tubercles, progressively earlier acquisition of primary ribs only and development of a ventrolateral horn at an early ontogenetic stage.

Plesiacanthoceras muldoonense is represented by abundant well-preserved material from the Frontier formation at USGS Mesozoic locality D9801 (south of Lone Bear Road in SW1/4 Sec. 13, T.42N., R.82 W., Johnson County, Wyoming) and USGS Mesozoic locality 23459 (near head of Fisher Draw, about 4.5 km (2.7 miles) south of Kaycee in Sec. 25, T.43 N., R. 82 W., Johnson County, Wyoming). These show inner whorls like those of *Conlinoceras gilberti* and *C. tarrantense*, with alternately long and short ribs, conical inner and clavate outer ventrolateral and siphonal tubercles to a diameter of around 25 mm (Pl. 16, figs. 1–6), beyond which the outer ventrolateral and siphonal tubercles decline, disappearing by 30–40 mm diameter. The ribbing pattern modifies so that all ribs are long, with an umbilical bulla that migrates out to an inner flank position and inner ventrolateral tubercles that strengthen into a clavate upward-directed ventrolateral horn to give a quite distinctive whorl section. Ribbing declines on the outer whorl and tubercles dominate; there may be looping of riblets between ventrolateral horns, while the adult aperture shows the development of a terminal flared ventral rib.

In *Plesiacanthoceras wyomingense* the timing of ontogenetic development of tubercles is again modified, the siphonal row disappears by 10 mm or so, secondary ribs by 10 mm (Pl. 16, figs. 7 and 8), but inner and outer ventrolateral tubercles are present and well-differentiated (Pl. 16, figs. 11–15) to a diameter of 110 mm in microconchs and 160–170 in macroconchs, beyond which the outer ventrolaterals decline and a massive inner ventrolateral horn develops, projecting outwards and above the venter. Adult *P. wyomingense* develop the same high, bar-like rib at the adult aperture as do ancestral *P. muldoonense*.

P. wyomingense is the largest species of the lineage, and retains the 'juvenile' characters of well-differentiated inner and outer ventrolateral tubercles to a diameter where all *P. muldoonense* are horned and adult. It is thus a hypermorphic giant. In spite of this, continuity of characters links the lineage into a single generic grouping in our view; resemblance to *Acanthoceras* and *Cunningtoniceras* in part reflects remote ancestry; in part evolutionary convergence. Old World *Acanthoceras* and *Cunningtoniceras* typically have a broad E/L and a narrow L. The New World taxa also have a broad E/L, but L is broad.

Occurrence. Middle and upper Cenomanian of the US Western Interior and Gulf Coast.

Plesiacanthoceras bellsanum (Stephenson, 1953a)

Plate 2, figs. 4–8; Plate 12, fig. 9, text-fig. 23C

1953a *Mammites bellsanus* Stephenson, p. 204 (*pars*), pl. 49, fig. 3; pl. 51, figs. 8–11.

1971 *Mammites ? bellsanus* Stephenson; Kennedy, p. 122.

Types. The holotype is USNM 105983, paratypes are USNM 105984–6, Templeton Member of the Woodbine Formation, *Plesiacanthoceras wyomingense* zone, branch of Cornelius Creek, 4.3 km (2.7 miles) north 5° east

of Bells, Grayson County. One of the paratypes, USNM 105986, is a *Metoicoceras latoventer* Stephenson, 1953a.

Dimensions	D	Wb	Wh	Wb:Wh	U
USNM 105983	88·7 (100)	38·6 (43·5)	42·7 (48·1)	0·9	20·0 (22·5)
USNM 105985	75·5 (100)	33·3 (44·1)	38·3 (50·7)	0·86	12·2 (16·2)

Description. USNM 105984 shows the earliest growth stage: up to a diameter of 6 mm approximately the shell is globose, smooth, non-tuberculate, bearing only low irregular folds and constrictions (Pl. 12, fig. 9). A fragment at a diameter of 27 mm shows a feeble siphonal clavus, as in *Plesiacanthoceras wyomingense* (Pl. 16, figs. 7 and 8). In middle growth coiling is fairly evolute, with 46% of the previous whorl covered. Whorl section compressed, with maximum breadth at umbilical bulla. Ornament consists of alternately long and short ribs. The former arise at elongate umbilical bullae, 11 per whorl, are rursiradiate, weakened at mid-flank but strengthened into prominent rounded inner ventrolateral tubercles, connected by a broad swelling to strongly clavate outer ventrolaterals with a markedly asymmetric profile. Most ribs are long at the smallest diameter visible; as size increases shorter ribs arise around mid-flank and strengthen into inner and outer ventrolateral tubercles that match those on the long ribs. There are no siphonal tubercles.

USNM 105985 is in a more robust shell, but has weaker umbilical bullae; USNM 105986 is a *Metoicoceras latoventer*; it is very compressed, and has very strong umbilical bullae.

Suture with broad bifid E/L and U₂, L narrower (text-fig. 23C).

Discussion. *P. bellsanum* is easily separated from *Acanthoceras amphibolum* by the very early loss of siphonal tubercles and persistence of alternately long and short ribs into middle growth plus separation of inner and outer ventrolateral tubercles to a large size. It is close to *P. wyomingense*, which has very flat sides, larger outer ventrolateral clavi in middle growth and enormous finger-like ventrolateral horns when adult (Pl. 16, figs. 7 and 8, 11–15).

Occurrence. *Plesiacanthoceras wyomingense* zone of north-central Texas only.

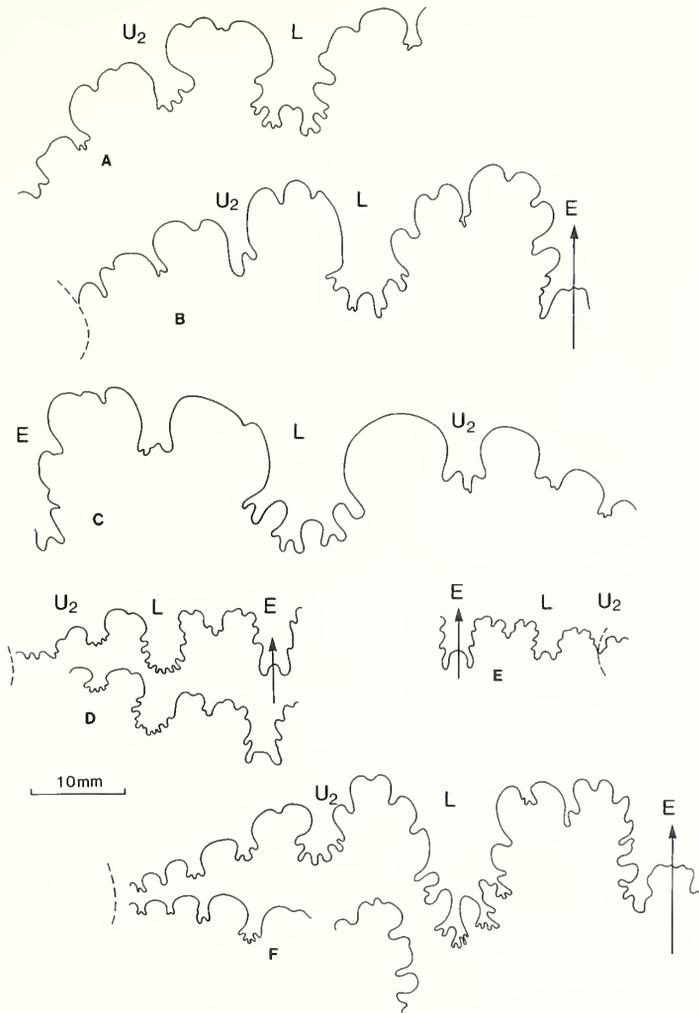
Genus PLESIACANTHOCERATOIDES nov.

Type species. *Protacanthoceras vetula* Cobban, 1987b (p. 21, pl. 10, figs. 1–28; text-fig. 16). Middle Cenomanian *Acanthoceras amphibolum* zone Belle Fourche Shale of the Black Hills area of eastern Wyoming and basal Eagle Ford Group of north central Texas.

Diagnosis. Progenic dwarf. Macroconchs adult at 30 mm or less diameter, microconchs about 60% of diameter of corresponding macroconchs. Whorls subquadrate, middle growth stages with primary ribs with umbilical bullae or not alternating with shorter intercalatories, all ribs with conical inner and clavate outer ventrolateral and siphonal tubercles, constrictions sometimes present. Adult body chambers show crowding and strengthening of ventral ribs and decline of ventral tubercles. Suture simple with broad, little-incised E/L, narrower L and small U₂.

Discussion. *Plesiacanthoceratoides* is a homoeomorph of *Protacanthoceras* Spath, 1923, but whereas the latter is a progenic dwarf derivative of *Acanthoceras rhotomagense*, the former is derived from *Plesiacanthoceras*. Five successive species/subspecies of *Plesiacanthoceratoides* occur in the U.S. Western Interior. The oldest species appears in association with *Plesiacanthoceras muldoonense*. *Plesiacanthoceratoides vetula* (Cobban, 1987b), described below, from the lower part of the *Acanthoceras amphibolum* zone is succeeded by two new subspecies of a third species in the upper part of the *A. amphibolum* zone and a fourth in the *Plesiacanthoceras wyomingense* zone.

Occurrence. Middle and low upper Cenomanian. North-central Texas, Wyoming and Montana.



TEXT-FIG. 24. External sutures. A and B, *Metoicoceras latoventer* Stephenson, 1953a, USNM 105998, 106000. C and D, *M. swallowi* (Shumard, 1860), USNM 105991, 105993. E, *Plesiacanthoceratoides vetula* (Cobban, 1987b), USNM 388189. F, *Metoicoceras geslinianum* (d'Orbigny, 1850), USNM 22938.

Plesiacanthoceratoides vetula (Cobban, 1987b)

Plate 9, figs. 1–25, 28; text-fig. 24E.

Types. Holotype is USNM 388189, paratypes USNM 388190–7, from the middle Cenomanian *Acanthoceras amphibolum* zone fauna of the Belle Fourche Shale at USGS Mesozoic locality D5900, on the Old Woman anticline south-west of the Black Hills, head of Elm Creek in W1/2 sec. 14, T. 36 N, R. 62 W., Niobrara County, Wyoming.

Material. Figured specimens USNM 420287 to 420292, from the concretions in the lower part of the Eagle Ford Group at USGS Mesozoic locality D12626, 8.9 km (5.2 miles) northeast of Mansfield, Tarrant County, Texas. *A. amphibolum* zone. Twelve unfigured specimens, USNM 420293, from the same locality.

<i>Dimensions</i>		D	Wb	Wh	Wb:Wh	U
Macroconchs						
USNM 420287	c	19.3 (100)	10.2 (52.8)	9.4 (48.7)	1.09	2.9 (15.0)
USNM 420288	c	19.0 (100)	9.6 (50.5)	8.9 (46.8)	1.08	2.6 (13.7)
USNM 420289	c	20.3 (100)	10.5 (51.7)	9.4 (46.3)	1.12	3.4 (16.7)
Microconch						
USNM 420290	c	13.8 (100)	8.0 (57.9)	6.7 (48.5)	1.19	1.6 (11.6)

Description. Markedly dimorphic, macroconchs 20 mm in diameter, microconchs two thirds diameter of macroconchs. Coiling very involute with tiny, deep umbilicus. Whorl section depressed, quadrate in intercostal section, polygonal in costal section, with greatest breadth at umbilical bullae when present and below mid-flank when not. Earliest ornamented stages bear 14 ribs per whorl, limited to the outer flank, with conical inner, clavate outer ventrolateral and siphonal tubercles. As size increases, ribs extend down the flank and are irregularly long and short, long ribs extending to the umbilical shoulder, where they may develop feeble bullae, with in adults, up to 18 ribs of which 6 or 7 are bullate. Periodic broad, deep constrictions are present on the phragmocone, flanked by ribs, while there are occasional non-tuberculate ribs in early and middle growth.

Adult body chambers show a crowding of ribs and strengthening ventrally to produce a marked ventral chevron; whereas tubercles dominate ribs on the phragmocone, the reverse is true on the last part of the body chamber. There is a marked ventral lappet at the adult aperture.

Suture line very simple with broad bifid E/L, narrow L and little incised U₂.

Discussion. Middle growth stages with constrictions are very close to those of juvenile *A. amphibolum amphibolum*. Mature body chamber ornament of *P. vetula* and disparate size immediately distinguishes the two.

Occurrence. *A. amphibolum* zone of north-central Texas and Wyoming.

Subfamily MAMMITINAE Hyatt, 1900 p. 588

(= Buchiceratinae Hyatt, 1903, p. 26; Metoicoceratidae Hyatt, 1903, p. 115; Fallotitinae Wiedmann, 1960, p. 741)

Genus METOICOCERAS Hyatt, 1903, p. 115

Type species. By subsequent designation by Shimer and Shrock 1944, p. 591: *Ammonites swallowi* Shumard, 1860 (p. 591).

Metoicoceras swallowi (Shumard, 1860)

Text-fig. 24C and D.

1860 *Ammonites swallowi* Shumard, p. 591.

1953a *Metoicoceras swallowi* (Shumard); Stephenson, p. 207, pl. 51, figs. 1-3; pl. 52, figs. 1-5 (with full synonymy).

1953a *Metoicoceras swallowi macrum* Stephenson, p. 209, pl. 51, figs. 4-7.

Discussion. Stephenson described all of the surviving material of this species in detail as well as the early uncertainties surrounding it. His variety *macrum*, described as more compressed and with feebler ornament than the nominate subspecies, is regarded as a strict synonym. As already noted (p. 81) there are no longer outcrops at the type locality and the exact age of the species is unknown. All that can be said is that the suture with its little-incised elements (text-fig. 24C and D) suggests it may be from quite a high horizon in the Cenomanian, and is very distinct from that of *M. latoventer* (text-fig. 24A and B), but closer to that of *M. geslinianum* (d'Orbigny, 1850) (text-fig. 24F).

Occurrence. Templeton Member of Woodbine Formation in Lamar County (see Stephenson 1953a p. 209 for details).

Metoicoceras latoventer Stephenson, 1953a

Plate 17, figs. 1 and 2; text-fig. 24A and B

- 1953a *Metoicoceras latoventer* Stephenson, p. 209, pl. 53, figs. 1–9; pl. 54, figs. 9–11.
 ?1953a *Metoicoceras crassicostrae* Stephenson, p. 210, pl. 58, figs. 6–8.
 1953a *Manmites? bellsanus* Stephenson, p. 204 (*pars*), *non* pl. 49, fig. 3; pl. 51, figs. 8–11.

Types. The holotype of *M. latoventer* is TMM 2574, from the Templeton Member of the Woodbine Formation, 6.4 km (4 miles) east of Whitesboro; one paratype is in the same collection. Paratypes USNM 105998–105601, 106002a–j are from gullies just south of the old Sherman Highway, 4.5 km (2.8 miles) east of the centre of Whitesboro, also from the Templeton. The holotype of *Metoicoceras crassicostrae* is USNM 106003 from the Templeton Member on Cornelius Creek, 4.3 km (2.7 miles) north 5° east of Bells in Grayson County. All *Plesiacanthoceras wyomingense* zone.

Material. OUM KT3926–7, 3929–3936, from the Templeton Member of the Woodbine Formation, gullies just south of old Sherman Highway, 4.5 km (2.8 miles) east by south of the centre of Whitesboro, Grayson County. *Plesiacanthoceras wyomingense* zone. USNM 105986, a paratype of *Manmites? bellsanus* Stephenson, 1953a, is from the same horizon and locality as the holotype of *Metoicoceras crassicostrae* (see above).

<i>Dimensions</i>	D	Wb	Wh	Wb:Wh	U
USNM 105998	12.3 (100)	7.0 (56.9)	5.4 (43.9)	1.30	2.2 (17.9)
USNM 106001	24.0 (100)	13.4 (55.8)	10.9 (45.4)	1.23	4.9 (20.4)
USNM 106002	c 65.0 (100)	27.7 (42.6)	30.7 (41.2)	0.9	15.8 (24.3)
USNM 106000	76.3 (100)	31.0 (40.6)	33.4 (43.8)	0.93	18.9 (24.8)
Holotype of <i>M. crassicostrae</i> USNM 106003	94.5 (100)	37.8 (40.0)	40.8 (43.2)	0.93	25.1 (26.6)

Discussion. Stephenson (1953a) provides a careful account of this species, and his description is not repeated here. The holotype of *M. latoventer* is an adult, as in the largest paratype figured by Stephenson (1953a, pl. 53, figs. 8 and 9), 113–120 mm in diameter. There are no significant differences between these specimens and the holotype (and only known specimen) of *M. crassicostrae* (Pl. 17, figs. 3 and 4), a near complete adult 94.5 mm in diameter, and we suspect but cannot prove them conspecific. *M. crassicostrae*, now dated as from the Texas equivalents of the US Western Interior *Plesiacanthoceras wyomingense* zone, is the oldest species of the genus. It, like *Metoicoceras praecox* Haas, 1949 (p. 15, pls. 5–7; text-figs. 5–9) of the *Calycocheras canitaurinum* zone, differs from all other species of the genus in the presence of feeble siphonal tubercles in early growth, up to a diameter of 20–25 mm in *M. latoventer* and 28–34 mm in *M. praecox*. Whereas *M. praecox* has the compressed whorl section and low broad ribs seen in later *Metoicoceras* species (including the type), *M. latoventer* has an only slightly compressed whorl even when adult, with persistent inner ventrolateral tubercles to the beginning of the outer whorl whereas these are lost at an early ontogenetic stage in later species and even lost in some variants beyond a diameter of 20 or so millimetres. This, plus the presence of a siphonal tubercle in youth suggests the origin of *latoventer*, and hence *Metoicoceras*, lay in some contemporary acanthoceratines such as *Plesiacanthoceras*, where there are parallel trends of progressively earlier loss of siphonal clavi and differentiated inner and outer ventrolateral tubercles. *Thomelites* Wright and Kennedy, 1973, suggested as a possible ancestor to *Metoicoceras* (e.g. Wright and Kennedy 1981, p. 40) may thus be no more than a convergent compressed acanthoceratine and not a close ally or ancestor.

Occurrence. As for types.

Suborder ANCYLOCERATINA Wiedmann, 1966, p. 54
 Superfamily TURRILITACEAE Gill, 1871, p. 3
 Family HAMITIDAE Gill, 1871, p. 3
 Genus HAMITES Parkinson, 1811, p. 145

(= *Torneutoceras* Hyatt, 1900, p. 586 (objective synonym); *Stomohamites* Breistroffer, 1940 p. 85; *Hamitella* Breistroffer, 1947 p. 100 (84), *nom. nov. pro. Helicoceras* d'Orbigny, 1842 p. 611, *non* Koenig, 1825 p. 19)

Type species. Hamites attenuatus J. Sowerby, 1814 (p. 137, pl. 61, figs. 4 and 5) by the subsequent designation of Diener (1925, p. 88).

Hamites cimarronensis (Kauffman and Powell, 1977)

Plate 15, figs. 11, 13, 15, 17, 19–21

1953a *Hamites* ? sp. Stephenson, p. 197.

1977 *Stomohamites simplex cimarronensis* Kauffman and Powell, p. 97, pl. 9, figs. 1, 3 and 4; text-figs. 5 and 6.

Type. Holotype is USNM 167160, the original of Kauffman and Powell (1977, pl. 9, fig. 1) from USGS Mesozoic Locality 30235 in Cimarron County, Oklahoma. It is from the Hartland Member of the Graneros Shale, of middle Cenomanian age.

EXPLANATION OF PLATE 15

Figs. 1, 3, 5, 6, 10, 12, 16, 18, 22, 23, 25. *Turrilites* (*Turrilites*) *acutus* Passy, 1832, including transitional forms to *T. (T.) costatus* Lamarck, 1822 (figs. 10, 23). 1 is TMM 21055; 3 is USNM 420302; 6 is USNM 420305, 10 is TMM 35359; 16 is USNM 420303, 23 is USNM 420308; 25 is USNM 420304, from the basal shell bed of the Bluebonnet Member, Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County, *Acanthoceras bellense* zone. 5 is USNM 420311; 12 is USNM 420310; 18 is USNM 420312; 22 is USNM 420309, all from USGS Mesozoic locality D12626, roadside 8.9 km (5.5 miles) north-east of Mansfield, Tarrant County, basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone.

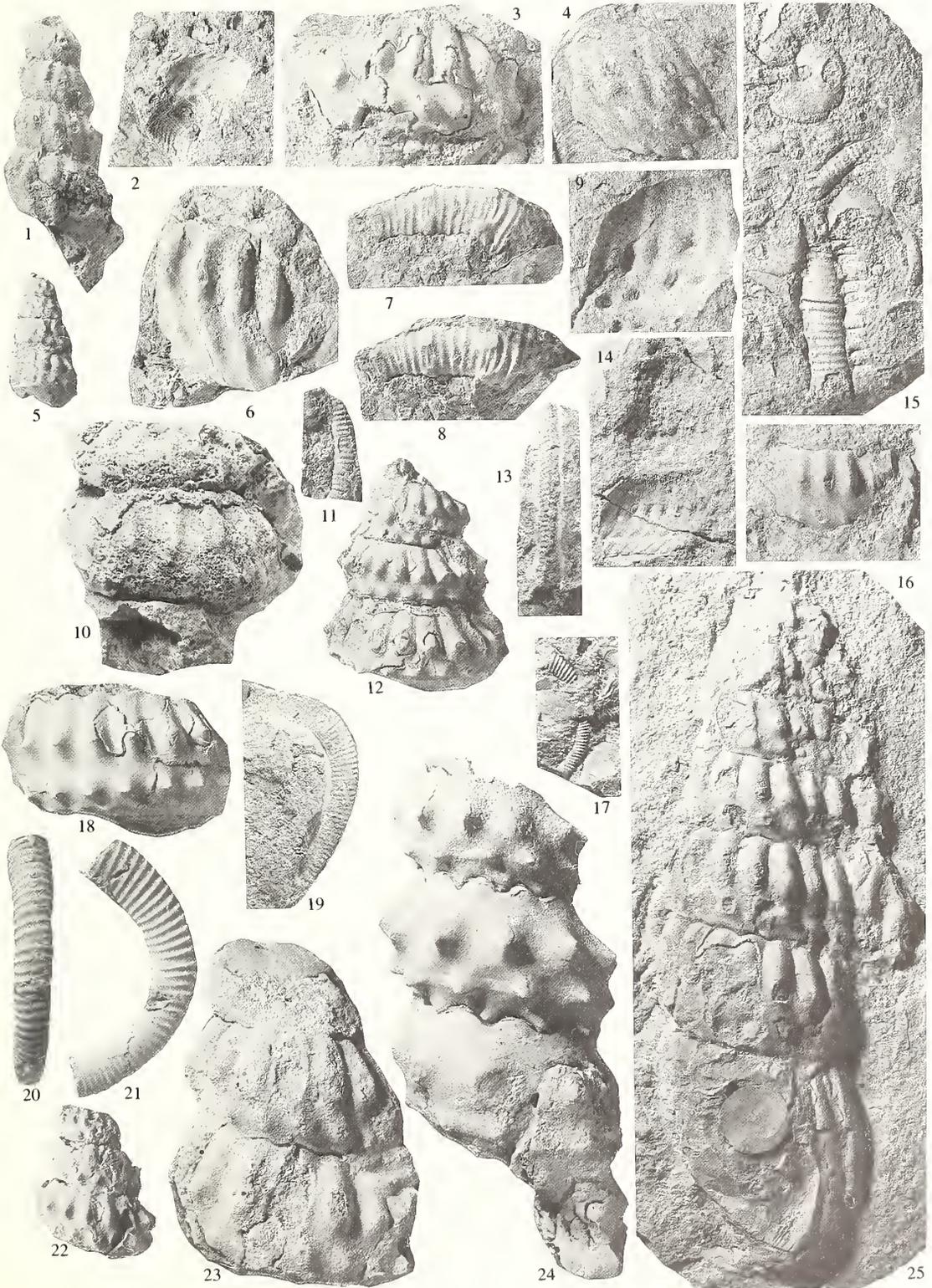
Figs. 2, 4, 9, 14. *Ostlingoceras* (*Ostlingoceras*) *davisense* Young, 1958. Specimens are from USGS Locality 14598, temporary exposure 0.8 km (0.5 mile) east of South Bosque, near railroad, McLennan County, Pepper Shale (inferred); *Forbesiceras brundrettei* zone.

Figs. 7 and 8. *Anisoceras* cf. *plicatile* (J. Sowerby, 1819), USNM 420299, 0.3 km (0.2 mile) south of Mountain Creek, 6.1 km (3.8 miles) north-east of town square in Alvarado, Johnson County. Basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone.

Figs. 11, 13, 15, 17, 19–21. *Hamites cimarronensis* (Kauffman and Powell, 1977). 11, USNM 420297; 17, USNM 420298, from USGS Mesozoic locality D9502, concretion in field 0.5 km (0.3 mile) north-west of Lillian, Johnson County, basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone. 13, 19, USNM 424123, from USGS locality 14591, abandoned brickpit on Cloice Branch, near Waco, McLennan County. 15, USNM 420296, from the Moody Hills opposite Baggett station about 7.2 km (4.5 miles) south of McGregor, McLennan County. Both *Acanthoceras amphibolum* zone. 20 and 21, USNM 420294, from Bird Creek, 6.4 km (4 miles) east-north-east of Belton, Bell County, *Acanthoceras bellense* zone.

Fig. 24. *Turrilites* (*Turrilites*) *dearingi* Stephenson, 1953a. USNM 420316, from roadcut on east side of Texas highway 360, 1.9 km (1.2 miles) south of bridge over Trinity River, Tarrant County. Tarrant Formation, *Conlinoceras tarrantense* zone.

Figures 20 and 21 are $\times 2$; the remainder are $\times 1$.



Material. USNM 420294 and 420295, from the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group, Bird Creek, Bell County; USNM 420296 from the same horizon near Waco, *Acanthoceras bellense* zone. USNM 420297 and 420298 from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone, USGS Mesozoic locality D9502, concretion in field 0.5 km (0.3 mile) NW of Lillian, Johnson County. A specimen from USGS Locality 14591, abandoned brickpit on Cloice Branch near Waco, McLennan County. OUM KT3937–3939 from the Templeton Member of the Woodbine Formation, *Plesiachanthoceras wyomingense* zone, gullies just south of old Sherman Highway, 4.5 km (2.8 miles) east by south of Whitesboro, Grayson County.

Discussion. Kauffman and Powell (1977) based their *Stomohamites simplex cimarronensis* on a series of crushed fragments. They differentiated it from *H. simplex* of d'Orbigny (1842, p. 550, pl. 134, figs. 12–14) (see Kennedy and Juignet 1983, p. 13, figs. 15a–d; 17a–w; 36j; 37v and w) because it had four shafts rather than three, and was larger. The complete adult form of *H. simplex* is unknown to us, whereas the reconstruction given by Kauffman and Powell (1977, text-fig. 5) shows a smaller shell than is represented by English specimens of *H. simplex* (Kennedy 1971, pl. 1, figs. 1–8). Instead, *H. cimarronensis* differs from *H. simplex* in its dense ribbing, with a rib index of up to 8 at apparent whorl heights of 11–28 mm. In *H. simplex*, the index ranges from 4.5 to 7.

Occurrence. *Acanthoceras bellense*, *Acanthoceras amphibolum* and *P. wyomingense* zones in central Texas. Similar fragments are widespread in this interval in the US Western Interior north as far as Wyoming.

Family ANISOCERATIDAE Hyatt, 1900, p. 587
 (= Algeritidae Spath, 1925, p. 190)
 Genus ANISOCERAS Pictet, 1854, p. 705

Type species. By original designation: *Hamites saussureanus* Pictet, 1847, p. 374, pl. 13, figs. 1–4.

Anisoceras cf. *plicatile* (J. Sowerby, 1819)

Plate 15, figs. 7 and 8

compare:

- 1819 *Anisoceras plicatile* J. Sowerby, p. 281, pl. 234, fig. 1.
 1983 *Anisoceras plicatile* (J. Sowerby); Kennedy and Juignet, p. 25, fig. 16a–m, p and q; 19a–c; 341, m (with synonymy).

Material. USNM 420299–420300, from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone, concretion on hillside 0.3 km (0.2 mile) south of Mountain Creek and west of secondary road, 6.1 km (3.8 miles) north-east of town square in Alvarado, Johnson County.

Discussion. Whorl section is slightly compressed oval with a rib index of 6. Rounded lateral tubercles are linked by groups of 2 or 3 ribs to larger, rounded ventrolateral tubercles, linked over

EXPLANATION OF PLATE 16

Figs. 1–6, 9, 10. *Plesiachanthoceras muldoonense* (Cobban and Scott, 1973). 1–3, USNM 388117; 4–6, USNM 388114; 9 and 10, USNM 388121, from calcareous siltstone concretions in the Frontier Formation at USGS Mesozoic locality 23459, near head of Fisher Draw about 4.5 km (2.7 miles) south of Kaycee in sec. 25, T. 43 N., R. 82 W., Johnson County, Wyoming.

Figs. 7, 8, 11–15. *Plesiachanthoceras wyomingense* (Reagan, 1924). 7 and 8, USNM 388164; 11–15, USNM 388165, all from the Belle Fourche Shale at USGS Mesozoic locality 22871, about 9.6 km (6 miles) north-east of Alzada in the SE $\frac{1}{4}$ sec. 6, T. 95 N., R. 59 E., Carter County, Montana.

All figures are $\times 1$.



KENNEDY and COBBAN, *Plesiacanthoceras*

the venter by groups of 2–3 ribs with 2–3 intercalatories between. With such small fragments confident identification is impossible.

Occurrence. As for material.

Family BACULITIDAE Gill, 1871, p. 3
Genus SCIPONOCERAS Hyatt, 1894, p. 578

(= *Cyrtochilus* Meek, 1876, p. 392 (*non* Jakowlew, 1875, p. 252); *Cyrtochilella* Strand, 1929, p. 8).

Type species. By original designation: *Hamites baculoide* Mantell, 1822 (p. 123, pl. 23, figs. 6 and 7).

Sciponoceras? sp.

Plate 12, figs. 12–14

Material. TMM 2425, from the base of the Bluebonnet Member of the Lake Waco Formation of the Eagle Ford Group at TMM locality 245-T-24, about 0.8 km (0.5 mile) south-east of Round Rock, Williamson County. *Acauthoceras bellense* zone.

Description. Specimen is wholly septate with a maximum whorl height of 21.5 mm, and retains extensive areas of recrystallized shell. Whorl section compressed oval with whorl breadth to height ratio 0.8. Dorsum somewhat flattened, flanks very broadly rounded, venter rounded, only slightly narrower than dorsum. Shell surface ornamented by closely and evenly spaced growth lines and riblets. These are somewhat effaced on the dorsum, markedly concave on the dorsolateral area but markedly prorsiradiate and straight on the lateroventral region, intersecting the line of the venter at 18°, strengthening, and crossing the venter in a linguoid peak. This same ornament is present on the internal mould. There are no constrictions visible. Imperfectly exposed sutures have rectangular, bifid elements.

Discussion. This remarkable species differs from all other described Cenomanian Baculitidae in the absence of constrictions, the presence of which differentiate *Sciponoceras* from *Baculites*. The latter is known from the Turonian onwards, and we doubt that the present specimen suffices to extend the range of the genus back for nearly half a stage. In consequence we refer it to *Sciponoceras?* sp.

Occurrence. As for material.

Family TURRILITIDAE Gill, 1871, p. 3
(= Pseudhelicoceratinae Breistroffer, 1953, p. 1350)
Genus and Subgenus OSTLINGOCERAS Hyatt, 1900, p. 587

Type species. *Turrilites puzosianus* d'Orbigny, 1842 (p. 587, pl. 123, figs. 1 and 2) by original designation.

Ostlingoceras (Ostlingoceras) brandi Young, 1958.

1958 *Ostlingoceras brandi* Young, p. 287, pl. 40, figs. 4 and 5, 7; text-fig. 1 n.

1959 *Ostlingoceras brandi* Young; Young, p. 37, pl. 8, figs. 2, 7.

1965 *Ostlingoceras (Ostlingoceras) brandi* Young; Clark; p. 37, pl. 8, figs. 2, 7.

Type. Holotype is TMM 10281 from the base of the Boquillas Formation on the NE flank of the Davis Mountains, Jeff Davis County, Texas. *Forbesiceras brundrettei* zone.

Material. One specimen from USGS locality 14592, old brickpit on Cloice Branch, 1.3 km (0.8 mile) east of South Bosque, McLennan County. Probably from the Pepper Shale; *Forbesiceras brundrettei* zone.

Discussion. Specimen is an external mould of a single whorl. It shows low, even, rounded, oblique ribs, without tubercles on the outer whorl face, weakening markedly towards the base of the whorl. The lower surface bears much finer, markedly prorsiradiate riblets and growth striae.

Occurrence. *F. brundrettei* zone. In addition to the present record it occurs at Gold Hill and Chispa Summit as well as the type locality, in Trans-Pecos Texas.

Ostlingoceras (Ostlingoceras) davisense Young, 1958

Plate 15, figs. 2, 4, 9, 14

1958 *Ostlingoceras davisense* Young, p. 289, pl. 39, figs. 29, 34.

1965 *Ostlingoceras (Ostlingoceras) davisense* Young; Clark, p. 36, pl. 8, figs. 1, 3.

Type. Holotype is TMM 10286, from the base of the Boquillas Formation on the north-east flank of the Davis Mountains, Jeff Davis County, Texas.

Material. Three specimens from USGS Locality 14598, temporary exposure 0·8 km (0·5 mile) east of South Bosque, near railroad, McLennan County. *F. brundrettei* zone, Pepper Shale (inferred).

Discussion. Specimens are external moulds only. Ornament consists of low, oblique, prorsiradiate ribs with a weak tubercle on the upper third of the outer whorl face, a second two thirds down the face and two closely spaced tubercles at the lower whorl suture, the lowermost concealed below the suture. The species is in some respects transitional to *Mariella*.

Occurrence. *F. brundrettei* zone. In addition to the present record the species occurs at Gold Hill and Chispa Summit as well as the type locality in Trans-Pecos Texas.

Genus and Subgenus *TURRILITES* Lamarck, 1801, p. 102

(= *Euturrilites* Breistroffer, 1953, p. 1351; *Turbinites* Dubourdieu, 1953, p. 42 *non* Martin 1809, pl. 38).

Type species. *Turrilites costatus* Lamarck, 1801 (p. 102) by original designation.

Turrilites (Turrilites) acutus Passy, 1832

Plate 12, fig. 10; Plate 15, figs. 1, 3, 5, 6, 10, 12, 16, 18, 22, 23, 25.

1832 *Turrilites acutus* Passy, p. 334, pl. 16, figs. 3 and 4.

1977a *Turrilites acutus* Passy, Cobban, p. 22, pl. 4, figs. 4 and 5.

1977b *Turrilites acutus* Passy; Cobban, figs. 2i, 2k.

1983 *Turrilites (Turrilites) acutus* Passy; Kennedy and Juignet, p. 51 (with synonymy).

1985 *Turrilites (Turrilites) acutus* Passy; Atabekian, p. 77, pl. 28, figs. 5–13; pl. 29, figs. 1–10; pl. 30, figs. 1–11 (with synonymy).

Lectotype. The original of Passy (1832, pl. 16, fig. 3) designated by Juignet and Kennedy (1976, p. 65), and from the middle Cenomanian Rouen Fossil Bed of Côte Ste Catherine, Rouen, Seine-Maritime, France. It is in the collections of the Sorbonne, now in the Université Paris VI (Pierre et Marie Curie), Paris.

Material. Numerous specimens: USNM 420309–420313, from USGS Mesozoic locality D12626, roadside 8·9 km (5·5 mile) north-east of Mansfield, Tarrant County, in a loose concretion. One specimen, USNM 420308, from USGS Mesozoic locality D9502, concretions in field just east of gravel road, 0·5 km (0·3 mile) north-north-west of Lillian, Johnson County. Six specimens USNM 420307, from concretion on hillside 0·3 km (0·2 mile) south of Mountain Creek, 6·1 km (3·8 miles) north-east of the town square in Alvarado, Johnson County. All are from the basal part of the Eagle Ford Group, *Acanthoceras amphibolum* zone. USNM 420301–420306 and OUM KT2058 are from the basal shell bed of the Bluebonnet Member of the Lake Waco Formation on Bird Creek, 6·4 km (4 miles) east-north-east of Belton, Bell County, *Acanthoceras bellense* zone.

Discussion. The specimens from the *A. amphibolum* zone are very typical representatives of this well-known species. Most of those from the *A. bellense* zone are equally unexceptional, but a few (e.g. Pl. 15, fig. 23) are transitional to *T. costatus*. Clark (1965) illustrated and described specimens from

what he spoke of as Tarrant Formation on Pepper (e.g. Bird) Creek that are actually from the basal shell bed of the Bluebonnet Member. The original of his pl. 20, figs. 1, 2 and 7 seem to be transitions from *T. acutus* to *T. costatus* (e.g. Pl. 15, figs. 1, 10, 23 herein). The same author's *T. scheuchzerianus* (1965, pl. 20, fig. 6) is no more than a worn example of this passage form, as are others cited by him on p. 54.

Occurrence. *Turrilites acutus* first appears in the middle of the middle Cenomanian, where it is widespread and common; it ranges to the lower part of the upper Cenomanian, where it is generally rare. It is known from western and eastern Europe, the USSR, North Africa, Nigeria, Angola, Zululand, Madagascar and Mozambique. In the United States there are records from California, Texas, New Mexico and Colorado; in the Western Interior and Texas it ranges from the *Acanthoceras bellense* zone to the *A. amphibolum* zone, being particularly widespread in the latter.

Turrilites (Turrilites) dearingi Stephenson, 1953a

Plate 12, figs. 5 and 6, 11; Plate 15, fig. 24

- 1953a *Turrilites dearingi* Stephenson, p. 197, pl. 44, figs. 6–8.
 1965 *Turrilites (Turrilites) dearingi* Stephenson; Clark, p. 55, pl. 20, fig. 4.
 1971 *Turrilites dearingi* Stephenson; Kennedy, p. 31.
 1976 *Turrilites dearingi* Stephenson; Juignet and Kennedy, p. 65.

Types. Holotype is USNM 105956, paratype JPC 4134 (cast is OUM KT6105 and USNM 105957), both from the Tarrant Formation at USGS locality 20788, small branch of Big Bear Creek, 2.4 km (1.5 miles) east of Euless, Tarrant County. *Conlinoceras tarrantense* zone.

Material. USNM 420136, plus casts of two specimens in the Gerry Kienzlen Collection (Dallas, Texas) (casts USNM 420314, 420315; OUM KT 6106–7), all from the same horizon as the types, roadcut on east side of Texas Highway 360, 1.9 km (1.2 miles) south of bridge over Trinity River, Tarrant County.

Description. Coiling sinistral; apical angle 21° approximately; whorls in close contact. Intercostal section shows concealed upper surface of whorls markedly concave, outer face evenly convex, lower face convex. Costal section shows outer whorl face with strikingly concave upper, middle and lower sections. There are 13–18 ribs per whorl. They arise at the crenulated upper whorl suture and are feebly prorsiradiate, strengthening into a strong pointed tubercle at the junction of upper and middle sectors of the outer whorl face. A low, broad prorsiradiate rib connects to a smaller, feebly clavate pointed tubercle at the junction of the middle and lower sections of the outer whorl face, and a further broad prorsiradiate rib connects to a slightly smaller tubercle of similar shape to those in the second row. This third row of tubercles is housed in a marked notch in the suture between the whorls, such that all three rows of tubercles are visible. The lower whorl face bears faint ribs that correspond to grooves in the upper whorl face of the succeeding whorl. Some specimens show a faint spiral ridge linking the lower two rows of tubercles.

Sutures not seen.

Discussion. Stephenson (1953a) compared this species only with the Lower Cenomanian *Turrilites bosquensis* Adkins, 1920 (a *Wintonia*) and Clark (1965) with *Turrilites morrisii* of Sharpe (1857) (= *carcitanensis* Matheron, 1842) (a *Neostlingoceras*). Instead, it is a close ally of *Turrilites acutus*

EXPLANATION OF PLATE 17

Figs. 1 and 2. *Metoicoceras latoventer* Stephenson, 1953a. TMM 21677, a paratype from the Templeton Member 4 miles east of Whitesboro, Grayson County.

Figs. 3 and 4. *Metoicoceras crassicosatae* Stephenson, 1953a. The holotype USNM 106003, from the Templeton Member on a branch of Cornelius Creek 4.4 km (2.75 miles) north 5° east of Bells, Grayson County.

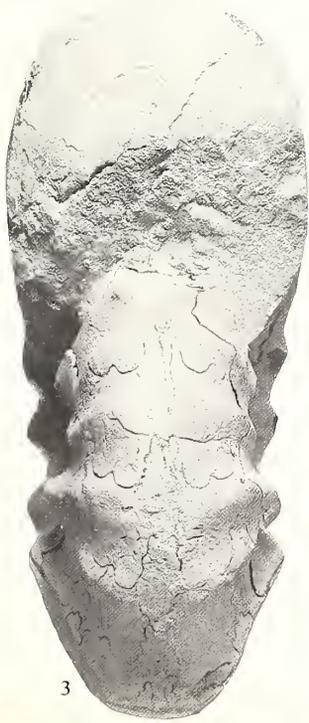
All figures are natural size.



1



2



3



4

Passy, 1832 (p. 334, atlas, p. 7, pl. 16, figs. 3 and 4) from which it differs only in that the lowest row of tubercles is only slightly smaller than the second row and is much more conspicuous, not being concealed by the succeeding whorl. In the lectotype of *T. acutus* and topotypes this tubercle is far less conspicuous, although European *T. acutus* show the same range of rib density. Kennedy (1971, p. 31) thought *T. dearingi* might be an aberrant *T. acutus*, while Juignet and Kennedy (1976, p. 65) regarded it as a synonym of *T. acutus*. Of the five specimens before us, the types and the large Conlin specimen (Pl. 15, fig. 24) show the prominent lowest row of tubercles to advantage, and if this is a consistent difference, it suggests that *T. dearingi* is probably a local subspecies of *T. acutus*. It is kept separate here, but whether treated as a species or subspecies of *T. acutus* is of no importance.

Occurrence. *Conlinoceras tarrantense* zone. Tarrant Formation of north-east Texas only.

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THE ACTINOPTERYGIAN FISH *PROHALECITES* FROM THE TRIASSIC OF NORTHERN ITALY

by ANDREA TINTORI

ABSTRACT. The bony fish *Prohalecites* is redescribed from new well-preserved material from the locality of Ca' del Frate (northern Italy), dated close to the Ladinian–Carnian boundary. A few poorly preserved specimens from the type locality, Perledo (Ladinian), have also been restudied. The specimens represent several ontogenetic stages as evidenced by vertebral column development, and it is concluded that in structure *Prohalecites* is intermediate between the Parasemionotidae and *Dapedium* plus the Pholidophoridae, being closer to the last two. In fact *Prohalecites*, though similar to some of the Parasemionotidae in the dermal skull covering, has a splint-like quadratojugal, similar in shape and position to that of the Pholidophoridae, but not fused to the quadrate (as is the case for *Dapedium*), and ural neural arches approaching the uroneural condition of the Pholidophoridae.

NEW finds in the Kalkschieferzone (top member of the Meride Kalk) near Ca' del Frate (Viggiú, Varese) offer an opportunity for a revision of the genus *Prohalecites* Deecke 1889, so far known only from the Ladinian of Perledo (Como). New stratigraphical data (Gaetani *et al.*, in prep.) point to an uppermost Ladinian to lowermost Carnian age, which is somewhat older than previously thought (Tintori *et al.* 1985). The Kalkschieferzone is characterized by more or less marly limestone, often in thin laminated layers. The depositional environment was marine, but probably influenced by continental areas; this hypothesis is supported by the presence of the conchostracan crustacean *Palaeolimnadia*, a fresh-water dweller (Tintori, in press). The body parts and eggs of these organisms are often well preserved because of the total lack of oxygen in the fossilization environment.

Prohalecites has not been found in the Besano–Monte San Giorgio Scisti Ittiolitici di Besano (Grenzbitumenzone) (Tintori and Renesto 1983), which includes the Anisian–Ladinian boundary. Unfortunately most of the original material used by Bellotti (1857), Deecke (1889) and De Alessandri (1910) has been lost or destroyed during the last World War. Furthermore, no material has been collected in the Calcare di Perledo–Varenna (Calcare di Perledo in Tintori *et al.* 1985) for at least fifty years since the cessation of quarrying.

MATERIAL

So far only the topmost part of the Ca' del Frate horizon (now thought to be the basal part of the Kalkschieferzone of the Meride Kalk) has been extensively studied. Most of the *Prohalecites* specimens come from only two bedding planes. Those from the lower, paler bedding planes (a few cm below the upper darker one) are generally smaller. This does not represent a taxonomic difference but rather a mass mortality event which affected a school of juvenile specimens, perhaps in a different season (summer?) from the later event which caused the mortality at the upper level. A great number of *Palaeolimnadia* has been found on a bedding plane similar to the upper one, and it is hypothesized that this upper deposition may have occurred during the rainy season (autumn/winter?), the Conchostraca having been transported into the Ca' del Frate marine environment by river flooding from a nearby island (Tintori, in press).

On both surfaces the small fishes occur at an average of about one in 100 cm² and, even though most of them show more or less the same orientation, a few specimens are randomly scattered. The

alignment may be due to a weak bottom current, but this seems unlikely since the fishes are always complete and their bones articulated. Most of the larger fishes, as well as some of the smaller, have the skull crushed dorso-ventrally, showing either the skull-roof or the gular region with the jaws and sometimes part of the snout. This kind of preservation is related to the very wide head of *Prohalecites*. The body is usually preserved in lateral view, but occasionally it is irregularly twisted. Thus the sea bottom must have had very low energy currents and a very high sedimentary rate to cause rapid burial of the dead fishes by the calcareous mud. Anoxic conditions were also present (see above).

SYSTEMATIC PALAEOLOGY

Subclass ACTINOPTERYGII Cope 1871

Infraclass NEOPTERYGII Regan 1923

Genus PROHALECITES Deecke, 1889

PROHALECITES PORROI (Bellotti, 1957)

Plate 1; Text-figures 1-9

- 1857 *Pholidophorus porro* Bellotti, p. 430.
 1853-1860 *Pholidophorus porro* Bellotti; Costa, p. 65, pl. 5, fig. 9-9b.
 1866 *Pholidophorus porro* Bellotti; Kner, p. 185.
 1889 *Prohalecites porro* (Bellotti); Deecke, p. 125, pl. 7, figs. 5-7.
 1895 *Prohalecites* (?) *porro* (Bellotti); Woodward, p. 489.
 1910 *Prohalecites porroi* (Bellotti); De Alessandri, p. 137, pl. 9, figs. 4-5.

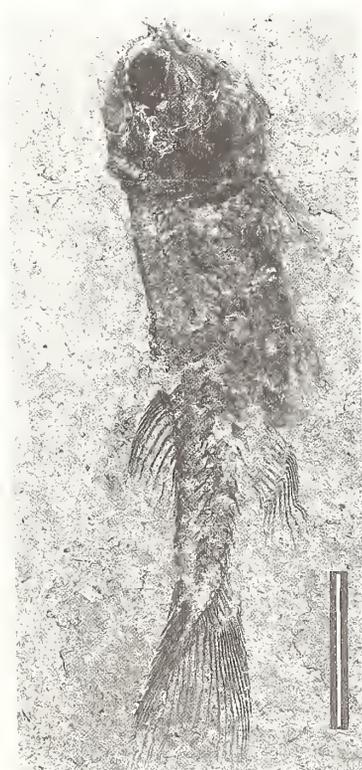
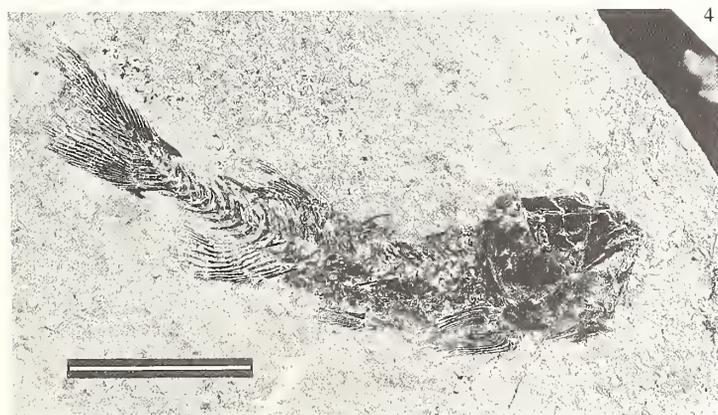
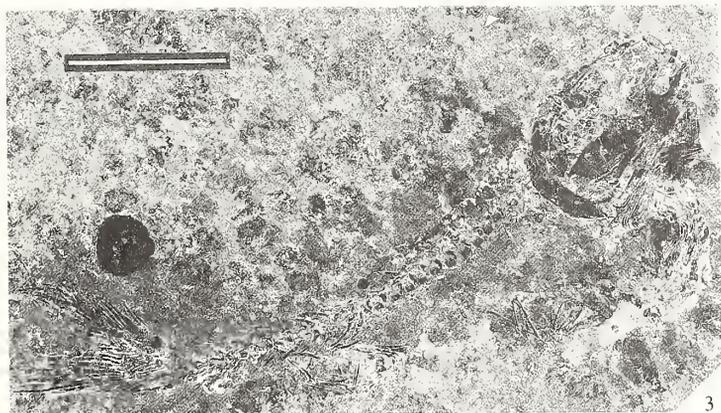
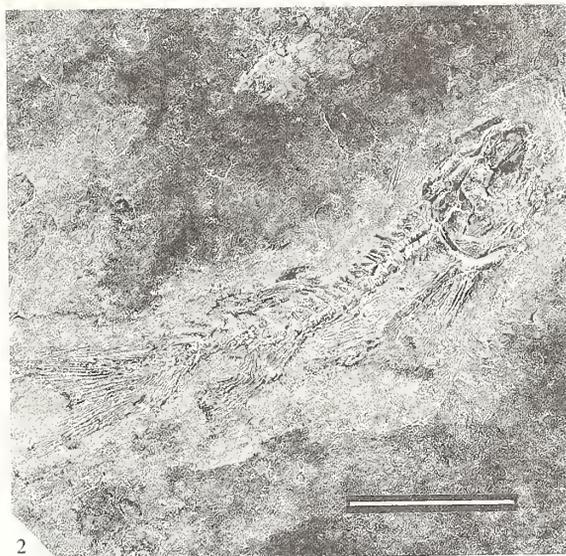
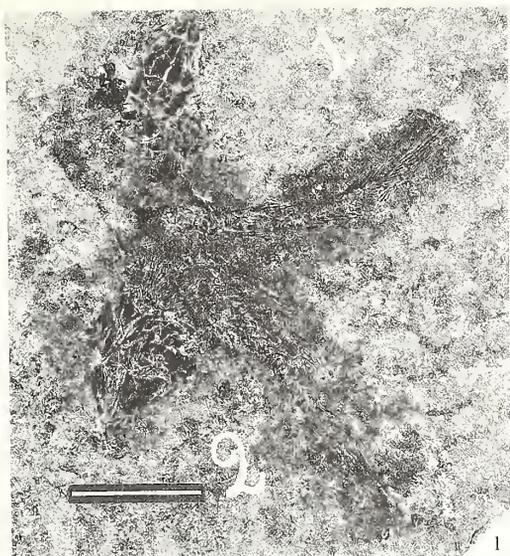
Diagnosis (emended). Very small naked fish. Rostral followed by broad contiguous nasals. Maxilla short, no supramaxilla, quadratojugal splint-like. Preopercular made from two bones, the dorsal one being tube-like. Five infraorbitals. Parietals sometimes fused. Unpaired median extrascapular often present. Vertebral segments about 33 with hemichordacentra. Epineurals and supradorsal present. Vertebral column diplospondylous in the caudal region; unpaired median neural spines; ural-neural arches as primitive uroneurals; ural chordacentra; a few urodermals present.

Type specimens. The original material described by Bellotti (1857) was destroyed during the last World War. However I do not think it necessary to designate a neotype, the species being easily recognizable and the only one in the genus. The following material can be considered as topotypes: eleven specimens of which one is from the Curioni collection in the Museum of the Geological Survey of Italy in Rome (no catalogue number), seven are from the Ruppel collection in the Senckenberg Museum in Frankfurt am Main (SM P1239a,b; P1245-7-8; P1251-4; P1262), one is from the Paläontologisches Institut und Museum der Universität in Zürich (PIMUZ AI-551), and two are from Costa's collection in the Museo di Paleontologia dell'Università di Napoli (MPUN M172-3-4; M174, being the counterpart of M173).

There are no accurate locality data with these specimens, although they are probably from the quarries in the middle to upper part of the Calcare di Perledo-Varenna. The available specimens are small and poorly preserved, some of them being only counterparts. Latex peels have been made, but are uninformative. Nevertheless, the fishes' position is interesting: they are often in lateral view but, as in several Ca' del Frate specimens, the entire skull-roof is visible. No single bone shape is detectable, owing to a peculiar kind of

EXPLANATION OF PLATE I

Prohalecites porroi (Bellotti 1857). Scale bars, if not otherwise stated, 10 mm. 1, two specimens (MCSNIO P370/1-2, 38 and 36 mm s.l.) on one of the two major fossiliferous surfaces (the darker one), both dorso-ventrally crushed. 2, mature specimen (MCSNIO P349a, 30 mm s.l., see also text-fig. 7B) with skull in lateral view; note thoracic hemichordacentra and stout paired neural arches as well as pleural ribs articulating with parapophyses. 3, mature specimen (MCSNIO P373/1, 41 mm s.l., see also text-figs. 4A, 7C); note thoracic hemichordacentra with no intercalaries. 4, young specimen (MCSNIO P341/1, 31 mm, see also text-fig. 7A) with small hemichordacentra only in the middle of the caudal region; skull shows inner surfaces of the roofing bones and of the left lower jaw as well as external surface of the right side bones. 5, young specimen (MCSNIO P376, 23 mm s.l.) with no hemichordacentra (scale bar, 5 mm).



preservation in which the original bone is usually no longer present: only a rough natural mould shows the general shape of the fish.

Other material. The 334 specimens stored in the Museo Civico di Storia Naturale di Induno Olona, Varese (MCSNIO P328 to P416). Three more specimens from Ca' del Frate, but labelled as from Besano, are in the British Museum (Natural History) collection (BMNH P.19471–3; C. Bender Collection, purchased in 1935). The new specimens considered in this paper were prepared mainly with dilute acetic acid, but mechanical techniques were used on occasion. Most of the observations concern a few dozen specimens.

Horizon and locality. The topotypes are from near Perledo (Como, northern Italy), most probably from the upper part of the Calcare di Perledo–Varenna (Scisti di Perledo *auct.*; Upper Ladinian, Middle Triassic). The other material is from the Kalkschieferzone (upper member of the Meride Kalk) near Ca' del Frate (Viggiù, Varese, northern Italy).

DESCRIPTION

Skull and lower jaw

The nasals (text-figs. 2,3) are joined along their whole length; the posterior nostril must have opened on the lateral side of the nasal where a notch is present, while the anterior one presumably opened along the anterior margin. The rostral (text-figs. 2–4) contains the ethmoid commissure and there is a lacuna in the bony cover of the snout where the supraorbital sensory canal may have joined the ethmoid commissure itself. The true position of the antorbital (text-fig. 2) is not clear: it probably touched the corresponding nasal but not the rostral.

The skull roof is very wide in the orbital region and the frontals (text-figs. 2,3) are very broad posteriorly. The parietals (text-figs. 2,3) are sometimes fused, giving rise to a large shield posterior to the frontals. The parietal pit-lines are seen as grooves, lacking the thin ganoine layer which elsewhere covers these bones.

The dermopterotic (text-figs. 2,3) is trapezoidal. The sensory canal branches at about the posterior third to connect with the preopercular sensory canal. In at least one specimen the dermopterotics seem to have fused to the adjoining roofing bones.

The extrascapulars (text-figs. 2,3) are unusual: three to four bones carry the temporal commissure. Between the two lateral bones sometimes there is a third, narrow, unpaired element with two symmetrically arranged pores. Paired median extrascapulars are present in several other specimens.

Posterior to the antorbital and to the postero-lateral corner of the nasal there are three supraorbitals (text-figs. 2,3), the first of which is somewhat larger than the other two. The supraorbitals are followed by the dermosphenotic and the infraorbital series comprising five elements (text-figs. 2,3). The two most dorsal infraorbitals bear up to three denticles on their posterior margins.

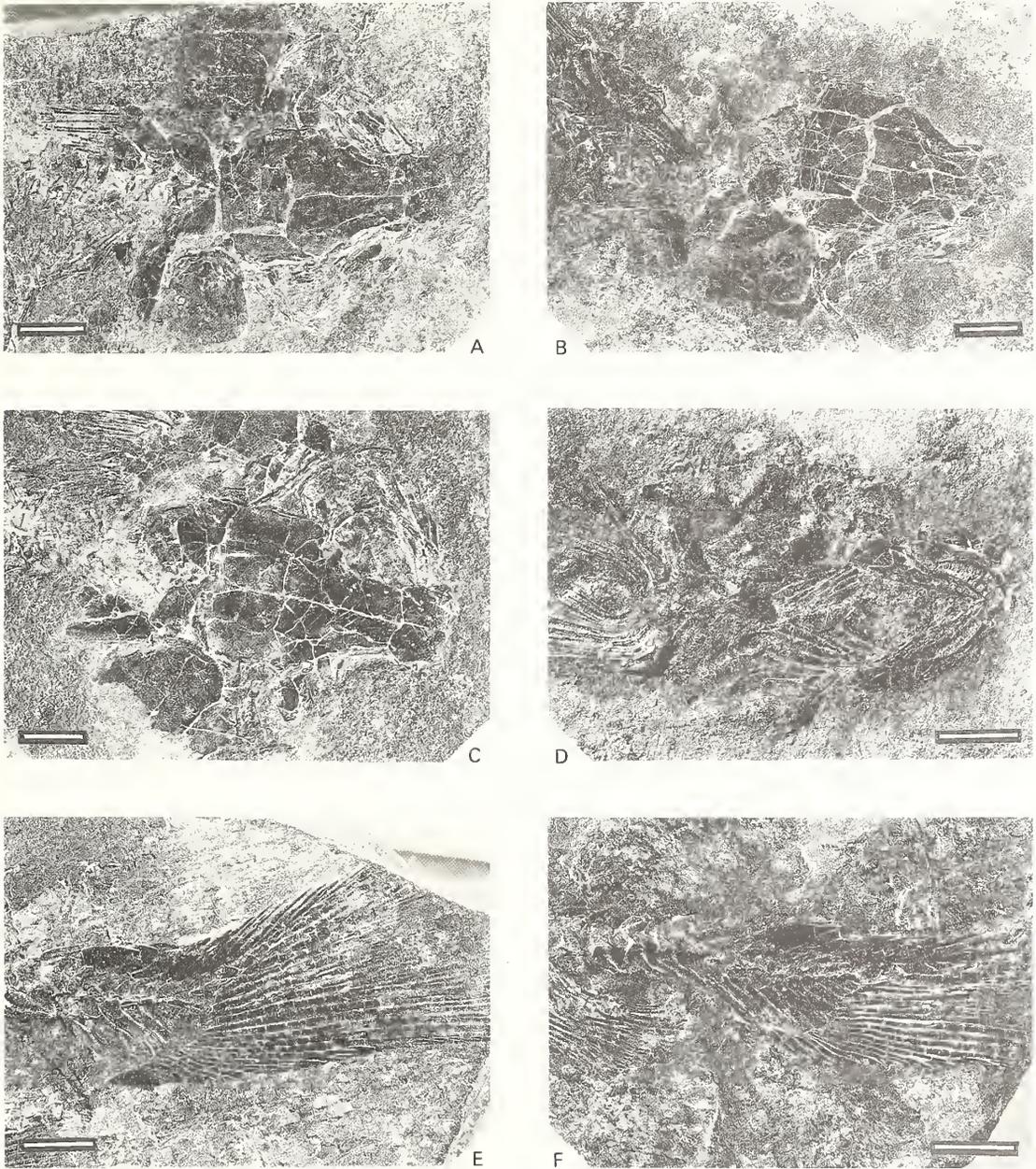
Only one suborbital (text-figs. 2,3) the upper, is known with certainty: it completely covers the uppermost part of the preopercular. Traces of a second suborbital have been seen only in MCSNIO P362 from Ca' del Frate and in MPUN M173 from Perledo, but from the configuration of the cheek we can infer that a second suborbital was probably present.

The maxilla (text-figs. 2,4) is about half as long as the lower jaw, ending free below the middle of the orbit. The whole oral margin bears about 20 teeth and it is thickened, especially in the central part. No traces of a supramaxilla have been detected. The teeth are very long and conical: the dentition is remarkably powerful for such a small fish.

The premaxilla (text-figs. 2,4) is triangular: the oral margin bears seven or eight teeth similar to those of the maxilla. A stout nasal process is present lying under the rostral and possibly reaching the nasal. Both the maxilla and the premaxilla are ornamented with flecks of ganoine. The lower jaw (text-figs. 2,4) bears a very high coronoid process. The dentary is the largest bone, with about 20 teeth. The sensory canal ran only in the dentary, probably being free for a short distance between the hind tip of the dentary itself and the ventral preopercular. Dorsal to the angular is the surangular which shows a very small exposed area, much as in *Amia*, and it is seen in only one specimen (MCSNIO P370/3). A notch is present in the lower half of the posterior margin which presumably received the articulatory head of the quadrate. However, it is not clear whether the notch is a true articulatory notch or is like the feature found in the same position in *Amia*. The true articulation pattern is not detectable.

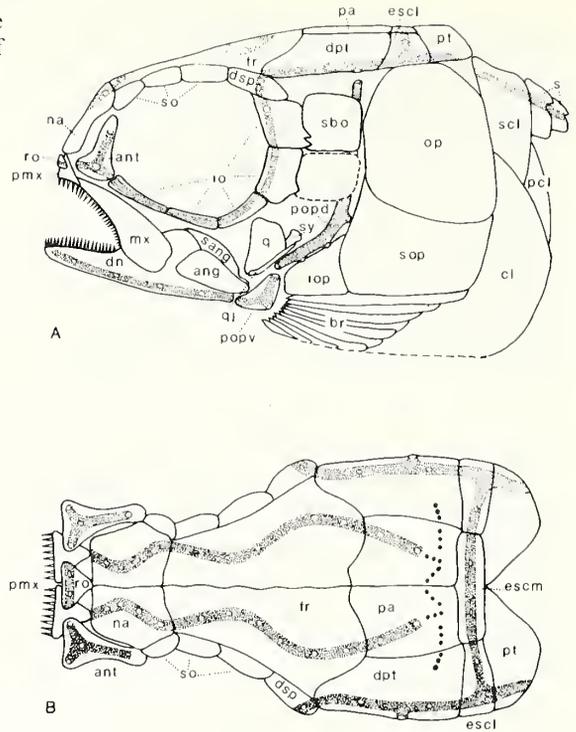
The opercular (text-figs. 2–4) is very broad. The subopercular is subtriangular and the interopercular is small and trapezoidal. All the opercular bones are ornamented with small tile-like ganoine flecks.

The branchiostegal rays (text-figs. 2,4) are at least ten in number, gently decreasing in size forwards. The



TEXT-FIG. 1. *Prohalecites porroi* (Bellotti 1857). A, head of a 33 mm long specimen (MCSNIO P328/1, see also text-fig. 3B); note the fused parietals and the unpaired median extrascapular. B, head of a 35 mm long specimen (MCSNIO P379) with fused parietals. C, head of a mature fragmentary specimen (MCSNIO P353); note the S-shaped left dorsal preopercular and the two right lateral line scales behind the supracleithrum. D, ventral view of a 35 mm long specimen (MCSNIO P370/3). E, caudal fin of a 30 mm long specimen (MCSNIO P335, see also text-fig. 9B). F, caudal fin of a 33 mm long specimen (MCSNIO P411). Scale bars, 2 mm. Lengths of fishes quoted are standard lengths (s.l.).

TEXT-FIG. 2. *Prohalecites porroi*. Restoration of the skull. A, lateral view; B, dermal skull roof. Length of skull, c. 10 mm.

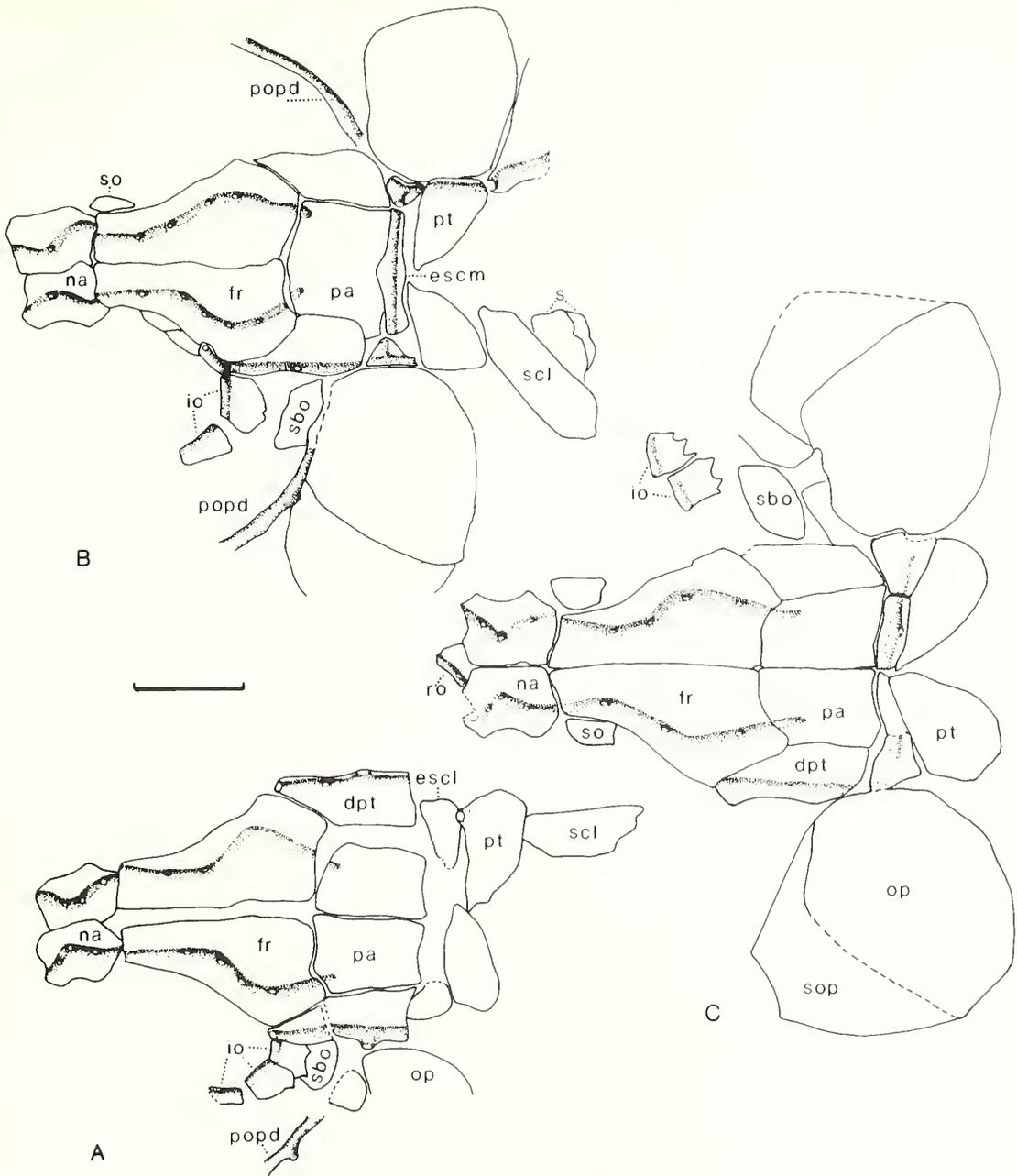


three most dorsal ones follow the usual pattern, with the ventral edge overlapping the preceding ray. This pattern reverses at the fourth ray so that, starting from the fifth, the dorsal margin overlaps the following one. This arrangement is described by Zambelli (1975, 1978, 1981) for all the Norian pholidophorids from Northern Italy.

The dorsal preopercular (text-figs. 2–4) is a very slender bone, gently bent forwards ventrally. Its ventral region is partially exposed and has two or three very short, backwardly-directed pegs, enveloping the branches of the sensory canal. The ventral preopercular lies just behind the lower jaw articulation and in front of the interopercular. It is a small triangular bone bearing the connection between the mandibular and the preopercular sensory canals. A pore is present at the postero-ventral corner of the bone, at the end of a branch leaving the main canal where it bends sharply upwards. A bone in a similar position, also bearing part of the preopercular sensory canal, is present in *Cleithrolepis* and was named quadratojugal by Wade (1935) and Hutchinson (1973). In *Cleithrolepis*, however, the bone is close to the posterior end of the maxilla, which is as long as the lower jaw. Later, Wade (1941) named this bone the 'second preopercular'. Furthermore, Daget (1964) pointed out that the quadratojugal always lies close to the posterior end of the maxilla and in front of the preopercular, having no sensory canal. The quadratojugal (*sensu* Daget 1964) is present in a few actinopterygians (Patterson 1973, p. 249; Gardiner 1984), sometimes bearing traces of the vertical pit-line (*Pteronisculus*, Nielsen 1942; *Canobius ramsayi*, Westoll 1944). Patterson (1973) seems to agree with the interpretation of Daget (1964), not citing *Cleithrolepis* in his list. I also consider this bone as a ventral preopercular, both because of the presence of the sensory canal and its position relative to the very short maxilla. So far, *Prohalecites* is the only fish having a similar bone associated with a short maxilla.

The parasphenoid (text-fig. 5) has a median rounded keel and two lateral wings. Between the keel and each wing there is a groove as in *Huletia* (Schaeffer and Patterson 1984). The ascending processes arise at the level of the buccohypophysial canal opening, and have a small stout basipterygoid process anteriorly. The posterior portion of the parasphenoid is a flat lamina which is partly seen in only one specimen. No traces of dentition can be seen.

In a few specimens otoliths are visible: in MCSNIO P391/1 (s.l. 24 mm) four otoliths are present just behind the parasphenoid. The anterior two are smaller and may be utricular (lapilli) while the posterior are somewhat bigger and are considered as saccular (sagittae). Otoliths are visible in small specimens; this may simply be due

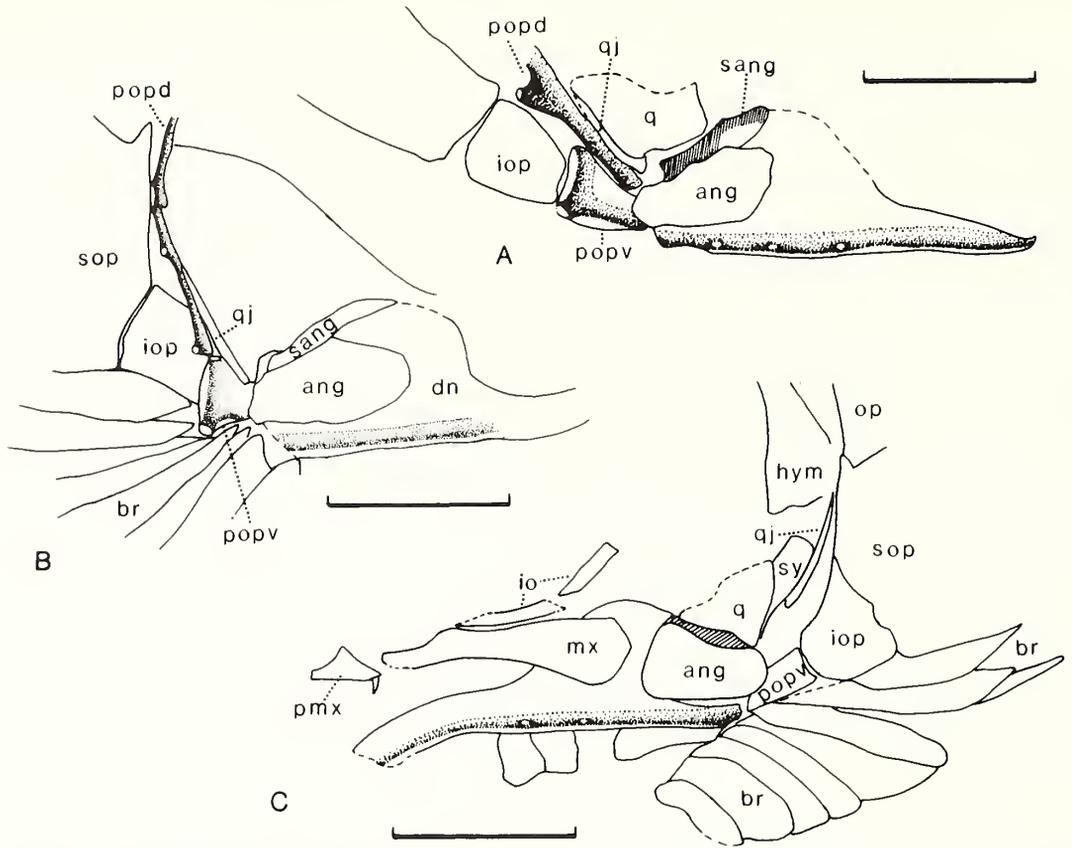


TEXT-FIG. 3. *Prohalecites porroi*. Skull bones as preserved in A, MCSNIO P362, s.l. 35 mm; B, MCSNIO P328/1, s.l. 33 mm (see also text-fig. 1a); C, MCSNIO P377, s.l. 35 mm. Scale bar, 2 mm.

to the thickness of the bones in the juvenile stage: they break up easily above the hard masses of the otoliths themselves.

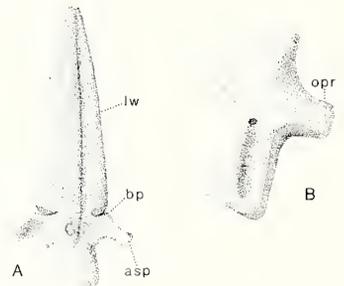
The hyomandibular (text-figs. 4,5) is large and powerful and perforated by the hyomandibular nerve.

The quadrate (text-figs. 2,4) has a stout articular head, which is buttressed by the anterior end of the quadratojugal (*sensu* Patterson 1973). The quadratojugal is applied to the posterior margin of the quadrate,



TEXT-FIG. 4. *Prohalecites porroi*. Lower jaw and associated preopercular bones as preserved in A, MCSNIO P373/1, s.l. 41 mm (see also pl. 1, fig. 3, text-fig. 7C); B, MCSNIO P373/2, s.l. 37 mm; C, MCSNIO P338, s.l. 33 mm. Scale bars, 2 mm.

TEXT-FIG. 5. *Prohalecites porroi*. Restoration of A, the parasphenoid (dorsal view); B, the hyomandibular (side view).



but it does not fuse to it; the splint-like bone is very similar to that of *Dapedium* and *Lepidotes* (Patterson 1973, p. 293).

The symplectic (text-figs. 2,4) is a triangular bone lying on the inner side between the quadrate and the quadratojugal. It is much larger than the quadratojugal and extends upwards much beyond the quadrate, though not reaching the hyomandibular. So far, no trace of a condyle for articulation with the lower jaw has been detected. However, the proximal tip lies close to the quadrate articular head.

The whole palate is ossified and sutures between the different bones are hard to detect. Some teeth may be present in the anterior region. All the bones, except the quadratojugal, show a cancellous structure.

The ceratohyals are never clearly visible, but possibly there is a small ceratohyal followed by a larger epihyal. The hypohyals are stout and heavily ossified and must have been only weakly tied to each other.

Girdles

In the pectoral girdle the scapulocoracoid is a large plate with a pronounced antero-ventral process. The scapular foramen, close to the antero-dorsal corner, is small and round. On the inner side, a smaller foramen is present ventral to the scapular. In the coracoid region, very close to the posterior margin, there is a large elongated fenestra. At least four elongated, strong pectoral radials are visible which are enlarged distally where they articulate with the lepidotrichia.

The cleithrum (text-fig. 2) is strongly convex and the anterior region is much larger than the posterior one. The external surface shows the same ornamentation as the supracleithrum, i.e. elongated ganoine flecks more or less parallel to the posterior edge.

The supracleithrum (text-figs. 2,3) is narrow and elongated, somewhat wider in the upper region where the sensory canal crossed the whole bone. Posterior to the supracleithrum there are two scales bearing the lateral line. The postcleithrum (text-fig. 2) is elongated dorso-ventrally, with a gently rounded posterior edge. Its outer surface is smooth.

Axial skeleton

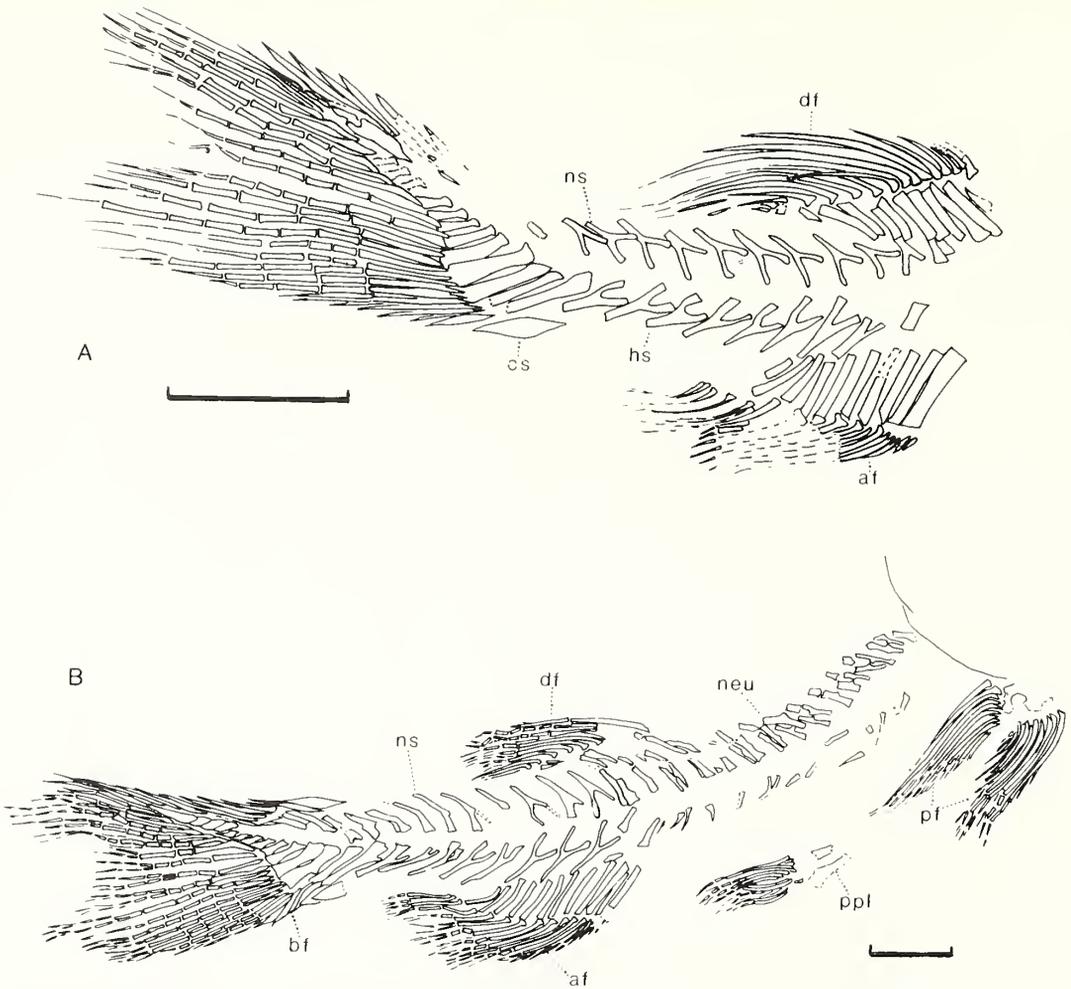
The vertebral segments (text-figs. 6-8) number about 33, 20 or 21 of which are in the caudal region. The vertebral centra consist of crescentic hemichordacentra throughout the length of the body. Usually the dorsal and ventral hemicentra do not meet though they are opposite to each other in the caudal region. However, in a couple of specimens a few centra are ring-shaped, showing that fusion has occurred between the two opposing hemicentra.

In the anterior trunk region only dorsal precentra, probably related to cartilaginous intercalaries, and ventral centra with parapophyses, are present. Fully mature specimens show neural arches bearing hemicentra from the 10th-11th vertebral segment. The whole preural part of the caudal region is diplospondylous. Although precentra become larger and larger back to the middle of the caudal region they do not reach the size of centra.

Hemicentra are not present in juvenile specimens: recently Schaeffer and Patterson (1984) described a similar situation for *Hueltia americana* and *Todiltia schoewei*, confirming what Patterson (1973) wrote about *Euricormus*' hemichordacentra. In *Prohalecites*, chordacentra commence in the anterior caudal region in specimens of about 30 mm standard length. Initially, both ventral and dorsal centra appear in that region. Then ventral centra develop anteriorly (but parapophyses are not firmly fixed to them at this stage) and also posteriorly in the ural region. Finally, the dorsal centra reach their full extent and precentra appear. The latter are largest in the mid caudal region. The size of the precentra gives information about two possible growth gradients of the hemichordacentra, as already suggested by Schaeffer and Patterson (1984) for *Hueltia*: backwards in the trunk region and centrifugally from the middle caudal region. That this is the usual pattern is confirmed by observations on Norian Pholidopleuridae now being made by the author.

The neural arches and spines are paired from the first to the 14th-16th segment; then median spines are present. In young individuals, the paired arches and spines are rectangular; in adults they become thinner and more elongated. Supraneurals are present from the first vertebral segment back to the second neural spines beneath the dorsal fin radials. Their proximal ends lie between the distal ends of the paired spines. Paired elongated bean-like bones flank the dorsal tip of the supraneurals, at least in the anterior trunk region. They are in line with the distal parts of the dorsal fin radials (see below). Unfortunately, these bones have been seen only in one of the largest specimen (MCSNIO P413). Similar bones are also known in *Cleithrolepis* (Wade 1935, fig. 25, and p. 54; Patterson pers. comm.), though here they do not have the one-to-one relationship with the supraneurals. Epineurals are well developed as posterolaterally directed outgrowths from the neural arches. They reach their maximum length between the 7th and 10th abdominal neural arches. A small forwardly-directed process is set halfway along the anterior edge of each abdominal neural arch. At the same level, there are rod-like thickenings on the medial surfaces of the arches that may be considered to be supradorsals. These thickenings, and the anterior process, mark the position in life of the longitudinal ligament, as in *Amia* and *Salmo* (Jollie 1973).

Neural and haemal arches become tightly bound to supporting hemicentra in mature specimens. There are large parapophyses beneath the notochord in the abdominal region, which bear long slender pleural ribs. Posterior to the 13th or 14th vertebra there are rather expanded haemal arches, bearing long haemal spines, which are much enlarged in the last three or four pre-ural vertebrae.



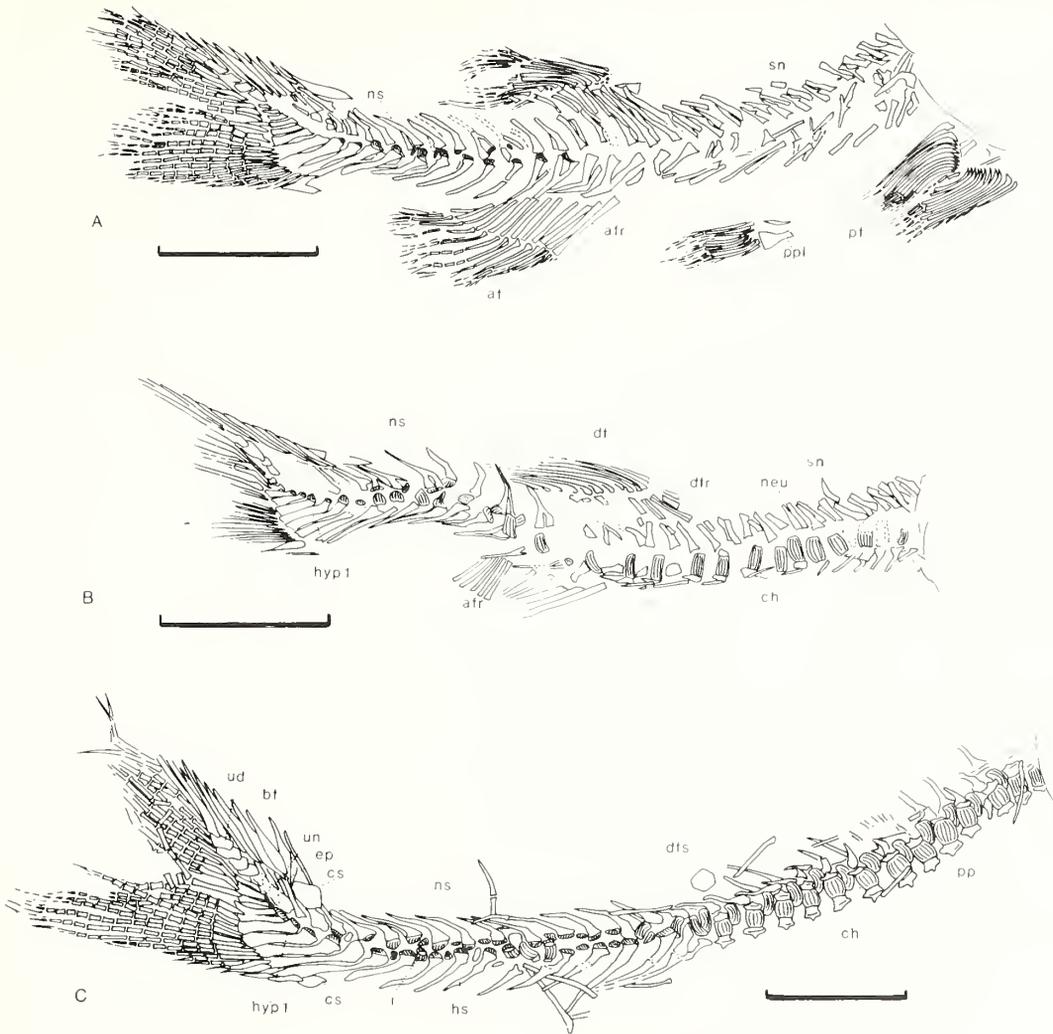
TEXT-FIG. 6. *Prohalecites porroi*. Axial skeleton and fins as preserved in A, MCSNIO P400, s.l. 19 mm; and B, MCNSIO P392, s.l. 27 mm. Scale bars, 2 mm.

No intercalaries have been observed except a few paired interventrals in the middle of the caudal region. However, external surfaces of the dorsal precentra are never completely exposed.

Paired fins

The pectoral fins (text-figs. 6–8) are large, their length being usually somewhat less than the head length. Each fin consists of 10 to 12 lepidotrichia preceded by two spines. The leading lepidotrich bears slender fringing fulcra. The proximal segment is very long and the more distal segments somewhat shorter. Each lepidotrich bifurcates only once or twice and always well beyond the commencement of segmentation. The insertion of the pectoral fins is ventral, very close to the mid-line.

The pelvic fins (text-figs. 6–8) are small, with only six to eight long lepidotrichia and two short anterior spines in each. Slender fringing fulcra are present on the leading lepidotrich. The structure of the lepidotrichia is similar to that of the pectoral fin. A pair of long slender bones is the only endoskeletal support of the fins. Each bone has an asymmetrically enlarged distal end.

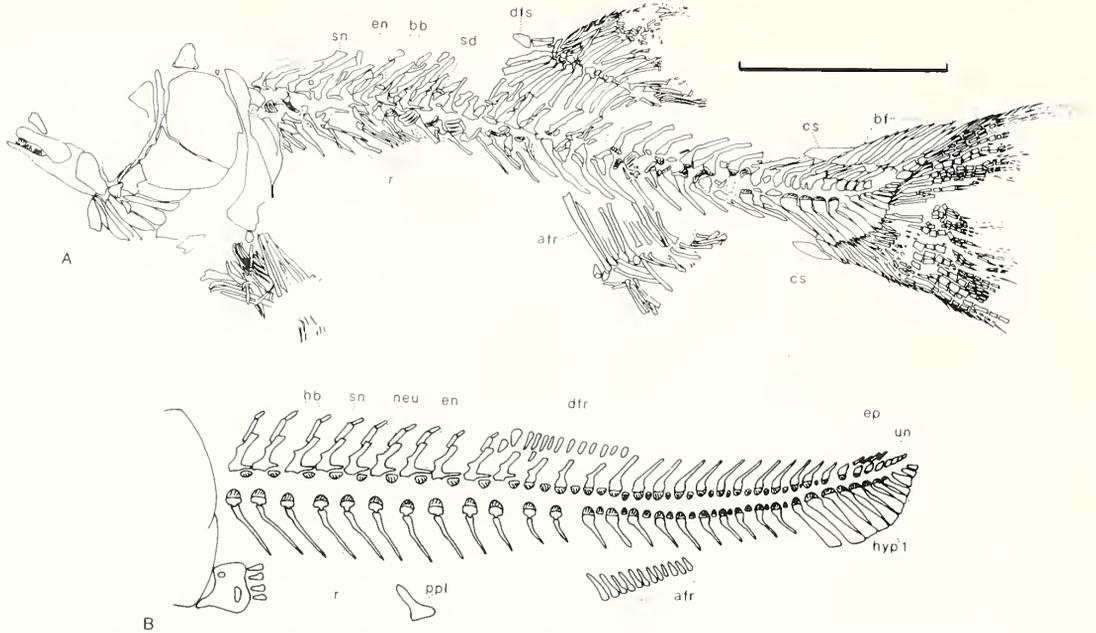


TEXT-FIG. 7. *Prohalecites porroi*. Axial skeleton and fins as preserved in A, MCSNIO P341/1, s.l. 31 mm (see also pl. 1, fig. 4); B, MCSNIO P349a, s.l. 30 mm (see also pl. 1, fig. 2); C, MCSNIO P373/1, s.l. 41 mm. (see also pl. 1, fig. 3, text-fig. 4A). Scale bars, 5 mm.

Unpaired fins

The dorsal fin (text-figs. 6–8) is inserted about half way between the skull roof and the beginning of the caudal fin. The fin is short: 10 to 12 lepidotrichia are preceded by an oval median scale and four or five basal fulcra. The first lepidotrich is unbranched and short, bearing only one or two fringing fulcra. All of the main lepidotrichia branch once; their proximal segment is very long and usually there are two or three more segments before the branching. The general shape of the fin is triangular. The radials are equal in number to the lepidotrichia and the first is much larger than the others and also supports the basal fulcra. Each radial is composed of a long slender proximal part and a couple of very short distal bones which are close to the articulation with the lepidotrichia.

The anal fin (text-figs. 6–8) originates a little more posteriorly than the dorsal. Its shape and size are also comparable, with 12 lepidotrichia, a few basal fulcra and a median scale. Fringing fulcra are borne by the first two lepidotrichia, the second of which is the longest in the fin.

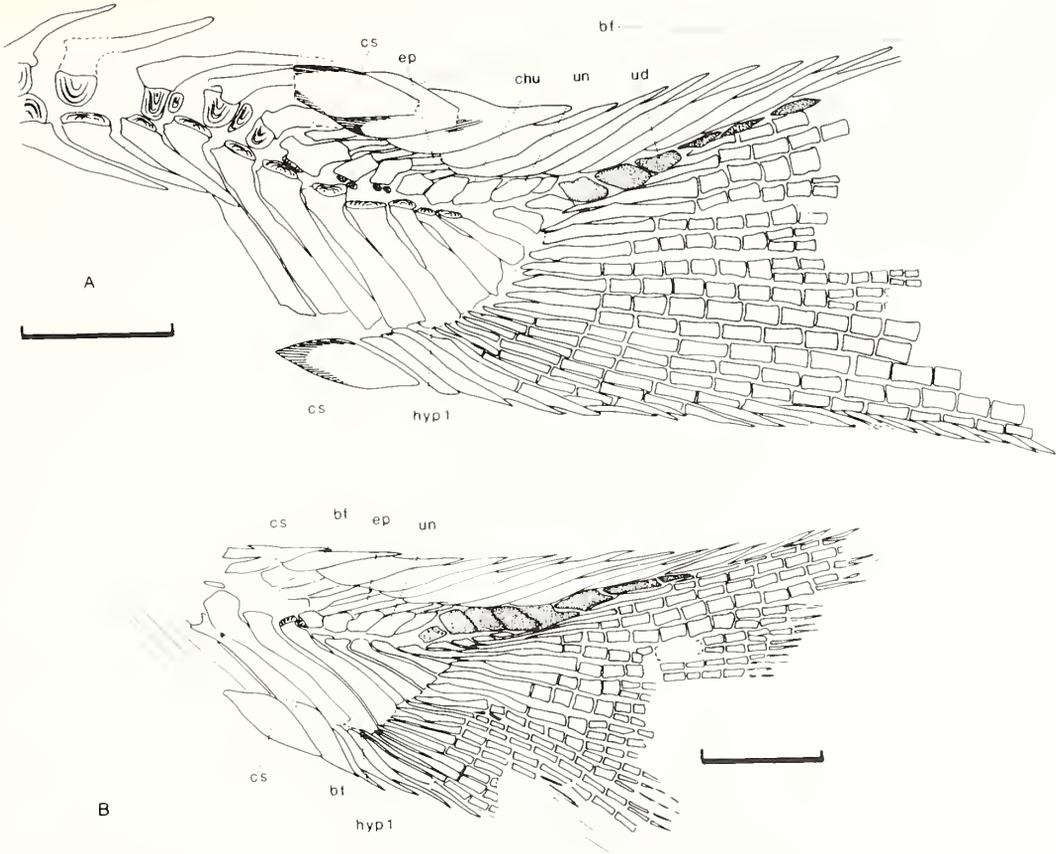


TEXT-FIG. 8. *Prohalecites porroi*. A, MCSNIO P413 as preserved, s.l. 43 mm; scale bar, 10 mm; B, restoration of the axial skeleton.

The caudal skeleton (text-figs. 6–8) is sometimes well exposed but, owing to the small size of the fishes, some structures, such as the ural neural arches, are difficult to interpret.

The striking similarity to the caudal skeleton of the Pholidophoridae (Patterson 1968) helps to determine where the ural structures begin. In a few specimens, a small anterior process is visible at the base of the haemal spine; easier to detect is a change in the anterior outline of the arches from convex to concave or straight. Both these features, together with the upward flexure of the posterior outline of the haemal spines, occur on the fifth elongated haemal spine, which is therefore considered to be the first hypural. The complete hypural series is composed of only six or seven elements. The first two or three, together with the last four haemal spines, support the lower lobe of the fin. The notochord was calcified even in the ural region, but usually only ventral hemicentra are present, as far as the sixth ural centrum. The last dorsal hemicentrum may be the first preural or the first ural. In a couple of specimens two hypurals are borne by a single hemicentrum, much larger than the others: the first and the second urals in one specimen, the second and the third in the other. In at least one of these specimens there is one more double hemicentrum in the caudal region but in a dorsal position; it bears two pairs of neural arches which are fused into a single median neural spine. Furthermore, in this specimen, a ring-shaped centrum is found in the middle of the caudal region. In the light of these facts the occasional fusion of the ural ventral hemicentra is considered an individual malformation rather than an indication of relationship (Patterson 1973; Schaeffer and Patterson 1984).

Again, as in the Pholidophoridae s.s., the last three preural neural spines, which remain unpaired, gradually decrease in length. Posterior to them there are three or four long epurals. There are six or seven ural neural arches in one-to-one correspondence with the hypurals. They are always preserved in lateral view so that it is impossible to determine whether or not they lack a median spine. The first two or three are rather similar to each other and, though smaller, do not differ in shape from the last preural neural arches. The more posterior ural neural arches are small, longitudinally elongated and close to each other, giving rise to a continuous cover over the neural canal and approaching or even touching the hypural bases. Though similar to those of pholidophorids in their general aspect, these ural neural arches are surely more primitive. *Dapedium* too has similar structures, but its preural neural arches are paired (Patterson 1973). On the other hand, the modified arches are hollowed anteriorly to receive the posterior edge of the preceding arch, as illustrated in *Pholidophorus bechei* by Patterson (1968), and they also closely resemble the last three ural neural arches in



TEXT-FIG. 9. *Prohalecites porroi*. Caudal fin as preserved in A, MCSNIO P331, s.l. unknown; B, MCSNIO P335, s.l. 30 mm (see also text-fig. 1E). Urodermal shaded. Scale bars, 2 mm.

Leptolepis coryphaenoides (Patterson 1968). I therefore consider these ural neural arches to be uronurals, comparable to those of *Dapedium* and of the Pholidophoridae s.s. (Patterson 1968, 1973).

The caudal fin is moderately forked and almost symmetrical in its outline. There are 14 to 18 principal lepidotrichia, seven or eight in the lower lobe and seven to ten in the upper. The lowermost and perhaps the uppermost two principal lepidotrichia are unbranched: all the others branch once or twice. In the lower lobe, the leading ray bears fringing fulcrum in its distal part, and is preceded by three or four unbranched but segmented shorter rays, which also bear a few fringing fulcrum. Usually, four basal fulcrum are present; they are preceded by a median scale with a short anterior process. This latter scale is considered to be a caudal scute. In the upper lobe, the proximal ends of the lepidotrichia become more and more asymmetrical upward, so that long, downwardly bent processes overlap the complete series of the upper hypurals. Along the upper margin of the fin there is a caudal scute, larger than the ventral one, and ten basal fulcrum followed by slender fringing fulcrum on the uppermost lepidotrich. The anterior tips of the basal fulcrum lack ganoine, but the remainder of their surface is enamelled, even where covered by the preceding fulcrum.

Squamation

Most of the body of *Prohalecites* was naked or covered by very thin scales which have left no trace. In several specimens, however, the body outline is shown by small carbonized patches, much closer to each other in the abdominal region. The only known scales are ganoine-covered; for example, the two at the beginning of the lateral line just posterior to the supracleithrum, or the median ones in front of the unpaired fins. At the base

of the upper lobe of the tail there is an elongated patch of eight to ten scales, arranged in a long row of six to eight scales with one or two more rounded ones dorsally. They are clearly homologous to the urodermals of some pholidophorids (Patterson 1968). The scales of the main row show more or less the same shape as the posterior uroneurals, but each slightly overlaps the following one. The two upper urodermals are overlapped by the epaxial basal fulcra. The whole urodermal scale patch covers the proximal ends of the upper lobe lepidotrichia, but seems to lie just posterior to the last uroneural and hypural; thus the uroneurals form a continuous series with the urodermals, except that the two are distinguished by the marginal overlapping of the urodermals.

TAXONOMIC REMARKS

Relationships of Prohalecites

No detailed anatomical description of *Prohalecites* has been made since that of De Alessandri (1910), but the genus was often mentioned or listed in papers concerning Triassic fish faunas. Brough (1939, p. 107) considered *Prohalecites* as a possible sub-holostean while both Griffith (1977, p. 81) and Patterson (1981, p. 217) tentatively ascribed the genus to primitive teleosts, perhaps in the light of its original designation as '*Pholidophorus*'.

Even now, after a much more detailed description, the taxonomic position of *Prohalecites* is difficult to define owing to the presence of both advanced and primitive characters. In many respects (especially the axial skeleton), it seems to fit rather well in the Pholidophoridae s.s.

Outside the Pholidophoridae, chordacentra are known in the Pholidopleuridae and Caturidae (Patterson 1973), Ophiopsidae (Bartram 1975), *Hulettia*, and immature *Todiltia* (Schaeffer and Patterson 1984), as well as in several other groups. Furthermore, they seem to be present also in other undescribed genera from the Italian Upper Triassic (pers. obs.).

The caudal endoskeleton shows more or less the same organization as in pholidophorids, with ural neural arches slightly modified and approaching the uroneural stage. The dermal skull also shows a striking resemblance to the pholidophorids in the position and shape of the quadratojugal, even though this bone is not yet fused with the quadrate in *Prohalecites*. The infraorbitals are also very similar in shape apart from the postero-ventral one. Many other characters, however, are remarkably different: for example the snout pattern has large contiguous nasals, the preopercular is double and shows a tube-like dorsal part, the maxilla is very short, and there are no supramaxillae. Thus, *Prohalecites* cannot be placed in the Pholidophoridae *sensu* Nybelin (1966), or even as emended by Zambelli (1981), or *sensu* Patterson (1973).

The dermal skull pattern of *Prohalecites* is much like that of advanced Parasemionotidae (*sensu* Patterson 1973), genera such as *Promecosomina* and especially *Paracentrophorus* and *Phaidrosoma* (Griffith 1977), but Parasemionotidae have no vertebral centra (Patterson 1973), while *Paracentrophorus* has no fringing fulcra (Gardiner 1960). *Prohalecites* also shows some resemblance to the Caturidae, but their quadrate and symplectic articulation with the lower jaw is so far unknown in *Prohalecites*.

The very short maxilla, without any supramaxilla, is here considered a derived character which might have formed either by the shortening of a long toothed maxilla and the concomitant loss of the supramaxilla, or directly from a maxilla not yet provided with a supramaxilla. This opinion is in contrast with that of Schaeffer and Patterson (1984) who consider the lack of supramaxillae as a primitive character in *Hulettia*, as in all the other chondrosteans with long maxillae. In some Parasemionotidae, *Promecosomina* and *Phaidrosoma* for instance, the supramaxilla is also absent and the maxilla is rather short.

Among Triassic fishes, the Semionotidae with grinding dentition also show a short maxilla, but this is usually toothless. The caudal endoskeleton of *Prohalecites* is rather similar to that of *Dapedium* (Patterson 1973, fig. 27), which is, in my opinion, close to *Pholidophorus bechei* (Patterson 1968, fig. 5). In many other respects, apart from the large contiguous nasals in *Dapedium* and some other genera, the narrow but single opercular and the splint-like quadratojugal in *Lepidotes* and *Dapedium* (Patterson 1973), the Semionotidae are quite different from *Prohalecites*. The heavy scale covering, lack of chordacentra (but *Tetragonolepis* apparently does have them; Patterson 1973,

p. 294), small mouth, and body more or less elevated are in contrast with the characters of *Prohalecites*.

Since no trace of scales is preserved in any specimen, the body of *Prohalecites* is considered naked. This helps little in the search for possible relatives; among the inferred ancestors, none shows thin or absent scales, but scales are wanting in a few Pholidophoridae and Caturidae. This lack of a scale covering led Woodward (1895) to consider *Prohalecites porroi* all as immature specimens. However, De Alessandri (1910) pointed out that, though the smallest specimens may well be young, the large ones show adult characters, especially in body proportions. Though De Alessandri's arguments are perhaps superficial, the ontogenetic development of the vertebral column described herein proves without doubt that *Prohalecites porroi* represents a naked species of about 40 mm standard length. Moreover, fishes other than *Prohalecites* are uncommon in the Ca' del Frate beds, comprising less than 10% of the total collected specimens from about ten other species. None of the latter shows any tendency towards a reduction in scale covering.

Less important characters, such as fusion of the parietals and the presence of a median extrascapular, are found in *Amia*, *Sinamia*, and *Ikechaoamia* (Patterson 1973; Stensio 1935; Su Tetsao 1973; Zhang Mi-man and Zhang Hong 1980; Jain 1985). However, this character alone is not sufficient to prove a relationship, because fusion of the parietals has occurred several times in different groups, including the Pholidophoridae themselves (Zambelli 1975, 1978), while a median extrascapular is common in many stem-group neopterygians.

In *Prohalecites*, a ventral preopercular separates the interopercular from the hind edge of the lower jaw as in Macrosemiidae. This was considered a unique specialization of that family by Bartram (1977). Apart from this last character, and the partial fusion between the quadratojugal and quadrate, macrosemiids and *Prohalecites* are very different in other features.

Recently, Schaeffer and Patterson (1984) gave a detailed description of *Hulettia americana*, a mid-Jurassic fish, which is rather similar to *Prohalecites* in many features. Major differences between the two genera are the position of the rostral, which is anterior to the totally contiguous nasals in *Prohalecites*, and the caudal endoskeleton. In this latter, *Prohalecites* shows hemichordacentra and ossified ural neural arches, which can be considered as uroneurals *sensu* Patterson (1973); none of these characters is present in *Hulettia*.

The fact that *Prohalecites* is a neopterygian is proved by the presence of several characters among those listed by Patterson (1973), such as the reduced body lobe of the tail, dorsal and anal fin radials equal in number to their lepidotrichia, premaxilla with nasal process, coronoid process of the lower jaw, suspensorium vertical, tube-like dorsal preopercular and loss of clavicles. However, problems arise when to evaluate closer relationships. Similarities between *Prohalecites* and the Parasemionotidae and Caturidae for example are not substantiated and there is no articulation between the symplectic and the lower jaw in *Prohalecites* itself. This articulation, however, is also not recorded in Parasemionotidae s.l. such as *Paracentrophorus*, *Promecosomina*, and *Phaidrosoma* which are the closest to *Prohalecites* at least in the skull-bone pattern. On the other hand, the presence of chordacentra in *Prohalecites* makes it difficult to put all these genera together.

What relationships exist with the Pholidophoridae is difficult to determine: very close similarities are seen in the caudal endoskeleton and in a few characters of the dermal skull. That the quadratojugal is not completely fused with the quadrate is primitive with respect to the pholidophorids, but the juxtaposition of these elements is similar. Unfortunately, there is a lack of neurocranial information for *Prohalecites*.

It is also worth considering the similarities between *Prohalecites* and *Dapedium*. Once more, the caudal skeleton as well the lower jaw joint are very similar in the two. On the other hand, the similarities of *Prohalecites* both with *Dapedium* and with the Pholidophoridae is consistent with Olsen's (1984) view that *Dapedium* was the closest relative of *Pholidophorus*.

In conclusion, *Prohalecites* is clearly more advanced than the Parasemionotidae and somewhat more primitive than *Dapedium* and the Pholidophoridae; moreover, it is certainly closer to the last two than to the former. Nevertheless, I think it better to leave *Prohalecites* as a Neopterygian *incertae sedis* because its characters do not perfectly fit in any of these cited groups.

Species of Prohalecites

Other problems arise at the species level because of the different preservation of the Perledo and Ca' del Frate specimens. A comparison between the two groups of specimens show that they are very similar in most of the known characters. According to De Alessandri (1910) the standard length range is 20–45 mm, comparable with the 19–43 mm range of my specimens. Fin positions and lepidotrichia number are also similar in each, except for the caudal fin. In the latter, De Alessandri recorded 25–26 segmented rays with six more 'anterior rays, small and shortening backwards'. Four of the Ladinian specimens (SM p1247, 54, 62 and MPUN M174), however, show a smaller caudal fin with less than 20 principal rays, as in the Ca' del Frate specimens; the others are too poorly preserved to count the lepidotrichia. Hemichordacentra are found in both groups, ranging in number from 32 (De Alessandri 1910) to 33–35 in the Ca' del Frate specimens. The scales also have the same distribution, few in number and only at the base of the upper lobe of the caudal fin.

The two most remarkable differences are the opercular shape, triangular in the Ladinian specimens (De Alessandri 1910) but rectangular in the Carnian, and the absence of teeth in the Ladinian specimens (De Alessandri 1910) compared with the well-toothed mouth of the new specimens. However, I have been able to prepare specimen MPUN M173, the only Perledo one with bone preserved: teeth are present at least on the lower jaw. Considering that two of the supposed differences resulting from De Alessandri's description proved to be untrue, we may have doubts regarding the other character. The Perledo specimens can easily be misinterpreted owing to their poor preservation.

On the basis of these considerations I include the new Carnian material in the existing *Prohalecites* species, *P. porroi* (Bellotti 1857), at least until new or better preserved material from Perledo, or from coeval beds, is found.

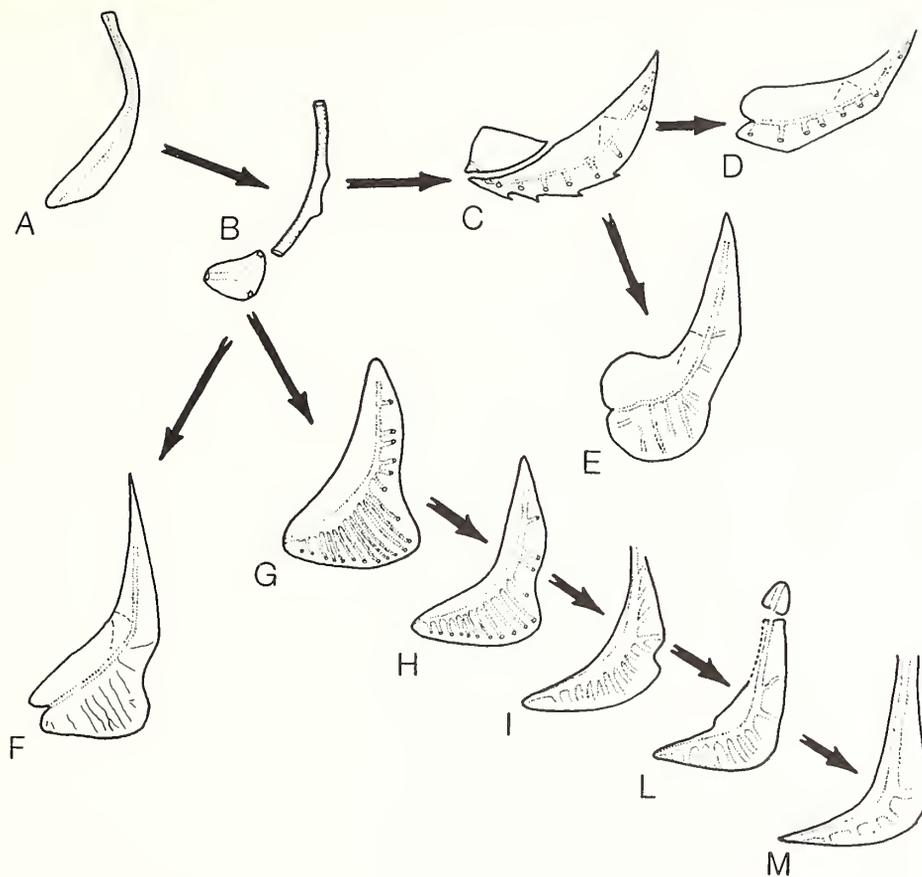
So far, *P. porroi* is still the only species of *Prohalecites* because '*Pholidophorus*' *microlepidotus* Kner 1866 is very different: it has cycloid scales, a large caudal fin with about 40 lepidotrichia, including few epaxial rays, no vertebral centra, and no pelvic fins (pers. obs.). Therefore, it cannot be related to *Prohalecites porroi*, even if Kner (1866) himself thought the two species very close to each other. On the other hand, Deecke (1889), in proposing the new genus *Prohalecites* for *Pholidophorus porroi*, also noticed some differences, which suggested that Kner's species should not be included.

GENERAL REMARKS

Nybelin (1966, 1974) placed great emphasis on the preopercular structure in establishing phylogenetic relationships, and subsequently the reduction of the dorsal limb of the preopercular has been used for hypothesizing relationships between *Amia*, gars, and teleosts (Olsen 1984).

The preopercular in the most advanced Parasemionotidae (*sensu* Patterson 1973), such as *Paracentrophorus*, *Promecosomina*, and *Phaidrosoma*, is very narrow, much like the dorsal preopercular in *Prohalecites*, but with no posterior branches of the sensory canal (Gardiner 1960). Lehman (1952) and Lehman *et al.* (1959) postulated that this narrow preopercular might well have been produced in some Parasemionotidae (*Thomasinotus*, *Stensionotus*, and *Jacobulus*) by separation of the suborbitals (fragmentation), thus losing the area in front of the sensory canal. A few very short branches of the sensory canal are found in *Prohalecites*, while in the Pholidophoridae they are longer and surrounded by laminar bone, and the posterior region is expanded. The ventral preopercular of *Prohalecites* has one long branch of the sensory canal, but it is expanded posteriorly so that it could bear additional branches.

In *Leptolepis normandica* (Nybelin 1974), as well as in some Recent teleosts such as the salmon, the preopercular comprises two bones; a ventral compound one, with canal elements attached to a laminar base early in ontogeny, and a small dorsal tubular bone called the suprapreopercle (Jollie 1984). The dorsal preopercular of *Prohalecites* is not strictly homologous to the suprapreopercle, since it is usually associated with three or four neuromasts, whereas the suprapreopercle has none (Jollie 1984). However, both the dorsal preopercular and the suprapreopercle are simple canal



TEXT-FIG. 10. Possible evolution of the preopercular bone(s). A, *Phaidrosoma huzensis*, after Griffith 1977, fig. 23; B, *Prohalecites porroi*; C, *Pholidoctenus serianus*, after Zambelli 1978, fig. 1; D, *Parapholidophorus nybelini*, after Zambelli 1975, fig. 1; E, *Pholidorhynchodon malzannii*, after Zambelli 1980, fig. 1; F, *Pholidophorus latiusculus gervasutii*, after Zambelli 1980, fig. 1; G, *Pholidophorus bechei*, after Nybelin 1966, fig. 16; H, *Pholidolepis dorsetensis*, after Nybelin 1966, fig. 16; I, *Proleptolepis furcata*, after Nybelin 1974, fig. 17k; L, *Leptolepis normandica*, after Nybelin 1974, fig. 2c; M, *Leptolepides sprattiformis*, after Nybelin 1974, fig. 30a.

bones. This may be interpreted as a tendency in neopterygians to have more than one bone along the preopercular sensory canal, but with only the ventral part as a compound (tubular plus laminar) bone.

The *Prohalecites* ventral preopercular resembles in shape the ventral region of the preopercular in a few pholidophorids, such as *Pholidophorus latiusculus*, *P. bechei*, and *Pholidolepis dorsetensis* (Nybelin 1966, p. 428), and *Pholidorhynchodon malzannii* (Zambelli 1981). Furthermore, in another pholidophorid, *Pholidoctenus serianus* (Zambelli 1978), the preopercular is double, its antero-ventral part bearing only a very short sensory canal. Zambelli (1978) noted that the two preopercular bones in *Pholidoctenus* are very similar in shape to the single preopercular of other Triassic pholidophorids, implying that the genus was derived from genera more advanced in other characters by splitting of the preopercular. Zambelli (1986) wrote that the anterior preopercular of *Pholidoctenus* was lost in the main pholidophorid lineage during the Jurassic, leaving the quadrate uncovered by dermal bone. In my opinion, this is incorrect, because in other pholidophorid genera the sensory canal ran ventral to the notch which Zambelli (1978, fig. 4) interpreted as the point of separation of the parts of the preopercular. Since, in Parasemionotidae, the preopercular is

presumed to have lost the sensory canal-free anterior region, it seems improbable that part of the sensory canal itself appeared again on a suborbital-like bone. I think that *Pholidoctenus* (which is a primitive genus because its nasals are contiguous for their whole length) could more easily have achieved its preopercular structure by ventral growth of the principal bone, while the primitively separate ventral bone shifts forward, losing most of its sensory canal. A further step was the fusion of the two bones (as is presumed to have occurred in the other Triassic genera) resulting in the absence of the sensory canal in the area anterior to the antero-ventral notch. The groove on the inner surface, starting from this notch, is here interpreted as a trace of fusion and not as an early stage of splitting (Zambelli 1978, 1986). Accordingly, I think that Nybelin's assumption (1966, p. 429) about the primitiveness of the preopercular sensory canal position on the bone is incorrect.

In more advanced Parasemionotidae, the narrow stage of the preopercular had already been reached, and in *Prohalecites*, as we have seen, it is just a tube of bone round the sensory canal. Acquisition of the inflated postero-ventral region, together with the long posterior branches of the sensory canal, could be achieved by the formation of a ventral preopercular as in *Prohalecites* and the subsequent fusion of these two preopercular bones. This fusion may have occurred more than once, giving two distinct patterns. The first is seen in *Pholidoctenus* and most of the other Triassic pholidophorids (text-fig. 10C, D, E) where the ventral preopercular is presumed to have fused along the antero-ventral edge of the dorsal preopercular.

The second pattern is thought to have developed from a more simple dorso-ventral fusion between the two bones, which often leaves a posterior notch, as in *Pholidophorus latiusculus* (text-fig. 10F) and a few Jurassic pholidophorids (*Pholidophorus bechei* and *Pholidolepis dorsetensis* as well as in *Proleptolepis* for instance; text-fig. 10G, H, I). If *Prohalecites* was ancestral to the Pholidophoridae, then a preopercular such as that of *Pholidoctenus* is primitive compared to that of the other late Triassic pholidophorids (with a deep antero-ventral notch), and *Pholidoctenus* and *Pholidorhynchodon* could not have been ancestral to the main Lower Lias pholidophorid to leptolepid lineage. Nybelin had already noticed this fact (1966, fig. 16) that all the Lias species are derived from unknown or hypothetical ancestral forms.

Recently, Zambelli (1986) also wrote that no Upper Triassic genus of his new subfamily Pholidophorinae (*Pholidophorus*, *Parapholidophorus*, *Pholidoctenus*, and *Pholidorhynchodon*) could be directly ancestral to teleosts, even if he supposed that *Pholidophorus* had to be the closest relative to Lias Pholidophoridae.

Finally, concerning the shape of the preopercular, *Amia* is like the Parasemionotidae, while gars, in which the ventral branch is well developed and L-shaped, are most like the leptolepids. If relationships between *Prohalecites* and the pholidophorids are to be strengthened, then this preopercular character could be of interest in relation to the different hypotheses (Patterson 1973; Olsen 1984) for gars, *Amia* and teleost relationships.

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Abbreviations

af, anal fin; afr, anal fin radial; ang, angular; ant, antorbital; asp, ascending process of parasphenoid; bb, 'bean' bone; bf, basal fulcra; bp, basiptyergoid process of parasphenoid; br, branchiostegal ray; ch, hemichordacentrum; chu, ural hemichordacentrum; cl, cleithrum; cs, caudal scute; df, dorsal fin; dfr, dorsal fin radial; dfs, dorsal fin scale; dn, dentary; dpt, dermopterotic; dsp, dermosphenotic; en, epineurals; ep,

epurals; escl, lateral extrascapular; escm, median extrascapular; fr, frontal; hs, haemal spine; hym, hyomandibular; hyp1, first hypural; i, intercalary; io, infraorbital; iop, interopercular; lw, lateral wing of parasphenoid; mx, maxilla; na, nasal; neu, paired neural arch and spine; ns, median neural spine; op, opercular; opr, opercular process of hyomandibular; pa, parietal; pf, pectoral fin; pcl, postcleithrum; pmx, premaxilla; popd, dorsal preopercular; popv, ventral preopercular; pp, parapophysis; ppl, pelvic plate; pt, posttemporal; q, quadrate; qj, quadratojugal; r, pleural ribs; ro, rostral; s, lateral line scale; sang, surangular; sbo, suborbital; scl, supraclithrum; sd, supradorsal; sn, supraneural; so, supraorbital; sop, subopercular; sy, symplectic; ud, urodermal; un, uroneural.

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THE CLASSIFICATION, ORIGIN AND PHYLOGENY OF THECIDEIDINE BRACHIOPODS

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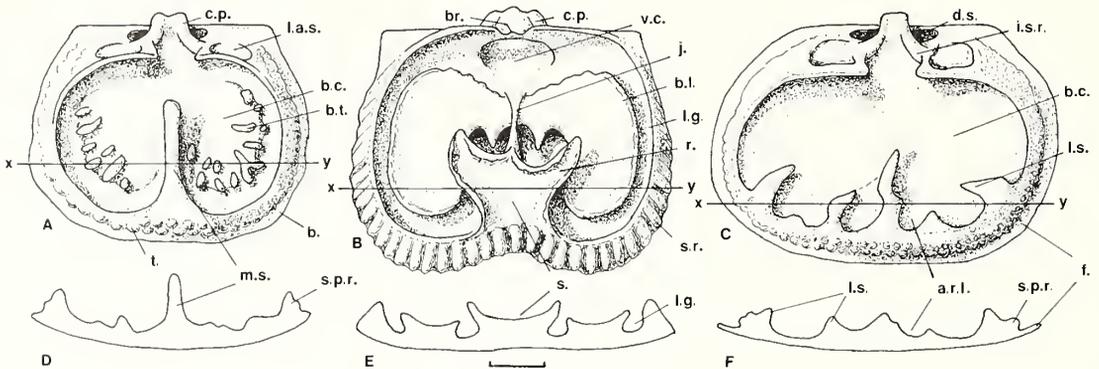
ABSTRACT. Recent studies on ontogeny and shell microstructure enable recognition of the inherent weakness of basing thecideidine taxonomy and phylogeny on morphological characteristics of separated brachial valves. Some previous assumptions are invalidated. The more robust components of lophophore supports are useful in determining relationships, but the form of the brachial lobes, because of their fragility, is less easy to establish, and, without the supporting evidence from sectioned complete shells, their value as taxonomic indicators is questionable. General evolutionary trends may be established through increasing complexity of lophophore supports, but for a clear understanding of thecideidine phylogeny detailed investigation of ontogeny and shell microstructure is required. Neotenous origin and the masking effects of convergent evolution have combined to obscure the line of thecideidine descent. However, shell microstructural evidence now points clearly to a spiriferacean ancestor. The high degree of external morphological similarity makes it essential to consider evidence compiled from studies of morphology, ontogeny and shell microstructure. A revised taxonomy assigning the Thecideidina, Thecospiracea and Bactryniidac to the Spiriferida is proposed.

THECIDEIDINE brachiopods have the dubious distinction not only of having previously been assigned to three articulate orders within the Brachiopoda but to the Mollusca also. Although some of the important early contributions must be mentioned, this paper is not an attempt to chronicle the many publications on thecideidine brachiopods. Much of the content of studies prior to 1965 was synthesized by Pajaud: his monograph (Pajaud 1970) is especially useful in providing fuller details of earlier works on the taxonomy and systematics of the group. Williams's (1973) review of the origin of the thecideidines provided an important summary of previous opinions about the systematic position of the group. The essential purpose of this review, therefore, is to consider the status of arguments advanced in the early 1970s in the light of further developments of the past twenty years. Although obviously interconnected, investigations relevant to this paper can broadly be grouped into studies aimed at the elucidation of taxonomy, ancestry and evolution using morphological, ontogenetic or microstructural evidence. This arrangement broadly reflects the chronological order of the major landmarks in the study of the group and thus serves as a useful framework around which to order the content of the paper.

THECIDEIDINE TAXONOMY

Although shells had been described earlier (Faujas 1798; Schlotheim 1813), the earliest use of 'thecidean' apparently dates from the introduction of the term by DeFrance (1822) to refer to the distinctive morphological characters of representatives of a newly designated genus *Thecidea*. It was, however, another eighteen years before the group emerged (Gray 1840) as a taxon of family rank containing six species, all assigned to *Thecidea*. After the establishment of the Thecideidae Gray, 1840, a series of classic descriptive works followed, notably those of Davidson (1851, 1854, 1874, 1876), D'Orbigny (1847), Eudes-Deslongchamps (1853), Lacaze-Duthiers (1861) and Moore (1854). These studies, although varying the generic spelling between *Thecidea*, *Thecidium* and *Thecideum*, introduced many new species. At about this time the expanding family attracted the interest of systematists (e.g. Dall 1870). Munier-Chalmas (1880, 1887) began the task of differentiating the taxa at generic level and, in view of the small size of many of the representatives,

it is perhaps a tribute to his observation and interpretative skills that the genera he created remain unmodified to the present day. At higher level, Waagen (1882) assigned the thecideans to the Terebratulacea, whereas Schuchert (1896) transferred them to the Strophomenacea. With only minor adjustments (Rollier 1915; Thomson 1915), this steady state persisted for half a century. However, beginning with the combination (Termier and Termier 1949) of thecideids and lyttoniids into a new superfamily Thecideacea, the next twenty years saw more changes than had been witnessed during the previous one hundred and fifty.

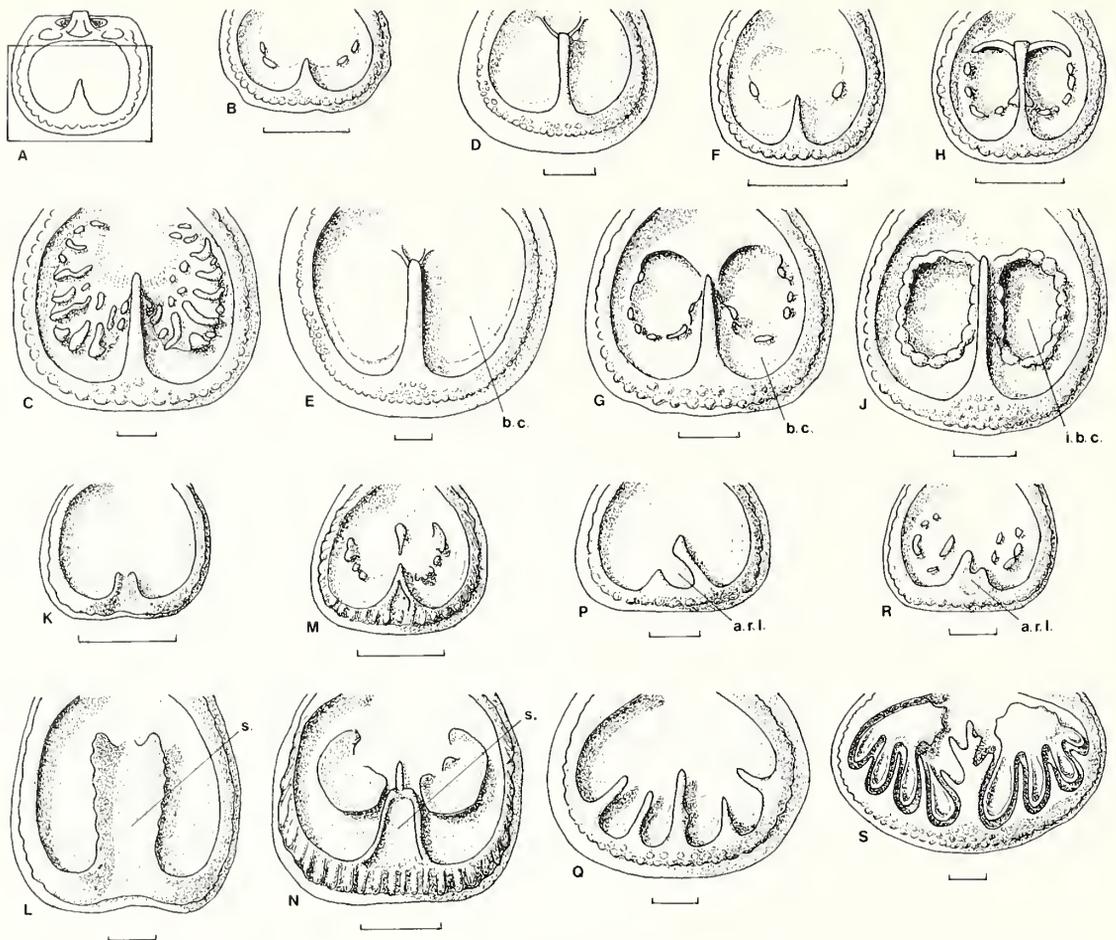


TEXT-FIG. 1. Drawings to show the internal morphology, typical of the principal types of thecideidine brachial valve. A, monoseptate form cf. *Moorellina* with blade-like median septum, brachial bridge broken. B, median septum with well-developed sinus cf. *Praelacazella*. C, polyseptate form cf. *Mimikonstantia*, bridge broken, lateral septa damaged. D-F, transverse sections, x-y, through brachial valves A-C respectively. Abbreviations: a.r.l., auxiliary resorption lobe; b., border; br., bridge; b.c., brachial cavity; b.l., brachial lobe; b.t., brachial tubercle; c.p., cardinal process; d.s., dental socket; f., flange; i.s.r., inner socket ridge; j., jugum; l.a.s., lateral adductor muscle scar; l.g., lophophore groove; l.s., lateral septum; m.s., median septum; r., ramulus; s., sinus; s.p.r., sub peripheral rim; s.r., serration rib; t., tubercle; v.c., visceral cavity. Scale bar represents 0.5 mm.

Elliott (1948) recognized two groups of thecideidines: (i) a thecideiform group, in which numerous septa (text-fig. 1C, F), supporting a multilobed lophophore, arose either from the valve margin or as lateral branches of a median septum; (ii) a thecidelliniform group, characterized by a single median septum and a bilobed lophophore (text-fig. 1A). In the latter group, Elliott (1948, p. 26) detected the incomplete record of a continuous line of descent, *Thecidella* (Lias)—*Bifolium* (Cretaceous)—*Thecidellina* (Recent). Subsequently, Elliott (1953) assigned all the monoseptate forms to the new subfamily Thecidellinae. He conceded that the classification of the heterochronous thecideiform branches was more difficult, as most of the stocks, with the exception of *Eolacazella*—*Lacazella*, were divergent. He recognized that *Davidsonella* was technically thecidelliniform, but argued that the very long brachial lobes showed the same functional attainment as the later thecideiform ptycholophe and included the genus, together with *Eudesella*, *Thecidiopsis*, *Thecidea*, *Eolacazella*, *Lacazella* and *Vermiculothecidea*, in the subfamily Thecideinae. Later, Elliott (1958) considered that intermediate forms between thecideidines and strophomenides or terebratulides were unlikely to be identified and proposed the elevation of the Thecideacea, as understood by Termier and Termier (1949), to subordinal rank to emphasize their distinctiveness. Pajaud's (1970) criticism of Elliott's classification was unjustified. His assertion that Elliott regarded *Thecidella*, *Moorellina*, *Bifolium* and *Thecidellina* as the trunk of a phyletic tree from which the ptycholophous forms branched was incorrect. Elliott clearly understood that two plexi of descent were involved, one rectilinear (Thecidellinae) and the other discontinuous (Thecideinae).

Although incorrect in several respects, e.g. the systematic position of *Thecidella* and *Lacazella*, Elliott's reasoning has stood the test of time (and an enlarged database) remarkably well and in it can be identified the root of all modern classification of the group. However, an important oversight on Elliott's part was his failure to recognize that in genera such as *Thecidella* the median septum was divided by the development of a trough-like depression (text-fig. 1B) or sinus (Baker and Laurie 1978, p. 564). Backhaus equated the median septum with ascending lophophore supporting elements. He coined the terms (Backhaus 1959, p. 12) *apparatus ascendens apertus* to describe the divided median septum (text-fig. 1E) as in *Lacazella*, and *apparatus ascendens clausus* to describe the blade-like median septum (text-fig. 1D) as in *Thecidellina*. Backhaus, like Elliott, also perceived two groups (= tribes of Backhaus 1959) but, unlike Elliott, noted that the *Praelacazella* species showed a progressive passage between the *Thecidella* species of the Lias and the *Lacazella* species of the Tertiary. A further problem stemmed from Elliott's (1948) account of the ontogeny of *Bifolium faringdonense*. Subsequent studies (Baker and Laurie 1978) showed that Elliott had unknowingly combined the ontogeny of the thecidellinin *B. faringdonense* with that of the lacazellin *Neothecidella parviserrata*. The earlier failure to recognize this mixed assemblage had led Backhaus (1959), Pajaud (1966a) and Smirnova and Pajaud (1968) to assign forms with an 'open' ascending apparatus to *Bifolium*. Worse, the authors shared a common view that a juvenile 'closed' ascending apparatus (i.e. undivided median septum) could give way to an open (divided median septum) form in the adult, thus paving the way for important misconceptions about thecidoidine phylogeny. It was only later that Pajaud and Smirnova (1971) showed that the form of the median septum is established very early and remains unaltered throughout ontogeny (text-fig. 2). They removed the 'open' *Bifolium lacazelliforme* types to *Praelacazella*.

Having established a marker (Pajaud 1963), and having published a series of short communications on preliminary notes and problems (Pajaud 1966a, 1966b), new genera (Pajaud 1966c, 1966d; Pajaud and Glazewski 1964; Pajaud and Patručius 1964; Termier, Termier and Pajaud 1966), mutation (Pajaud 1968a), neoteny (Pajaud 1968b), and ontogeny (Smirnova and Pajaud 1968), Pajaud then embarked on the monumental task of monographing all known thecidoidines. The monograph (Pajaud 1970) continued to include the Permian *Cooperina* Termier, Termier and Pajaud, 1966, despite the clear indication (Cooper and Grant 1969, p. 18) that *Cooperina* should be regarded as a productidine assigned to the Strophalosioacea. In view of the, then current, controversy surrounding thecidoidine ancestry, one can sympathize with the authors' eagerness (Termier, Termier and Pajaud 1966) to reveal to the scientific community the first Palaeozoic thecidoidine with such obvious links with the Strophomenida. Cooper and Grant were not to be denied, however, and had, understandably, retained the finest specimens in their own collections. The description and illustration of this material (Cooper and Grant 1975) closely following the systematic dismantling (Dagis 1973, p. 367; Williams 1973, p. 470) of Pajaud's (1970) arguments, dispelled any further doubt about the genus's productidine identity, although reassigned (Cooper and Grant 1975) to the Aulostegacea. Pajaud's reluctance to abandon the identification of *Cooperina* as a thecidoidine (Pajaud 1974; Patručius and Pajaud 1974) succeeded only in casting a shadow over a study (Pajaud 1970) which remains the most comprehensive statement on matters other than thecidoidine shell microstructure. Pajaud's (1970) proposal to elevate the Thecidoidina to a taxon of ordinal rank received little support from other workers, probably because it would have contributed nothing towards a better understanding of thecidoidine systematics, but would merely have frozen the uncertainty within the broader framework of ordinal relationships. Pajaud (1970, p. 74) constructed a taxonomy based on the philosophy that the recognition of genera should be based principally on the morphology of the brachial system. By comparing plans of the brachial structure he was able to identify what appeared to constitute natural groups with a high level of internal coherence. The scheme worked reasonably well up to subfamily level, but encountered difficulties when the phyletic relationship between subfamilies was considered. The principal source of the problems lay in the belief that polyseptate genera such as *Eudesella* arose from monoseptate genera such as *Moorellina* by simple mutation, that monoseptate juveniles of *Bosquetella*-type somehow metamorphosed into polyseptate adults of *Thecidiopsis*-type, and that *Thecidellina*-like



TEXT-FIG. 2. Drawings to show juvenile and adult phases in the brachial valve ontogeny of representative species of monoseptate (*apparatus ascendens clausus*), B–J, and polyseptate (*apparatus ascendens apertus*), K–S, thecideid genera. A, locational diagram. B, C, *Moorellina granulosa* (Moore). D, E, *Pachymoorellina dundriensis* (Rollier). F, G, *Rioultina ornata* (Moore). H, J, *Bifolium favingdonense* (Davidson). K, L, *Thecidella rustica* (Davidson). M, N, *Neothecidella parviserrata* Baker and Laurie. P, Q, *Munikonstantia sculpta* Baker and Elston. R, S, *Thecidiopsis tetragona* (Roemer). Abbreviations: *a.r.l.*, auxiliary resorption lobe; *b.c.*, brachial cavity; *i.b.c.*, intra-brachial cavity; *s.*, sinus. Scale bar represents 0.5 mm.

morphology arose neotenuously from *Backhausina*. It is now accepted (O. Nekvasilová, pers. comm. 1985) that the monoseptate specimens figured as juveniles of *Thecidiopsis bohémica* (Nekvasilová 1964, pl. 11, figs. 1–4) are in fact wrongly assigned to that species. Conversely, the detailed study of the ontogeny of *Thecidiopsis tetragona* revealed (Smirnova 1969) that brachial valves as little as 2.5 mm long already showed the development of lateral septa (text-fig. 1F) and confirmed that Pajaud was incorrect in the belief that the early ontogenetic development of *Thecidiopsis* passed through an auriform (entire median septum and auriform brachial lobes) phase. Although critical of the systematic schemes of Elliott and Backhaus, two thinly disguised groups (= clans) also emerged in Pajaud's (1970) classification. Pajaud's idea of a loose grouping into six subfamilies failed to appeal to Smirnova (1972, 1984) who, on the basis of detailed studies of ontogeny and comparative morphology, decided (Smirnova 1984, p. 109) that the fundamental shortcoming of all

existing classifications was the underrating of the importance of the type of lophophore. Smirnova, in resurrecting Elliott's (1965) family grouping, ascertained that the thecidellinid forms with their schizolophous lophophore (text-fig. 2A-J) differed sharply in ontogeny from the thecideid forms (text-fig. 2K-S) with their ptycholophous or thecidiolophous (Pajaud 1970) lophophore. Members of the Thecidellinidae Elliott, 1958 are characterized by a schizolophous lophophore and an undivided median septum which remained a stable character through the Mesozoic to Cenozoic history of the group. The taxon embraces the subfamilies Moorellininae Pajaud, 1966 and Thecidellininae Elliott, 1958. In the Thecideidae Gray, 1840, a complexly divided thecidiolophous lophophore is inherent, but it always originates as a concave plate dividing into separate lobes. The taxon embraces the subfamilies Thecideinae Gray, 1840, Davidsonellinae Pajaud, 1968, and Lacazellinae Backhaus, 1959. Arising from the more precise understanding of the various ontogenies, Smirnova (1972) recommended a certain amount of inter-subfamilial rearrangement of taxa, namely that *Eudesella* and *Konstantia* be transferred from the Moorellininae, as understood by Pajaud (1970), to the Thecideinae, and that the monoseptate genera *Bifolium* and *Bosquetella* be removed from the Thecideinae. *Bosquetella* was reassigned to the Moorellininae, *Bifolium*, along with *Rioulina* and *Elliottina*, being reassigned to the Thecidellininae. The only other important subsequent move (Smirnova 1984) was the transfer of *Glazewskia* from the Lacazellinae to the Thecideinae. Discovery of new sources of material enabled the restudy (Baker 1983) of the minute *Enallothecidea pygmaea* (Moore). The absence of a median septum and the incomplete sub-peripheral rim placed the genus close to the most primitive thecideidines. Other discoveries (Baker and Elston 1984) revealed that *Eudesella* was not the sole Early Jurassic polyseptate representative. Detailed study of the ontogeny of *Mimikonstantia* Baker and Elston, 1984 showed that, in its basic expression, it differed little from the development pattern described for *Thecidiopsis* by Smirnova (1969). The conclusion that *Mimikonstantia* was also related to *Konstantia* greatly strengthened Smirnova's (1972) argument for reassignment of *Eudesella* and *Konstantia* to the Thecideinae.

THECIDEIDINE ANCESTRY

A major problem posed by the study of the Thecideidina has always concerned the affinities of the suborder. The group has been identified as having originated from various articulate groups, with the Terebratulida (Elliott 1965), Spiriferida (Williams 1968, 1973) and, in particular, several strophomenide taxa (Rudwick 1968; Baker 1970; Pajaud 1970; Grant 1972; Dagens 1973) emerging as the main contenders. Clearly, their neotenous origin and the influence of palingenetic and proterogenetic processes have clouded the image of the line of thecideidine descent. Ideas in the late 1960s and early 1970s had been hampered by uncertainty regarding the Triassic spire-bearing *Thecospira*. Williams (1968, p. 48) revised an earlier opinion that the genus should be identified as a davidsoniacean (Williams 1953, p. 12) in favour of reassignment to the Spiriferida. This proposal was contested by Rudwick (1968, 1970), Baker (1970) and Dagens (1973), who favoured a strophomenide affinity for the genus. Williams, however, remained unconvinced by any counter arguments and reiterated (Williams 1973, p. 475) his earlier view that *Thecospira* should be regarded as a spiriferide, a view supported by Mackinnon (1974). Additionally, it was shown by Hölder (1975) that the brachial supports of complex thecideids were anatomically different from strophalosiacean productidines. In rejecting the views of other authors, Williams (1973, p. 441) declared that any attempt to identify the ancestor of the thecideidines must take account of the shell microstructure and the likelihood that the thecideidines arose neotenously or paedomorphically. After refuting the arguments in favour of a strophomenide ancestor, Williams was less certain about choosing between spiriferides and terebratulides as the probable ancestral stock. However, after citing cementation in *Thecospira* and recalling differences in the structure of the mantle edge in the thecideidines and terebratulides, Williams (1973, p. 475) finally emerged in favour of descent from a punctate spiriferide. The earlier identification of the Permian *Cooperina* as a thecideidine (Termier, Termier and Pajaud 1966) had sparked off similar controversy (Cooper and Grant 1969; Dagens 1973) before its productidine identity was finally confirmed (Cooper and Grant 1975).

An important development, however, had been the demonstration (Dagis 1973) that the shell microstructure of thecospirids is practically the same as that of early thecideidines and that, in the Thecospiracea, the hungarithecidids were probably ancestral to the thecideidines. Dagis perceived a similarity between plectambonitacean and thecospiracean shell microstructure but, because of the time gap, rejected any idea of a genetic link. However, after evaluation of other characters he considered that, although morphological resemblance to the davidsoniaceans may have been largely convergent, the thecospiraceans were descended from strophomenide ancestors which, by lineage therefore, were also ancestral to thecideidines.

Williams's (1973) meticulously detailed defence of his argument for spiriferide affinity left counter arguments difficult to sustain. The single weakness in Williams's thesis was his inability to demonstrate, other than at general level, any microstructure in the shells of spiriferides and thecideidines which represented unequivocal evidence of a genetic relationship. Because of the profound influence of neoteny in thecideidine evolution (Elliott 1953; Pajaud 1970; Williams 1973, 1984), I concluded (Baker 1984) that study of the characters of potentially ancestral adult shells would be unlikely to provide the key to the identification of the thecideidine ancestor. Also, within the Thecideidina the effects of neoteny suppression of some shell secretion processes were so dramatic that it became difficult to identify characters of phylogenetic significance. Eventually, cyrtomatodont teeth (Jaanusson 1971), secondary fibrous shell, and tubercles came to be recognized as characters which were sufficiently stable to survive all but the most drastic changes affecting the shell microstructure of later representatives of the group. It was perceived that such stable characters should be a feature of at least juveniles of the ancestral stock. The results of examination of the shell microstructure of juvenile representatives of potentially ancestral stock (Baker 1984) confirmed Williams's (1973) opinion and were positive enough to make his arguments in favour of spiriferide affinity virtually unassailable. The circle was closed, therefore, on the earlier demonstration (Dagis 1973) that the shell microstructure of thecospiraceans was almost identical with the microstructure of the majority of Early Jurassic thecideidines, since the confirmation of a genetic link between the thecideidines and spiriferides (Baker 1984) also established a genetic relationship for the thecospiraceans and spiriferides. The identification of the thecideidine tubercle as a structural homologue of the spiriferacean denticle pointed to a spiriferacean, rather than the suessiacean ancestor envisaged by Williams. Contrary to the opinion of Smirnova (1984, p. 115), I have never considered that the thecideidines might be descended from a terebratulide ancestor.

THECEIDINE PHYLOGENY

Elliott (1948, 1953) may be credited with the first attempt to elucidate the phylogeny of the, by then, numerous described species. Elliott envisaged, within the suborder, a palingenetic progression from a schizolophous monoseptate form to a ptycholophous polyseptate condition. He considered that the monoseptate genera like *Bifolium* and *Thecidellina*, appearing later, represented the heterochronous expression of the palingenetic trend. Backhaus (1959) rejected Elliott's views, making the important observation that thecideidine lophophore supports developed from the two basic, *apparatus ascendens clausus* and *apparatus ascendens apertus*, patterns. On this basis, Backhaus conceived the idea of two phyletic groups (tribes). He seems to have extrapolated from a thorough knowledge of Cretaceous thecideidines to a much more tenuous understanding of pre- and post-Cretaceous representatives of the suborder. Thus, his proposed phylogeny identifying *Moorellina*, despite its stratigraphic range, as a juvenile *Eudesella*, *Bosquetella* as a juvenile *Thecidiopsis*, and *Thecidellina* as the juvenile of some undiscovered ptycholophous adult, was manifestly suspect.

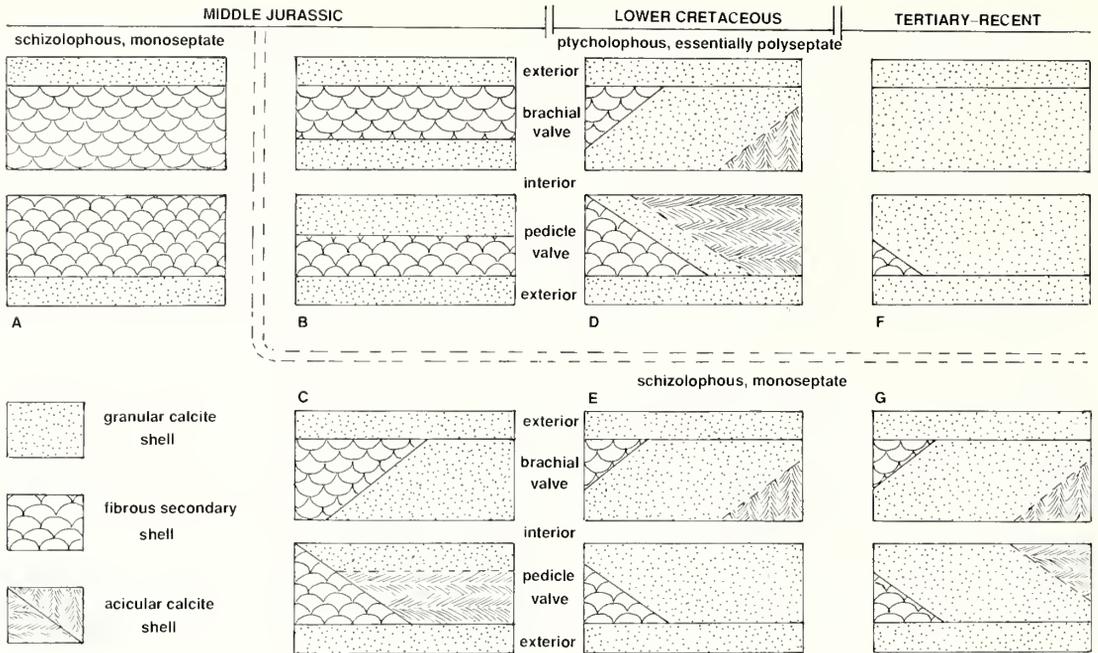
Rudwick's study of food-gathering mechanisms (Rudwick 1968) brought the problematical Triassic genera *Bactrynum* Emmerich, 1855, and *Thecospira* Zugmayer, 1880 into the picture, introducing the concept of the 'functional zone' as a measure of the phyletic relationship between the Thecideacea, Davidsoniacea and Lyttoniacea. Rudwick (1968, p. 353) included *Bactrynum* in the Thecideacea, arguing that the strophic hinge and articulation was quite unlike the aberrant

structures of the lytoniaceans and that the lophophore lay in lobed grooves like those found in polyseptate thecideidines.

Work on a very large collection of 2700 Early Cretaceous thecideid shells from Valanginian and Hauterivian bioherms in the Crimea (Smirnova 1969) enabled detailed study of the ontogeny of species of the thecidellinid genera *Bifolium* and *Bosquetella*, and the thecideid genera *Thecidiopsis* and *Praelacazella*. Close similarities in development suggested (Smirnova 1969, p. 64) that *Moorellina* was probably ancestral to *Bosquetella*. More important, the earliest stages in the development of both *Praelacazella* and *Thecidiopsis* were characterized by a broad median septum with a central sinus. In *Praelacazella* the structure was retained throughout all growth stages, whereas in *Thecidiopsis* it was quickly translated, though the development of a split in the median septum near the hinge-line, into the precursor of a polyseptate condition. The distinctiveness of the thecidellinid and thecideid ontogenetic development patterns provided interesting confirmation of Backhaus's (1959) idea of two phyletic groups. Additionally, within the groups, lineages showing parallel development were beginning to appear. *Moorellina*—*Bosquetella* and *Elliottina*—*Bifolium*—*Thecidellina* lineages were identified in the Thecidellinidae, and *Thecidella*—*Praelacazella*—*Lacazella* and *Eudesella*—*Thecidiopsis*—*Glazewskia* lineages were recognized in the Thecideidae. Smirnova's important contribution probably appeared too late to allow Pajaud (1970) the opportunity for comment. He was unenthusiastic about Rudwick's (1968) views on thecideid phyletic relations, in which he saw the resurrection of Elliott's ideas. However, Pajaud (1970, p. 79) did feel able to support the location of *Bactrynum* near to the Thecideidae in the Thecideacea. He appreciated the phyletic significance of Backhaus's two tribes and, with some modification of Backhaus's ideas, introduced a new phylogeny based on the concept of *Lacazella* and *Thecidellina* 'clans', embracing five subfamilies. Despite the weight of evidence against it, the Permian *Cooperina* was still identified at the base of the main trunk from which the two branches separated. Pajaud considered that the *Lacazella* clan, including the Davisonellinae and Lacazellinae, arose from a *Davidsonella*-type ancestor and that the evolution from the Lias to Recent followed a rectilinear pattern. The *Thecidellina* clan which included the Moorellininae, Thecideinae and Thecidellininae was also believed to have arisen from a *Davidsonella*-type ancestor. The evolution of the latter group was more complicated, and mutation was invoked (Pajaud 1968a) to explain the recurrent appearance of Jurassic and Cretaceous polyseptate forms, whereas neoteny was invoked (Pajaud 1968b) to account for the return to a monoseptate condition in the Tertiary.

Through his comprehensive survey of characteristically thecideid features, Williams (1973, p. 466) was able to identify a range of unifying characters in strong contrast to the profound evolutionary changes suffered by the shell microstructure and lophophore supports. In consideration of the ptycholophe as opposed to the thecidolophe (Pajaud 1970, p. 33), Williams concluded that both conditions could be regarded as equipotential adult elaborations of an immature schizolophe and may, therefore, have recurred many times in thecideid history. Unfortunately, although ignoring *Cooperina*, his chart showing the phyletic variation in thecideid shell microstructure (Williams 1973, fig. 100, p. 468) was based on Pajaud's phylogenetic reconstruction (Pajaud 1970, fig. 31, p. 82) and was, therefore, constrained by the same misconceptions which characterized Pajaud's phylogeny.

In a more recent contribution, Smirnova (1984) has shown that the early juveniles of the Lower Cretaceous *Bifolium mica* are very similar to adults of the Middle Jurassic *Riultina* and *Elliottina* which, in their adult morphology approach *Bifolium* and *Thecidellina*. On this basis, Smirnova detected a genetic relationship and rejected Pajaud's (1970) view that *Thecidellina* arose neotenuously from a Cretaceous thecideid which, instead of having a blade-like median septum, would be characterized by a concave median septum, quickly opening out to form lobes. It is now clear (author's unpublished work) that the adult *Bifolium faringdonense* has canopied brachial lobes like *Thecidellina*, offering further support for Smirnova's view. Although the development of the polyseptate condition from a concave triangular plate (Smirnova 1984) is a unifying character in the Thecideidae, representatives of the Thecideinae are characterized by lobes which are differentiated in a lateral direction, whereas representatives of the Lacazellinae are characterized by lobes which



TEXT-FIG. 3. Diagrammatic representation of the chronological succession of the principal events in the evolution of thecidid shell structure. Posterior and postero-lateral sectors of valve, left, anterior and antero-lateral sectors of valve, right. Horizontal lines indicate continuous layer, diagonal lines indicate restricted distribution. A, *Moorellina*, continuous fibrous secondary shell layer in both valves. B, *Mimikonstantia*, partially suppressed fibrous secondary shell. C, *Pachymoorellina*, partially suppressed fibrous secondary shell and introduction of acicular calcite tracts. *Thecidiopsis*, D, more strongly suppressed fibrous secondary shell, acicular calcite well-developed. E-G, fibrous secondary shell vestigial, restricted mainly to teeth and inner socket ridges, acicular calcite often well-represented but the shell is composed principally of granular calcite. E, *Bifolium*, F, *Lacazella*. G, *Thecidellina*. No lineage is implied.

are differentiated in a front to rear direction. In this respect, Pajaud's (1970) assignment of *Bactrynum* to a position near the Thecideidae seems reasonable. The two subfamilies of the Thecideidae appear to have showed parallel evolutionary development, expressed through a small number of lophophore lobes in the Lower Jurassic, becoming increasingly complex during the Upper Jurassic and Lower Cretaceous, with the maximum complexity reached simultaneously in both groups during the Upper Cretaceous. Changes at the Cretaceous/Palaeocene boundary led to the extinction of the specialized forms. The survival of thecideidines was attributed (Smirnova 1984) to the existence of 'primitive' forms able to adapt to life in various conditions and continue the existence of simply-organized genera in modern basins. Smirnova also studied the evolution of thecideid shell microstructure and reached essentially the same conclusion as Williams (1973, 1984), namely that the continuous fibrous secondary lining (text-fig. 3A) characteristic of early Jurassic shells had been reduced to vestigial patches on the teeth and sockets (text-fig. 3E) by the Early Cretaceous. Williams (1973, p. 469) envisaged that suppression of the fibrous secondary layer was accomplished rapidly, and placed the onset of the trend in late Jurassic time. Williams (1984, p. 739) regarded the suppression of fibrous secondary shell as an expression of neoteny. Smirnova (1984) was able to identify three stages to the suppression process which affected the brachial and pedicle valves differentially. Jurassic representatives were found to have a fibrous secondary layer in both valves. In the Lower Cretaceous, Berriasian to Hauterivian species showed a reduction (text-

fig. 3D) in the fibrous secondary layer in the brachial valve. The suppression of fibrous secondary shell was then extended to the pedicle valve also (text-fig. 3E-G), so that from the Barremian to the Present both valves were characterized by the complete reduction of the fibrous secondary layer, the end product being a granular calcite shell, with or without acicular calcite aggregations, in which the occurrence of fibrous secondary shell, if present at all, was restricted to the teeth and inner socket ridges. Study of a newly-discovered basal Middle Jurassic species (Baker and Elston 1984) cast some doubt on opinions about the timing of the onset of the evolutionary changes in shell microstructure. The shell microstructure of *Mimikonstantia* revealed that the onset of the neotenus suppression of fibrous secondary shell could be traced back at least as far as the beginning of the Middle Jurassic. Also, the shell microstructure resembles that of the Lower Cretaceous species *Thecidiopsis tetragona* and *T. lata*. The conclusion that *Mimikonstantia* and *Thecidiopsis* were phylogenetically linked (Baker and Elston 1984) offered indirect support for Smirnova's belief in a phylogenetic link between Jurassic and Cretaceous polyseptate forms. Consideration of the mechanical requirement for the multiplication of lateral septa suggested a possible sequence (Baker and Elston 1984, fig. 5, p. 790) in the development of a thecidiolophous form from a ptycholophous ancestor and thus, by implication, linked *Mimikonstantia*, *Thecidiopsis*, *Backhausina* and *Thecidea*, again supporting Smirnova's (1984, fig. 64, p. 110) ideas. The evidence indicated that Pajaud's (1970) tentative derivation of *Konstantia* and *Thecidiopsis* from monoseptate *Rioulina* stock was no longer tenable as *Mimikonstantia* pre-dates *Rioulina*. Recent studies (Baker 1989) also enable the origin of *Thecidiopsis* to be traced back to basal Middle Jurassic roots, although analysis of the shell microstructure of a newly designated genus indicates that both *Mimikonstantia* and *Eudesella* are slightly diverged from the main line of descent.

DISCUSSION

Ideas about thecideidine taxonomy, origin and phylogeny have been developed through consideration of morphological, ontogenetic and, more recently, shell microstructural evidence. The review would be incomplete without consideration of the value of the contribution made by each of these aspects.

The value of morphology

Because of their external morphological similarity and because their abnormally wide gape facilitates post-mortem liberation of brachial valves, the taxonomy of thecideidine brachiopods has traditionally relied heavily on the internal morphology of separated pedicle and brachial valves. Particular attention has always been paid to the skeletal supports for the lophophore. Although septa are usually sufficiently robust to provide reliable evidence of their location and general form, other structures, especially brachial and interbrachial lobes, are often fragile and finely sculptured and are almost invariably broken in separated brachial valves. Reservations about the reliability of the evidence as seen in separated brachial valves were expressed as early as the beginning of this century (Upton 1905, p. 91). Nekvasilová, after careful study of the Lower Turonian *Thecidiopsis (T.) bohémica imperfecta*, reached the conclusion (Nekvasilová 1967, p. 130) that, in thecideidines, determination based on the so-called brachial ridges as seen in detached brachial valves was quite inadequate, since such ridges may be a relic of structures whose complete shape may only be studied through sectioning of complete shells. She remarked on the similarity between the reconstructed brachial lobes of the Lower Turonian specimens and those of the Recent *Thecidellina blochmanni* Dall. Work on the ontogenetic development of *Moorellina granulosa* (Moore) showed that the brachial tubercles were the broken remains of much more elaborate structures (Baker 1969) which overarched the intra-brachial cavities. Perforate canopies have subsequently been identified (research in progress) in the Aalenian *M. dubia* and the Aptian *Bifolium faringdonense*. Clearly therefore, the development of the brachial lobes in the *Moorellina*—*Thecidellina* plexus of descent, as envisaged by Smirnova (1984), conformed to a more coherent pattern than became apparent from the study of separated brachial valves. Similarly, the radially disposed septa (Baker and Elston

1984) of the polyseptate *Mimikonstantia sculpta* are almost invariably broken in separated brachial valves.

Over-reliance on morphological evidence has been responsible for some of the most heated controversy surrounding the probable origin and systematic position of the Thecideidina. Termier, Termier and Pajaud's (1966) introduction of *Cooperina* as the first Palaeozoic thecideidina is a case in point. The authors' selective recognition of 'thecideidine' morphological characteristics prompted the omission of the obviously non-thecideidine aspects of the genus. Their arguments were systematically dismantled by Cooper and Grant (1969, p. 18) and finally refuted (Cooper and Grant 1975) through the description and figuring of the superb *Cooperina* specimens to which they had access. A similar selective approach was required to enable Grant (1972) to 'force' the conclusion (see Hölder 1975) of a genetic relationship between thecideidines and strophalosiacean productidines such as *Falafer*.

Rudwick (1968) recognized that in polyseptate thecideidines such as *Thecidiopsis* the primary lophophore lobe is that furthest from the mid-line in a postero-lateral position, and that in *Bactrynum* the primary lobe is located close to the median septum in an anterior position. In this respect the antero-postero extension of the lophophore lobes of *Bactrynum* resembles the development pattern of the lacazellins rather than the lateral extension pattern seen in the thecideins. Rudwick's error lay in the assumption that, in polyseptate thecideidines, growth without shell resorption was able to translate the juvenile arrangement into the adult complement of lateral septa. Study of the development of septa in relation to shell growth in polyseptate thecideacean species (Baker and Elston 1984) has shown that as the brachial valves increase in size, the zones of maximum growth acceleration (Baker 1970) become increasingly separated from the median septum. Therefore, in a shell which is increasing in width more rapidly than it is increasing in length, lateral migration of septa relative to the principal growth vectors is required, and a precisely-controlled process of shell accretion and resorption is necessary for this to be accomplished. On the other hand, if the brachial valve is increasing in length more rapidly than it is increasing in width, as in *Bactrynum*, zones of maximum growth acceleration will remain aligned essentially parallel with the median septum, and the antero-postero development pattern described by Rudwick (1968) will represent the optimum for the circumstances appertaining. This implies, therefore, that septal (and lophophore lobe) development patterns are a strategic response to shell growth requirements and present no real obstacle to the postulation of a genetic relationship between *Bactrynum* and thecideidines. The observation, in addition to the more general morphological considerations, that the shell succession in *Bactrynum* included a normally developed fibrous secondary layer and impersistent tubercles (Williams 1973, p. 475) further substantiated the view that the genus might reasonably be included in the Thecideidina. Although Rudwick was able to accept convergent evolution as the explanation for the morphological similarity between *Bactrynum* and lytoniacean genera, he firmly resisted the idea (Rudwick 1968, p. 329) that the morphological similarity between *Thecospira* and the davidsoniaceans could be similarly explained. By concentrating on cementation, lobed brachial grooves, pseudodeltidium and absence of pedicle foramen as prime evidence, Rudwick was able to assign the thecideidines (including *Bactrynum*) to the Davidsoniacea along with *Thecospira*. Williams (1973) was critical of Rudwick's selective approach and, as subsequent studies have shown (Baker 1984), convergent evolution in reef-associated faunas is probably common. Also, brachial grooves are not characteristic of all early thecideidines (Baker and Elston 1984). Cementation and a pseudodeltidium are also not as exclusive as Rudwick believed (Cooper and Grant 1975). Additionally, there is some evidence that very early thecideidines may have possessed a transient apical pedicle foramen (Baker 1983) and that, initially at least, the pseudodeltidium was located apically in the delthyrium. The accumulated evidence, reinforced by the discovery that the thecideidine tubercle should be regarded as homologous with the spiriferide denticle rather than the strophomenide taleola (Baker 1984) led to abandonment of the notion that the ancestors of the thecideidines were to be found among the strophomenides.

The value of ontogeny

Although some of the palingenetic and neotenuous processes thought to have been operative during thecideidine evolution subsequently proved to be questionable, it is probable that as many issues have been resolved through the interpretation of ontogeny as have been clouded by misinterpretation of morphology. It is unfortunate, therefore, that one of the earliest detailed studies (Elliott 1948) combined events in the ontogenies of *Bifolium* (text-fig. 2H, J) and *Neothecidella* (text-fig. 2M, N) into a single sequence, resulting in considerable taxonomic confusion until the error was noted and rectified (Baker and Laurie 1978). Similarly, it is now clear that the rioultinid (undivided median septum and auriform brachial lobes) brachial valves (text-fig. 2G) figured as juveniles of *Thecidiopsis bohemica* (Nekvasilová 1964, pl. 11, figs. 1–4) were wrongly identified (O. Nekvasilová, pers. comm. 1985). After a detailed study of available ontogenetic records, Pajaud (1970) concluded that the evolution of the lophophore supports followed a more complex pattern than the palingenetic (Elliott 1953, p. 698) or neotenuously-induced (Backhaus 1959, p. 77) progressions previously favoured. The real key to understanding phyletic relationships, however, was provided by Smirnova's (1969, 1984) correlation of the development of the lophophore supports in the various groups. The very large collections of material from the Crimea enabled considerable progress to be made in the detailed interpretation of the ontogeny (Smirnova 1969) of *Thecidiopsis*, *Praelacazella*, *Bosquetella* and *Bifolium*. The discovery that the ontogeny of *Thecidiopsis* (text-fig. 2R, S) did not pass through a rioultinid phase (Smirnova 1969) came too late, however, to prevent Pajaud (1970) from deriving *Thecidellina* neotenuously from *Thecidiopsis* stock. But, it was not until much later, that Smirnova formally rejected (Smirnova 1984) the citation of monoseptal forms such as *Bosquetella* as initial stages in the evolution of *Thecidiopsis tetragona* (Backhaus 1959) and *T. bohemica* (Nekvasilová 1964). Smirnova considered thecidellinin ontogenetic changes as being exemplified by the ontogenetic development of *Bifolium mica*. The ontogeny of *Bifolium* was traced via genetic links with *Elliottina* and *Thecidellina* and *Bosquetella* with *Moorellina*, thereby vindicating Elliott's remarkably perceptive observation (Elliott 1948) that although some species may have become extinct there is little doubt that most of the monoseptate, schizolophous species known, represent the broken record of a continuous series of thecidellinins from the Mesozoic to the present day. With allowance for a tachygenetic element, the correlation of the mechanics of shell growth with septal development pattern (Baker and Elston 1984) reveals a remarkable similarity between the early ontogeny of *Mimikonstantia* and *Thecidiopsis*, even down to the thickened triangular structure from which the lateral septa develop (text-fig. 2P, Q). According to Smirnova (1984) this triangular element could be correlated with the primitive divided median septum of some davidsonellins which was considered to link the Davidsonellinae with the Thecideinae and Lacazellinae in the Thecideidae. Evidence from ontogenetic studies has proved useful in the resolution of other taxonomic problems. Because Pajaud (1966b) had queried the validity of the species designation, Barczyk (1970, p. 653) was uncertain about the status of specimens of *Moorellina septata* (Moore) from the Upper Jurassic of Poland. Study of juveniles of a newly-designated Middle Jurassic genus (Baker 1989) shows that the specimens of *M. septata* queried by Pajaud as juveniles of *M. dundriensis* (Pajaud 1966b) in no way correspond to the latter.

The value of shell microstructure

The use of shell microstructure as an indicator of thecideidine relationships entered the arena relatively late, and for a variety of reasons (Grant 1972, p. 244; Williams 1973, p. 441), its potential value continued to be underestimated (Smirnova 1984). With the exception of three investigations of *Lacazella* shell microstructure (Davidson 1887, Oehlert 1887; Thomson 1927), thecideidine shell microstructure remained virtually unknown until Elliott's (1953, 1955) studies. The early studies were hampered by the difficulty of preparing sections and certain resolution deficiencies of optical microscopes. Also, by chance selection for study (Williams 1955) of a species in which fibrous secondary shell had been almost completely suppressed, it was not discovered that, in the majority of thecideidines, the shell microstructure differs in brachial and pedicle valves. Although Elliott

(1953, p. 695) observed 'the dark-coloured elements of typical pseudopunctuation are seen against clearer lamellar shell, but never so clearly as good examples of pseudopunctuation in certain Palaeozoic brachiopods', neither the resolution of the instruments nor the current state of knowledge enabled the observers to differentiate between taleolae and tubercle cores. Resolution problems were subsequently eliminated (Williams 1968) with the advent of scanning electron microscopy facilities, and the problems of section preparation were considerably alleviated by the use of cold-setting transparent embedding resins and the development of techniques (Baker 1970) for serially sectioning the very small shells at intervals of approximately 20 μm . The demonstration that the shell (text-fig. 3A) of the Middle Jurassic *Moorellina granulosa* was lined by a continuous layer of fibrous secondary shell (Baker 1970) caused Williams (1973) to modify his earlier conclusion (Williams 1968) that the shell microstructure (text-fig. 3F) of *Lacazella* was typical of the thecideidine model. Appreciation of the critical importance of precise location and orientation of section (Baker 1970) no doubt informed the ensuing study, of thecospiracean shell microstructure (Dagis 1973) the very detailed investigation of the Recent thecideidines *Thecidellina barretti* (Davidson) and *Lacazella mediterranea* (Risso) by Williams (1973), and studies of the shell microstructure of Lower Cretaceous species (Smirnova 1979, 1984). Even after the thecideidine structures had been identified as the cores of tubercles (Baker 1970), the pseudopunctuation signal was still so strong that it was easy to continue to regard them as being homologous with taleolae and, through association, perceive a relationship with strophomenides. Although concluding that thecospiraceans were closer to thecideidines than any other group, Dagis's opinion (1973) about the systematic position of the thecospiraceans and their relationship with thecideidines was also coloured by the strength of the historical association of both groups with the Strophomenida. It is unfortunate that, after demonstrating the genetic relationship, he then went on to parallel in thecospiraceans my misconception (Baker 1970) of the thecideidine tubercle as structurally homologous with the strophomenide taleola. Williams (1973), prompted by the discovery of fibrous secondary shell in early Middle Jurassic representatives of the group, undertook a critical survey of the shell microstructure of the majority of the described thecideidine genera. This study established that a continuous lining of fibrous secondary shell was the standard Lower to Middle Jurassic condition (text-fig. 3A) and the indications were that the onset of its neotenus suppression was not effected until the Upper Jurassic or Early Cretaceous (text-fig. 3D, E). Smirnova (1979), in pursuit of Williams's (1973) idea of a Late Jurassic to Early Cretaceous date for fibrous secondary shell suppression, studied the shell microstructure of three Lower Cretaceous species, *Thecidiopsis tetragona* (Roemer), *Thecidiopsis lata* Smirnova and *Praelacazella valangiensis* (de Loriol) in an attempt to find out if the change was abrupt or gradual. The differences in the microstructure of *T. tetragona* and *T. lata* and the similarity of *P. valangiensis* to both, helped to convince her that microstructure was of limited taxonomic value, but useful in dating the important steps in the structural evolution of the shell. This conviction was strengthened by a later study (Smirnova 1984) in which she deduced that, although the structural changes of the shell proceeded steadily, the disappearance of the fibrous secondary layer was quick and probably occurred in the first half of the Lower Cretaceous. Smirnova concluded that the degree of plasticity of microstructural changes in the thecideidine shell rendered shell microstructure almost valueless in the comparison of Mesozoic thecideidines and Triassic thecospirids with ancient Palaeozoic groups, and virtually useless for drawing conclusions about their hypothetical relationship. She felt that shell microstructure was only of value when its use was confined to the study of successive groups in time. The situation was envisaged as being most complicated from the Upper Cretaceous to Recent, as a consequence of the relative uniformity of shell microstructure (Smirnova 1984), when, the extreme difficulty of determining the relationship between layers of granular and acicular calcite rendered it of little use for systematization purposes. Work by Baker and Elston (1984) on newly-discovered Middle Jurassic material demonstrated, contrary to the view of Williams (1973) and Smirnova (1979, 1984), that although the fibrous secondary layer was still continuous, the trend towards its suppression (text-fig. 3B) was already established by the early Middle Jurassic. Subsequent investigations (Baker 1989) revealed that *Mimikonstantia sculpta* was not the only species affected.

In the contemporaneous *Pachymoorellina dundriensis*, fibrous secondary shell had already disappeared (text-fig. 3C) from the anterior and antero-lateral sectors of both valves.

CONCLUSIONS

The conjectural nature of some of the identifications of brachial lobe morphology has created taxonomic and phylogenetic problems. Until about the mid-1960s, interpretation was made more difficult because the size of most thecideacean representatives of the suborder fell outside the optimum resolution range for both conventional photography and reflected light photomicrography, so that the quality of plate figures was modest by current standards. Study of the detail of thecideidine morphology, and especially their shell microstructure was revolutionized by the advent of the scanning electron microscope. Considerable emphasis has been placed on the relative value of shell microstructure as a distinctive character. Although general shell fabric may not be diagnostic, structures such as tubercle cores, from a unifying point of view, show a remarkable continuity of expression throughout the history of the group. Also, it was only the demonstration that the thecideidine tubercle was probably the structural homologue of the spiriferacean denticle, rather than the strophomenide taleola, that enabled the link between thecideidines and strophomenides to be severed with confidence. The thecideidines represent a group whose classification is aided by the recognition of genera showing a high level of coherence from a genetic relationship point of view. Clearly, much remains to be discovered about the stratigraphic and geographical range of this still comparatively little-known group. Also, much more work is required on the detailed mapping of the various successions of shell microstructure, which is emerging as a taxonomic indicator of far greater potential than has hitherto been appreciated. However, in my opinion, sufficient information is now available to enable a reliable taxonomic and phylogenetic framework to be established.

RECOMMENDATIONS

Revised classification

Excluding the aulostegacean *Cooperina*, for the reasons given by Cooper and Grant (1969, 1975), Dagus (1973) and Williams (1973), the Thecideidina, as understood by Pajaud (1970, pp. 82–83) included twenty two genera distributed among five subfamilies. Apart from some rearrangement of genera and the resurrection of older family grouping (Smirnova 1984), Pajaud's framework has persisted, largely unaltered, to the present time. A further, subfamily Enallothecideinae Baker, 1983 and four additional genera *Enallothecidea* Baker, 1983, *Mimikonstantia* Baker and Elston, 1984, Pajaudina Logan, 1988 and *Pachymoorellina* Baker, 1989 may now be added. The general organization and shell microstructure of *Enallothecidea* is similar to that of early juvenile moorellinins prior to the full differentiation of the median septum. It is proposed, therefore, to reassign the Enallothecideinae to the Thecidellinidae. In view of the perceived relationship between *Bactrynum* and thecideidines, and the weight of evidence about the genetic relationship between thecospiraceans and thecideidines and their affinity with spiriferides a revised classification is proposed as follows:

- Order SPIRIFERIDA Waagen, 1883
- Suborder THECIDEIDINA Elliott, 1958
- Superfamily THECOSPIROIDEA Bittner, 1890
- Family THECOSPIRIDAE Bittner, 1890
- Genus THECOSPIRA Zugmayer, 1880
- Family THECOSPIRELLIDAE Dagus, 1973
- Genus THECOSPIRELLA Bittner, 1900

Family HUNGARITHECIDAE Dagus, 1973

Genus HUNGARITHECA Dagus, 1973

Superfamily THECIDEOIDEA Gray, 1840

Family THECIDELLINIDAE Elliott, 1958

Subfamily ENALLOTHECIDEINAE Baker, 1983

Genus ENALLOTHECIDEA Baker, 1983

Subfamily MOORELLININAE Pajaud, 1966

Genera MOORELLINA Elliott, 1953; PACHYMOORELLINA Baker, 1989; BOSQUETELLA Smirnova, 1969

Subfamily THECIDELLININAE Elliott, 1953

Genera RIOULTINA Pajaud, 1966; BIFOLIUM Elliott, 1948; THECIDELLINA Thomson, 1915

Family BACTRYNIIDAE Williams, 1965

Genus BACTRYNIUM Emmerich, 1855

Family THECIDEIDAE Gray, 1840

Subfamily DAVIDSONELLINAE Pajaud, 1966

Genera DAVIDSONELLA Munier-Chalmas, 1880; AGERINELLA Patruilius, 1964

Subfamily LACAZELINAE Backhaus, 1959

Genera THECIDELLA Oehlert, 1887; NEOTHECIDELLA Pajaud, 1970; PARABIFOLIUM Pajaud, 1966; PRAELACAZELLA Smirnova, 1969; VERMICULOTHECIDEA Elliott, 1953; DANELLA Pajaud, 1966; EOLACAZELLA Elliott, 1953; LACAZELLA Munier-Chalmas, 1880; PAJAUDINA Logan, 1988

Subfamily THECIDEINAE Gray, 1840

Genera EUDESELLA Munier-Chalmas, 1880; MIMIKONSTANTIA Baker and Elston, 1984; KONSTANTIA Pajaud, 1970; THECIDIOPSIS Oehlert, 1887; BACKHAUSINA Pajaud, 1966; PARATHECIDEA Backhaus, 1959; THECIDEA DeFrance, 1822; GLAZEWSKIA Pajaud, 1964

Elliottina Pajaud, 1963 is not included in the revised classification. The genus was never strongly placed and was soon relegated to sub-generic rank by Pajaud himself (Pajaud 1966*b*). The whole concept of the erection of a genus on the basis of the width of the ventral interarea is highly suspect in attached forms, where the morphology of the pedicle valve is so strongly influenced by the size and shape of the surface to which attachment is effected. It is rather surprising, therefore, that a new subfamily Elliottininae was proposed (Pajaud and Smirnova 1971) to include the resurrected *Elliottina* and also *Rioulina* and *Bifolium*. The Elliottininae was subsequently abandoned (Smirnova 1984), with *Rioulina*, *Bifolium*, and *Elliottina* being restored to the Thecidellininae.

The superfamily suffix -ACEA enjoys such a wide usage in current terminology that it would have caused considerable confusion to have changed it in the body of the paper. However, in compliance with the ICZN recommendation 29a (Ride *et al.* 1985, p. 55) -OIDEA is added to the superfamily stem as the preferred suffix in the revised taxonomy.

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TEUTHID CEPHALOPODS FROM THE LOWER JURASSIC OF YORKSHIRE

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ABSTRACT. Specimens of four teuthid species, *Loligosepia aalensis* (Zieten), *Jeletzkyteuthis agassizi* (Deslongchamps), *Teudopsis schuebleri* (Quenstedt) and *T. subcostata* (Münster), are described from the Whitby Mudstone Formation (Toarcian) of North Yorkshire. *Jeletzkyteuthis* nom. nov. is erected to replace *Loliginites* Quenstedt which is nomenclaturally invalid. This teuthid fauna is found to be similar to that of southern England, Normandy and southern Germany.

THE initial phase of fossil teuthid research took place during the first half of the nineteenth century. Most of the species' names still in use were first applied by workers such as Zieten (1830–32), Deslongchamps (1835), Buckland (1836), Quenstedt (1839, 1845–49), d'Orbigny (1842, 1845), and Münster (1843). Many of these authors directly compared their fossil specimens with the 'pens' of recent squid, and the genus *Loligo* was used for some of the named species (e.g. Zieten 1830–32; Buckland 1836).

Recently, interest in fossil teuthids has been rekindled by a number of works from the Tübingen school (e.g. Reitner and Engeser 1981, 1982; Engeser and Reitner 1983, 1985, 1986; Riegraf and Zügel 1984). However, despite the encouragement provided by Jeletzky (1966, p. 42) and Donovan (1977), little has been written on British teuthids in recent years. In this paper, I redescribe the teuthid specimens discussed by Simpson (1855, 1884) and Tate and Blake (1876) (see also Crick 1922, p. 288) from Yorkshire, figuring the type specimens of Simpson's species for the first time. Well-preserved teuthid specimens are rare due to their fragility and so new material is not readily available, requiring the re-examination of older collections. Fortunately, both Simpson and Blake carefully localized their material, and matrix lithologies allow reasonable stratigraphical control.

Interest in fossil teuthids in Britain probably began with Buckland (1836). He figured several specimens from the Lower Jurassic of Dorset which he assigned to *Loligo*, suggesting that they were similar to Zieten's (1830–32) *Loligo aalensis*. Voltz (1840) was later to reassign these forms to a new species, *Belopeltis bucklandi*. This is one of the oldest known species of *Loligosepia* (Sinemurian-Pliensbachian: Jeletzky 1966, p. 42), although earlier forms are known from Germany (Reitner 1978; Reitner and Engeser 1981). The majority of British nineteenth century discoveries were from southern England, as shown by Morris (1854, p. 303), Moore (1867) and Smithe (1877). Smithe (1877, p. 400) described a new species, *Beloteuthis glewensis*, from the sands overlying the Marlstone Rock Bed in North Gloucestershire which may represent the basal Toarcian (see Howarth 1980). Engeser and Phillips (1986) and Engeser (1988) have interpreted this as a species of *Teudopsis*. A revision of teuthids from the Fish and Insect beds (Toarcian) of southwest England was given by Crick (1921) who recorded two species, *Geoteuthis agassizi* (Deslongchamps) and *Teuthopsis [sic] brunelli [sic]* (Deslongchamps). These species may now be assigned to *Loligosepia aalensis* (Zieten) and *Teudopsis bunelii* Deslongchamps, respectively. A third species from the same horizon in Gloucestershire, *Teudopsis subcostata* (Münster), may be added to this list (BMNH C.5252). Moore (1867, p. 183) indicated that these teuthids were extremely common in southern England, and was able to suggest that they formed the stable diet of the contemporary ichthyosaurs, an idea supported by Pollard (1968) from the examination of ichthyosaur gastric masses.

Simpson (1855, 1884) was the first author to describe teuthids from Yorkshire. He erected four new species, *Sepia obtusalis*, *S. cuspidata*, *S. haustrum* and *S. incomposita*. Blake (*in* Tate and Blake

1876) re-examined Simpson's material, assigning *S. cuspidata* to the genus *Teudopsis*, and considering the nominal species *S. obtusalis* and *S. haustrum* junior synonyms of *Geoteuthis coriaceus* (Quenstedt). The types of these species are preserved in the Whitby Museum (WM). The fourth species, *S. incomposita*, is not mentioned in the WM catalogue, but Blake (*in* Tate and Blake 1876, p. 257) suggested that these specimens were in the York Museum collections. In any case, this species is actually based on fragments of fish vertebrae (Tate and Blake 1876, p. 257) and is therefore not dealt with here. Blake's specimens of this fish (*Gyrosteus mirabilis*) are certainly in the York Museum (Pyrah 1979, p. 417). Blake added two more species with his own *Beloteuthis leckenbyi* (now in the Sedgwick Museum), and a single specimen of *Beloteuthis subcostata* Münster (now in the British Museum (Natural History)) (see Crick 1922). These Yorkshire specimens were all collected from the Jet Rock (= Upper Lias Division 6 of Simpson, 1884) which is equivalent to the Jet Rock *sensu stricto* (*exaratum* Subzone) as defined by Howarth (1962, p. 386), and the lower part of the Jet Rock Member of Powell (1984). This original published information (Simpson 1855, 1884; Blake *in* Tate and Blake, 1876) is confirmed by the examination of the fossil matrices.

SYSTEMATIC PALAEOLOGY

All specimens are housed in Whitby Museum (WM), the British Museum (Natural History) (BMNH) and the Sedgwick Museum, Cambridge (SM). The descriptions given below are based purely on Yorkshire material and so little can be added to the original diagnoses. Most of the type specimens of the species described below are preserved in the Geologisches und Paläontologisches Institut, Tübingen (GPIT), West Germany.

The terms used below are discussed by Jeletzky (1966) (text-fig. 1). Recently, Engeser (1986, 1988) and Berthold and Engeser (1987) have suggested a revised taxonomy of the Coleoidea based on phylogenetic systematics. Jeletzky's (1966) less controversial classification is used below, however, as discussion of higher taxa is beyond the scope of this study, and as taxa of low rank remain unaffected. The synonymy lists follow the convention of Matthews (1973).

Subclass COLEOIDEA Bather, 1888

Order TEUTHIDA Naef, 1916

Suborder LOLIGOSEPIINA Jeletzky, 1965

Family LOLIGOSEPIIDAE Van Regteren Altena, 1949

(= *Belopeltidae* Naef, 1921)

Genus LOLIGOSEPIA Quenstedt, 1839

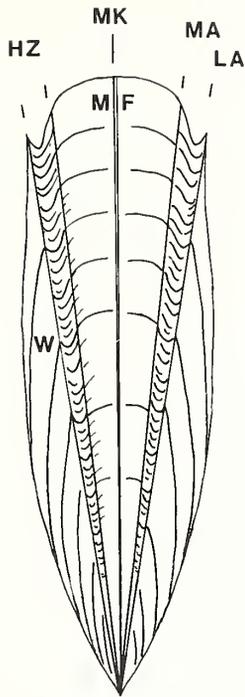
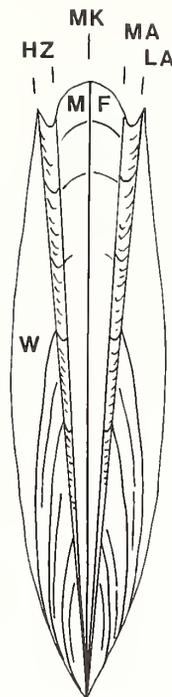
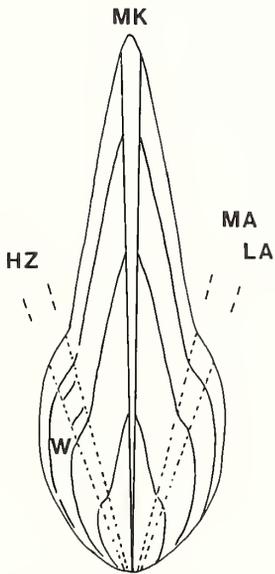
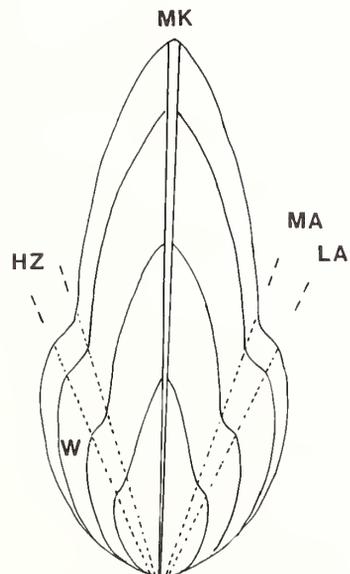
(= *Belopeltis* Voltz, 1840, (objective synonym); *Palaeosepia* Theodori, 1844, *Geoteuthis* Münster, 1843 (subjective synonyms))

Type species. *Loligo aalensis* Zieten, 1832, by monotypy.

Diagnosis. Large Loligosepiidae with gladius comprising relatively broad, smooth median field with central well-defined median keel and parallel striations; narrow hyperbolar fields with markedly anterior-concave growth lines; wings of parabolic form and with pointed anterior ends, generally extending for not less than one-third of the length of the median field. Large ink-sac present.

Range. This genus is known primarily from the Lower Jurassic (Sinemurian-Toarcian) of Europe (Jeletzky 1966; Reitner and Engeser 1981). However, Reitner (1978) has reported this genus from the Upper Triassic of Bavaria, although the specimens illustrated by him have markedly reduced wings.

Remarks. On the basis of the reconstructions given by Naef (1922, p. 129), specimens of *Loligosepia* may be distinguished from the similar genus *Parabelopeltis* Naef which has smaller hyperbolar zones with less anteriorly concave growth lines, and from *Jeletzkyteuthis* nom. nov. which has a narrower, elongate gladius with a narrow median field (text-fig. 1).

*Loligosepia aalensis**Jeletzkyteuthis agassizi**Teudopsis schuebleri**Teudopsis subcostata*

TEXT-FIG.1. Diagrammatic reconstructions of the four teuthid species under discussion, not to scale. Abbreviations: HZ, hyperbolar zone; LA, lateral asymptote; MA, median asymptote; MF, median field; MK, median keel; W, wing.

Loligosepia aalensis (Zieten, 1832)

Text-figs. 1, 2A–C, 3B, C

- *. 1832 *Loligo Aalensis* Zieten, p. 34, pl. XXV, fig. 4.
- . 1832 *Loligo Bollensis* Zieten, p. 34, pl. XXV, fig. 5. [Lectotype, here selected, Lower Toarcian, Posidonienschiefer, Boll, Southern Germany. Original in the GPIT].
- non 1832 *Loligo Bollensis* Zieten, p. 49, pl. XXXVII, fig. 1. [= *Teudopsis schuebleri* (Quenstedt)].
- . 1849 *Loliginites Bollensis* Zieten; Quenstedt, p. 508, pl. 32, figs. 11–13; pl. 33, figs. 1–5. [pl. 33, fig. 1 is Zieten's pl. XXV, fig. 5 specimen refigured].
- v. 1855 *Sepia haustum* Simpson, p. 21.
- v. 1876 *Geoteuthis coriaceus* Quenstedt; Blake (*in* Tate and Blake), p. 313, pl. IV, fig. 1.
- v. 1884 *Sepia haustum* Simpson; Simpson, p. 19.
- . 1920 *Geoteuthis Bollensis* (Schübler) Zieten; Bülow-Trummer, p. 253. [Full early synonymy].
- . 1921 *Geoteuthis agassizi* (Deslongchamps); Crick, p. 251, pl. A.
- . 1922 *Geoteuthis coriaceus* (Quenstedt); Crick, p. 288.
- . 1922 *Belopeltis Aalensis* (Zieten); Naef, p. 125, text-fig. 47b.
- . 1949 *Loligosepia aalensis* (Zieten); Van Regteren Altena, p. 58.
- . 1981 *Loligosepia aalensis* (Zieten); Reitner and Engeser, p. 427, text-fig. 2.
- . 1984 *Loligosepia aalensis* (Zieten); Riegraf *et al.*, p. 37.
- . 1988 *Loligosepia aalensis* (Schübler *in* Zieten); Engeser, p. 9. [Full synonymy].

Type specimen. Holotype, the original of Zieten (1832, p. 34, pl. XXV, fig. 4), from the Lower Toarcian of Aalen, southern Germany. Original in the GPIT.

Material. Nine specimens: WM 2, 3, 5; BMNH C.651, C.2699, C.2698, C.37529, C.46828 and C.12047 (the original of Tate and Blake 1876, pl. IV, fig. 1), all from the Jet Rock Member, Whitby Mudstone Formation (*falciferum* Zone), of Whitby, North Yorkshire.

Notes on Simpson's material. Simpson's (1855) nominal species *Sepia haustum* is a junior subjective synonym of *Loligosepia aalensis*. Two specimens are available in the Whitby Museum labelled *Sepia haustum* in Simpson's handwriting, namely WM 2 and 3 (text-fig. 2A, B). Specimen WM 2 is here designated lectotype (text-fig. 2B). Both specimens are preserved in concretions and are from Simpson's Upper Lias 6 division, equivalent to the Jet Rock *sensu stricto* of Howarth (1962).

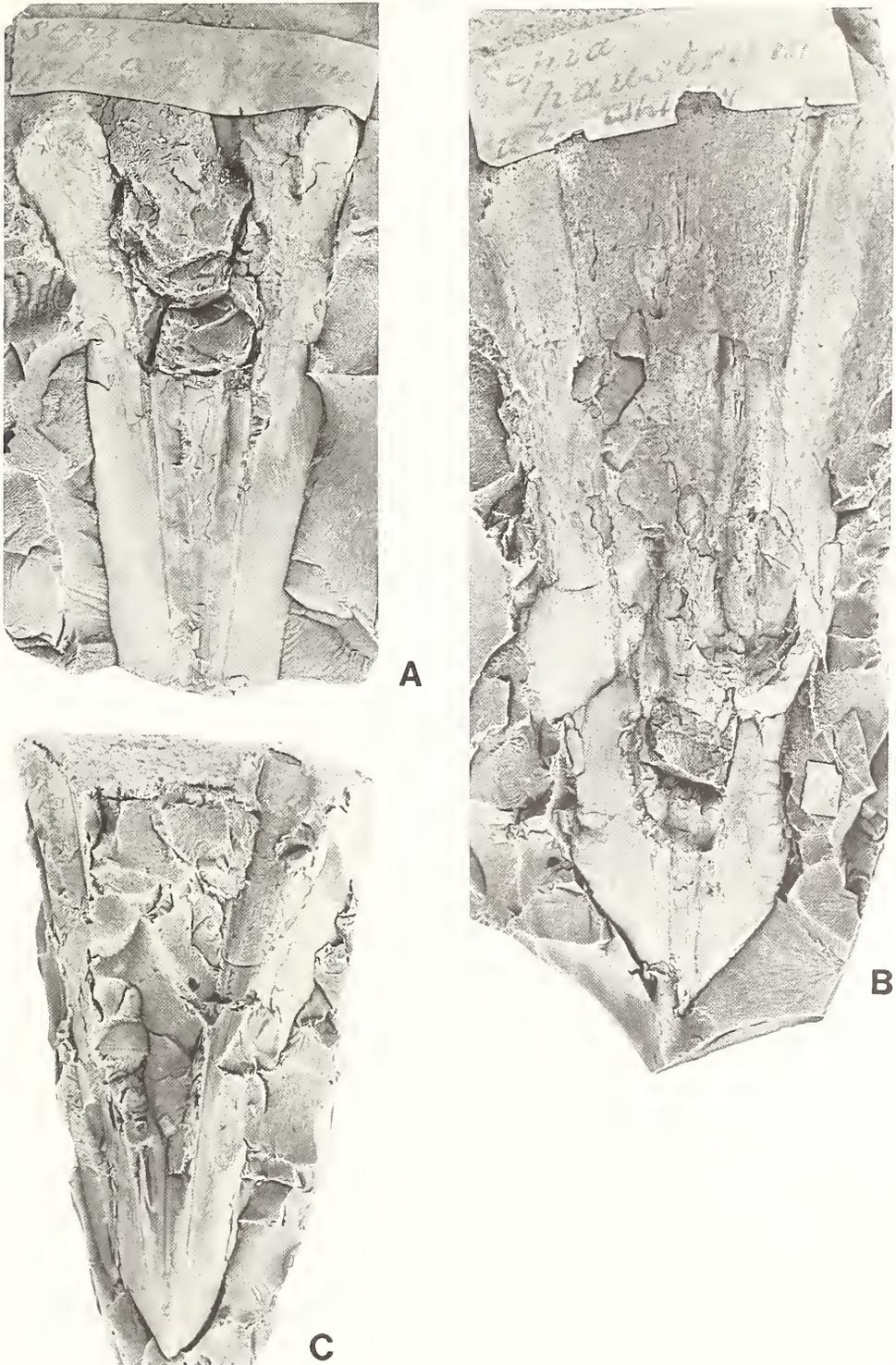
Diagnoses. See Quenstedt (1849, p. 508; '*Loliginites Bollensis*'), Naef (1922, p. 25; '*Belopeltis aalensis*') and Reitner and Engeser (1981, p. 427).

Description. Several specimens of this species have been recovered from the Toarcian of Yorkshire. The majority (BMNH C.651, C.2698, C.2699, C.12047, C.46828) are crushed and generally unrepresentative of the actual in-life gladius. However, two of the specimens (WM 5, text-fig. 2c; BMNH C.37529: text-fig. 3B, C) preserved in concretions are more representative of the original form of the shell. When flattened, the gladius has a rounded, obtuse posterior with fan-like anterior (text-fig. 2B). In concretions, the posterior is acute with the wings extended into the vertical plane to form a small conus (e.g. BMNH C.37529: text-fig. 3B).

The shell comprises a large (length 140 mm max.) gladius with a regular anteriorly-diverging, broad, median field with an apical angle of 18°. The median field is separated from the narrow hyperbolar zones by sharply-defined median asymptotes which are marked by a narrow, well-defined groove which expands anteriorly. Transverse growth lines are discernible on the lateral parts of the median field. A sharp median keel, bounded by grooves of an equivalent width, is accommodated in the central third of the median field. This third displays no growth lines, but has striations parallel to the keel.

The hyperbolar zones are each up to one-third of the width of median field, and display anterior-concave growth lines bounded by sharp asymptotes. The wings are parabolic in shape with correspondingly-formed growth lines. These are deflected sharply to the posterior at the lateral asymptotes. The wings are present along most of the preserved length of the specimens.

Remarks. Reitner and Engeser (1981) have recently discussed the differential diagnosis of this species within the genus *Loligosepia*. It can be distinguished from the coexisting species



TEXT-FIG. 2. *Lohigosepia aulensis* (Zieten), ventral views $\times 1$. A, WM 3, paralectotype of *Sepia haustum* Simpson. B, WM 2, lectotype of *Sepia haustum* Simpson. C, WM5.

Jeletzkyteuthis agassizi (Deslongchamps) by its broad median field and well-developed median keel. Riegraf (1987) recently described a large isolated ink-sac from southern Germany that he interpreted as belonging to *Loligosepia aalensis*.

Genus JELETZKYTEUTHIS nom. nov.
(nom. nov. for *Loliginites* Quenstedt, 1849)

Type species. *Teudopsis agassizi* Deslongchamps, 1835.

Derivation of name. In memory of Dr J. A. Jeletzky, 1915–1988.

Diagnosis. Large Loligosepiidae with smooth, narrow and elongate gladius comprising a narrow median field with median keel; hyperbolar zones equivalent in width to the median field with anterior-concave growth lines; wings of parabolic form similar to those of *Loligosepia*. Ink-sac present.

Range. Lower Jurassic (Toarcian) of Europe (Naef 1922).

Remarks. *Jeletzkyteuthis* is erected here as a replacement name for *Loliginites* Quenstedt, 1849, which Engeser (1988, p. 50) found was unavailable for the Principle of Priority under Article 20 of the *International Code of Zoological Nomenclature*, being originally used for fossil species of the Recent genus *Loligo* (Quenstedt 1849). Engeser (1988) further suggested that the type species of *Loliginites*, *L. coriaceus* Quenstedt (= *Teudopsis agassizi* Deslongchamps), was actually a plesiotoothid of the genus *Romaniteuthis* Fischer and Riou, 1982. However, forms formerly attributed to the genus *Loliginites* have much greater affinity to the Loligosepiidae than Plesiotoothididae, having well-developed wings, and relatively broad median fields with simple keels. *Romaniteuthis* is distinguished by its much reduced wings and conus, and its rounded, well-developed, keel (Fischer and Riou 1982; Riegraf and Zügel 1984). In consequence *Jeletzkyteuthis* nom. nov. is erected here for those narrow, elongate Loligosepiidae characterized by the species *Jeletzkyteuthis agassizi* (Deslongchamps) (see Naef 1922, text-fig. 47 and text-fig. 1 herein).

Jeletzkyteuthis agassizi (Deslongchamps, 1835)

Text-figs. 1 and 3A

- *. 1835 *Teudopsis Agassizi* Deslongchamps, p. 72, pl. 5, fig. 15.
- . 1849 *Loliginites coriaceus* Quenstedt, p. 512, pl. 34, figs. 5–8.
- v. 1855 *Sepia obtusalis* Simpson, p. 20.
- non 1876 *Geoteuthis coriaceus* Quenstedt; Blake (in Tate and Blake), p. 313, pl. IV, fig. 1 [= *Loligosepia aalensis*].
- v. 1884 *Sepia obtusalis* Simpson; Simpson, p. 18.
- . 1920 *Geoteuthis coriacea* Quenstedt; Bülow-Trummer, p. 253.
- non 1921 *Geoteuthis agassizi* Deslongchamps; Crick, p. 251, pl. A [= *Loligosepia aalensis* (Zieten)].
- . 1922 *Loliginites coriaceus* Quenstedt; Naef, p. 130, text-fig. 47c.
- . 1984 *Loliginites agassizi* (Deslongchamps); Riegraf *et al.*, p. 37.
- . 1988 *Romaniteuthis agassizi* (Eudes-Deslongchamps); Engeser, p. 51. [Full synonymy].

Type specimen. Holotype, the original of Deslongchamps (1835, p. 72, pl. 5, fig. 15), Toarcian, Curcy, Normandy, northern France. It is not known whether Deslongchamps's specimen still exists. However, Quenstedt's (1846–49) specimens of *Loliginites coriaceus* are preserved in GPIT.

Material. Three specimens, WM 1, BMNH 83685, C.3654, Lower Toarcian, Whitby Mudstone Formation, Jet Rock Member, (*falciferum* Zone), Whitby, North Yorkshire.

Notes on Simpson's specimens. Simpson's (1855) nominal species *Sepia obtusalis*, is a junior subjective synonym of *Jeletzkyteuthis agassizi*. Two specimens bear this name in the Whitby Museum Catalogue. Specimen WM 1 has a distinct well-preserved ink-sac, and is undoubtedly the specimen referred to by Simpson (1855, p. 20). This specimen is here designated lectotype of *Sepia obtusalis* (text-fig. 3A). It is preserved in bituminous shale and is undoubtedly from the Jet Rock Member. A second specimen, WM 5, bears no label, but is noted as *Sepia obtusalis* in the Whitby Museum catalogue. This is actually a representative of the species *Loligosepia aalensis* (Zieten) (text-fig. 2c; see above).

Diagnoses. See Quenstedt (1849, p. 512; *Loliginites coriaceus*) and Naef (1922, p. 130; *Loliginites coriaceus*).

Description. Few specimens of this species have been recovered from the Yorkshire Toarcian. The single WM specimen (text-fig. 3A) is fragmentary and worn, but comprises a posterior portion (length 50 mm) of a gladius slightly offset from a large, elongate ink-sac. The gladius fragment is flattened and narrow with a maximum preserved width of 19 mm. A central median field commences with an acute apex and remains narrow for its total length. The median field is slightly crushed and worn, but a narrow median keel can be discerned in its mid-part. The greater part of the width of the specimen is taken by the wings which are each up to three times the width of the median field. Preservation of this specimen is such that no growth lines can be discerned on the wings, and the hyperbolic zones cannot be identified, although the lateral asymptotes can be seen. Slightly oblique from the gladius is an elongate, flask-shaped ink-sac with a total length of 75 mm.

Specimen BMNH 83685 is rather better preserved, and comprises a narrow, elongate gladius 180 mm long. The median field is largely unornamented with a weak median keel. The hyperbolic zones are so narrow in its posterior as to be barely discernable; in the anterior they display anterior concave growth lines. The wings are three times as wide as the median field, extending for at least one half of the length of the gladius, and possess parabolic growth lines.

Remarks. These specimens are representative of the species *Jeletzkyteuthis agassizi*. Simpson's specimen, WM 1, is very close to Quenstedt's (1849, pl. 34, fig. 5). The specimen illustrated by Blake (in Tate and Blake 1878, pl. IV, fig. 1: BMNH C.12047) is more properly assigned to *Loligosepia aalensis* (Zieten) as it possesses a broader and more ornamented median field. *Jeletzkyteuthis agassizi* is clearly distinguished from *Loligosepia aalensis* (Zieten) by possessing a narrow, elongate and less ornamented gladius as illustrated by Naef (1922, text-fig. 47).

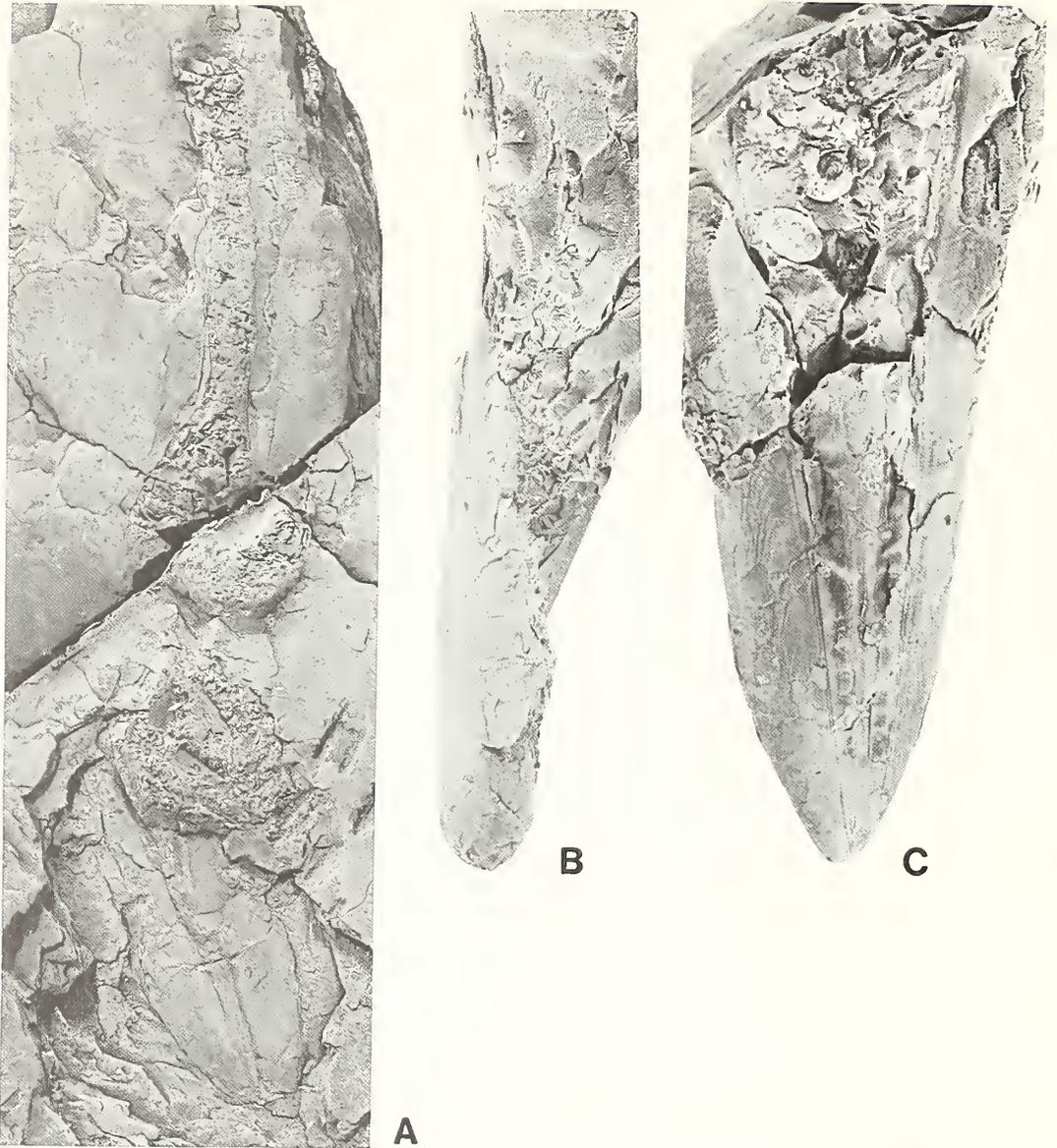
Suborder MESOTEUTHINA Naef, 1921
Family PALAEOLOLIGINIDAE Naef, 1921
Genus TEUDOPSIS Deslongchamps, 1835
(= *Beloteuthis* Münster, 1843 (Subjective synonym))

Type species. *Teudopsis bunelii* Deslongchamps, 1835, by subsequent designation (Woodward 1851–56, p. 69).

Diagnosis. Small to large, rhomboid to pyriform Palaeololiginidae comprising spoon-like gladius with posterior blade-like extension and rounded elliptical wings; median field restricted to well-developed keel or mid rib; hyperbolic zones developed as weak deflection of the growth lines.

Range. Lower Jurassic (Toarcian) to Middle Jurassic (Callovian) of Europe (Naef 1922; Fischer and Riou 1982). The species *Teudopsis brodiei* Caruthers reported from the Upper Jurassic of Dorset has recently been redescribed as an indeterminate plant fragment by Engeser and Phillips (1986).

Remarks. The nominal genus *Beloteuthis* Münster is a junior subjective synonym of *Teudopsis* Deslongchamps. Van Regteren Altena (1949) subsequently designated the species *Loligo bollensis* Zieten, 1832 as type of *Beloteuthis*. This is not without complication, however, as the nominal genera *Geoteuthis* Münster, 1843 and *Palaeosepia* Theodori, 1844 (junior subjective synonyms of *Loligosepia* Quenstedt) also share this type species. Although actually based on a different syntype



TEXT-FIG. 3. A, *Jeletzkyteuthis agassizi* (Deslongchamps), WM 1, $\times 1$. Ventral view of gladius and ink-sac. Lectotype of *Sepia obtusalis* Simpson. B, C, *Loligosepia aalensis* (Zieten), BMNH C.37529, $\times 1$. B, lateral view showing wings in lateral plane. C, ventral view.

of *Loligo bollensis*, they are junior objective synonyms of *Beloteuthis*. Fortunately, as already discussed, *Teudopsis* is the senior synonym. In addition, the lectotype of *Loligo bollensis* Zieten selected above is a specimen of *Loligosepia aalensis* (Zieten), thus making *L. bollensis* a junior subjective synonym of the same (see below).

Teudopsis was first recorded from Britain by Moore (1867, p. 303) and from Yorkshire, by Blake (*in* Tate and Blake 1876, p. 314). Crick (1921) described the type species *Teudopsis brunelli* [*sic*] from the 'Saurian and Fish Bed' (Lower Toarcian, *falciferum* Zone) of Alderton Hill in Gloucestershire.

This species is unknown in Yorkshire, but a single crushed specimen has been recovered from the Lower Toarcian (*falciferum* Zone) of Lincolnshire (BMNH C.46971).

Teudopsis schuebleri (Quenstedt, 1849)

Text-figs. 1 and 4A, C

- non 1832 *Loligo Bollensis* Zieten, p. 34, pl. XXV, fig. 4. [= *Loligosepia aalensis* (Zieten)].
 .1832 *Loligo Bollensis* Zieten, p. 49, pl. XXXVII, fig. 1.
 * .1843 *Loligo Schübleri* Quenstedt, p. 254.
 .1845 *Teudopsis ampullaris* Münster; d'Orbigny, p. 156, pl. 14, figs. 1, 2.
 .1845 *Teudopsis Bollensis* Zieten; d'Orbigny, p. 187, pl. 14, fig. 3.
 .1849 *Loliginites Schübleri* Quenstedt; Quenstedt, p. 499, pl. 32, figs. 14, 15.
 v. 1855 *Sepia cuspidata* Simpson, p. 21.
 .1858 *Loliginites Schübleri* Quenstedt; Quenstedt, p. 243, pl. 34, fig. 9.
 v. 1876 *Teudopsis cuspidatus* Simpson; Blake (*in* Tate and Blake), p. 314, pl. IV, fig. 3.
 v. 1884 *Sepia cuspidata* Simpson; Simpson, p. 19.
 1920 *Beloteuthis Schübleri* Zieten; Bülow-Trummer, p. 260. [Full early synonymy].
 .1922 *Teudopsis cuspidatus* (Simpson); Crick, p. 288.
 .1922 *Beloteuthis Bollensis* (Zieten); Naef, p. 144, text-fig. 53b.
 1949 *Teudopsis schübleri* (Quenstedt); Van Regteren Altena, p. 60.
 pars 1988 *Teudopsis bunelii* Eudes-Deslongchamps; Engeser, p. 77. [Includes *T. schuebleri* in synonymy].

Type specimen. Lectotype, here designated, the original of Quenstedt (1849, p. 499, pl. 32, fig. 15), from the Toarcian Posidonienschiefer of Holzmaden, southern Germany. The original is housed in the GPIT.

Material. Two specimens, WM 4 and SM J.35013 (the original of Blake *in* Tate and Blake 1876, pl. IV, fig. 3), from the Whitby Mudstone Formation, Jet Rock Member (*falciferum* Zone), of Whitby, North Yorkshire.

Notes on Simpson's specimens. Simpson's (1855) species *Sepia cuspidata* is a junior subjective synonym of *Teudopsis schuebleri*. Two specimens exist in the Whitby Museum that bear the label *Sepia cuspidata*. The first, WM 4 (text-fig. 4A), bears a label in Simpson's handwriting that reads '*Sepia cuspidata*, UL, Whitby'. This specimen is preserved in bituminous shale typical of the Jet Rock Member, and Simpson (1884, p. 19) recorded this species from his Upper Lias division 6 equivalent to the Jet Rock *sensu stricto* of Howarth (1962). This specimen is here designated lectotype. The second specimen, WM 682 (text-fig. 4B) is also labelled *Sepia cuspidata*, but close examination reveals that it is actually a skull of the fish *Saurorhynchus brevirostris* (Woodward) similar to that figured by Woodward (1899, text-fig. 1).

Diagnoses. See Quenstedt (1849, p. 499; *Loliginites Schübleri*) and Naef (1922, p. 144; *Teudopsis bollensis*).

Description. The Whitby Museum specimen (WM 4) consists of an elongate, conical, leaf-shaped gladius 120 mm long, with the posterior-most portion missing (text-fig. 4A). The gladius is flattened, but it is clear that the conus would have been spoon-like. The wings are represented by a slight lateral expansion in the posterior area with arcuate growth lines. Hyperbolic zones bounded by indistinct asymptotes are just discernible, and the growth lines are only slightly flexuous rather than notably anterior-concave. A relatively broad median keel, slightly displaced by compression in the posterior, is present for the length of the gladius and expands anteriorly to a maximum width of 4 mm. The keel is surrounded by an anterior blade-like extension with a posterior angle of divergence of 29°. Growth lines are discernible on the anterior extension, and mirror its leading edge.

The Sedgwick Museum specimen (SM J.35013) is a juvenile with a maximum length of 76 mm, preserved in three dimensions in a pyrite-skinned concretion (text-fig. 4C). The wings extend anteriorly for 34 mm from the spoon-like conus, and hyperbolic zones similar to the other specimen are seen on this example (text-fig. 4C). The median keel is well-developed with a relief of approx. 1 mm above the gladius, and it expands anteriorly to a width of 1.5 mm. The anterior blade-like extension consists of a platform containing the keel which has a border with a sub-relief of < 1 mm (text-fig. 4C). The anterior extension diverges posteriorly at an angle of 21°, and displays growth lines similar to those preserved on the WM example.

Remarks. Zieten (1832, pl. XXXVII, fig. 1) figured a specimen of this species from the Posidonienschiefer of southern Germany under the name *Loligo Bollensis*. Earlier in his monograph Zieten had used this name for a *Loligosepia*-like form now considered identical to his *Loligo aalensis* of the same work. The latter specimen is designated lectotype of *Loligo Bollensis* above, leaving the former specimen, a different species, without a name. Quenstedt (1839, p. 163, footnote) was aware of these problems, and later (Quenstedt 1843, p. 254) erected the name *Loliginites Schübleri* for the *Teudopsis*-like specimen of *Loligo Bollensis*.

Engeser (1988) considered the nominal species *Teudopsis schuebleri* a junior synonym of *Teudopsis bunelii* Deslongchamps. However, *T. schuebleri* can be readily distinguished from *T. bunelii* (syntype BMNH 74009, original of Deslongchamps 1835, pl. 3, fig. 3) by its elongate wing area, and its sharp, blade-like anterior extension which has a less regular form in *T. bunelii*. Both species can be distinguished from *T. subcostata* (Münster) in possessing a smaller form and less rhomboid shape (text-fig. 1).

Teudopsis subcostata (Münster, 1843)

Text-figs. 1 and 5A–C

- *. 1843 *Beloteuthis subcostata* Münster, p. 61, pl. V, fig. 2; pl. VI, fig. 2.
- . 1845 *Beloteuthis subcostata* Münster; d'Orbigny, p. 364, pl. 22, figs. 1–3.
- . 1849 *Loliginites subcostatus* Münster; Quenstedt, p. 501, pl. 32, figs. 7, 8.
- v. 1876 *Beloteuthis subcostatus* Münster; Blake (*in* Tate and Blake), p. 313.
- v. 1876 *Beloteuthis Leckenbyi* Blake (*in* Tate and Blake), p. 314, pl. IV, fig. 2.
- 1920 *Beloteuthis subcostata* Münster; Bülow-Trummer, p. 261. [Full early synonymy].
- . 1922 *Beloteuthis subcostata* Münster; Naef, p. 142, text-fig. 53a.

Type specimen. Lectotype, here designated, the original of Münster (1843, pl. 5, fig. 2) from the Toarcian Posidonienschiefer of Ohmden, southern Germany. The original of this specimen is believed to have been destroyed during the Second World War (W. Riegraf, pers. comm., 1988). However, Quenstedt's (1846–49) specimens from the same area are available in the GPIT for neotype selection.

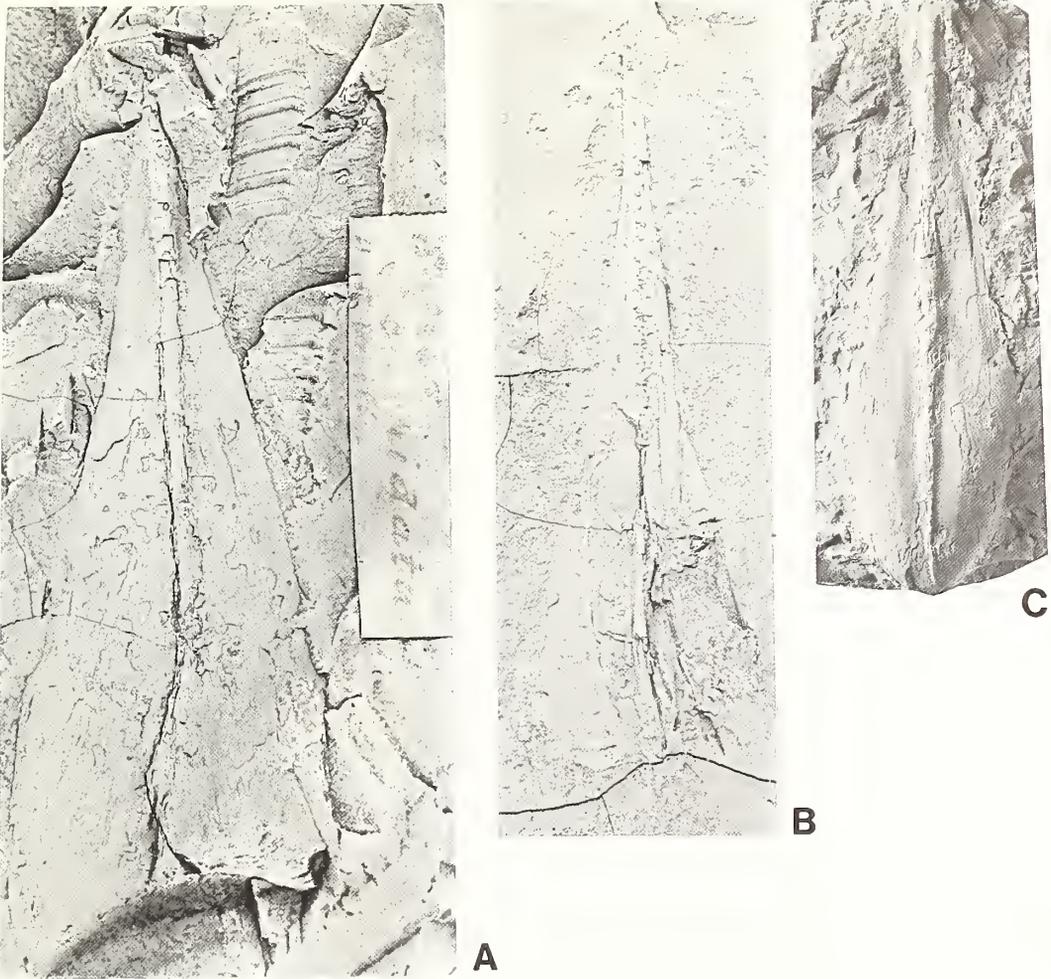
Material. Two specimens from the Toarcian Jet Rock Member (Whitby Mudstone Formation, *falciferum* Zone) of the environs of Whitby, North Yorkshire. The first, BMNH C.12046 (text-fig. 5A), was recorded by Blake (*in* Tate and Blake 1878, p. 314) from the *Serpentinus* Beds of Kettlewell. Only the Jet Rock *sensu stricto* of Howarth (1962) (*falciferum* Zone, *exaratum* Subzone) is exposed on the foreshore there. The second, SM J.35012 (text-fig. 5B, C) is the holotype of *Beloteuthis Leckenbyi* Blake. It was recorded by Blake (*in* Tate and Blake 1876, p. 314) as also from the *Serpentinus* Beds, and the specimen bears the label 'Whitby'. It is preserved in a small pyrite concretion or dogger, typical of the Jet Rock *sensu stricto* (Howarth 1962).

Diagnoses. See Münster (1843, p. 61; *Beloteuthis subcostata*), d'Orbigny (1845, p. 364; *Beloteuthis subcostata*), Quenstedt (1849, p. 501; *Loliginites subcostatus*) and Naef (1922, p. 142; *Beloteuthis subcostata*).

Description. The Yorkshire material comprises two specimens. The first, BMNH C.12046 (text-fig. 5A), is a large (length 240 mm), almost complete gladius of rhomboid shape, and is flattened. The second, SM J.35012 (text-fig. 5B, C), is smaller (length 100 mm), probably a juvenile, and is preserved in three dimensions.

The larger specimen (BMNH C.12046) is flattened with most of the gladius preserved, but with the wings present only as impressions. The wings are represented as small lateral extensions of the rhomb, and are present for almost half of the length of the gladius. Growth lines curve posteriorly, changing direction sharply at the lateral asymptotes, becoming almost straight in the hyperbolic zones and extending anteriorly to the median keel with a divergent angle of 54°. A broad, triangular anterior extension is present, with slightly curving leading edges (text-fig. 5A). A very broad median keel, reaching 10 mm at its widest, is central to the extension, and the surface of the central portion of the gladius is ornamented by lesser ridges and depressions that gradually diverge from the posterior (text-fig. 5A).

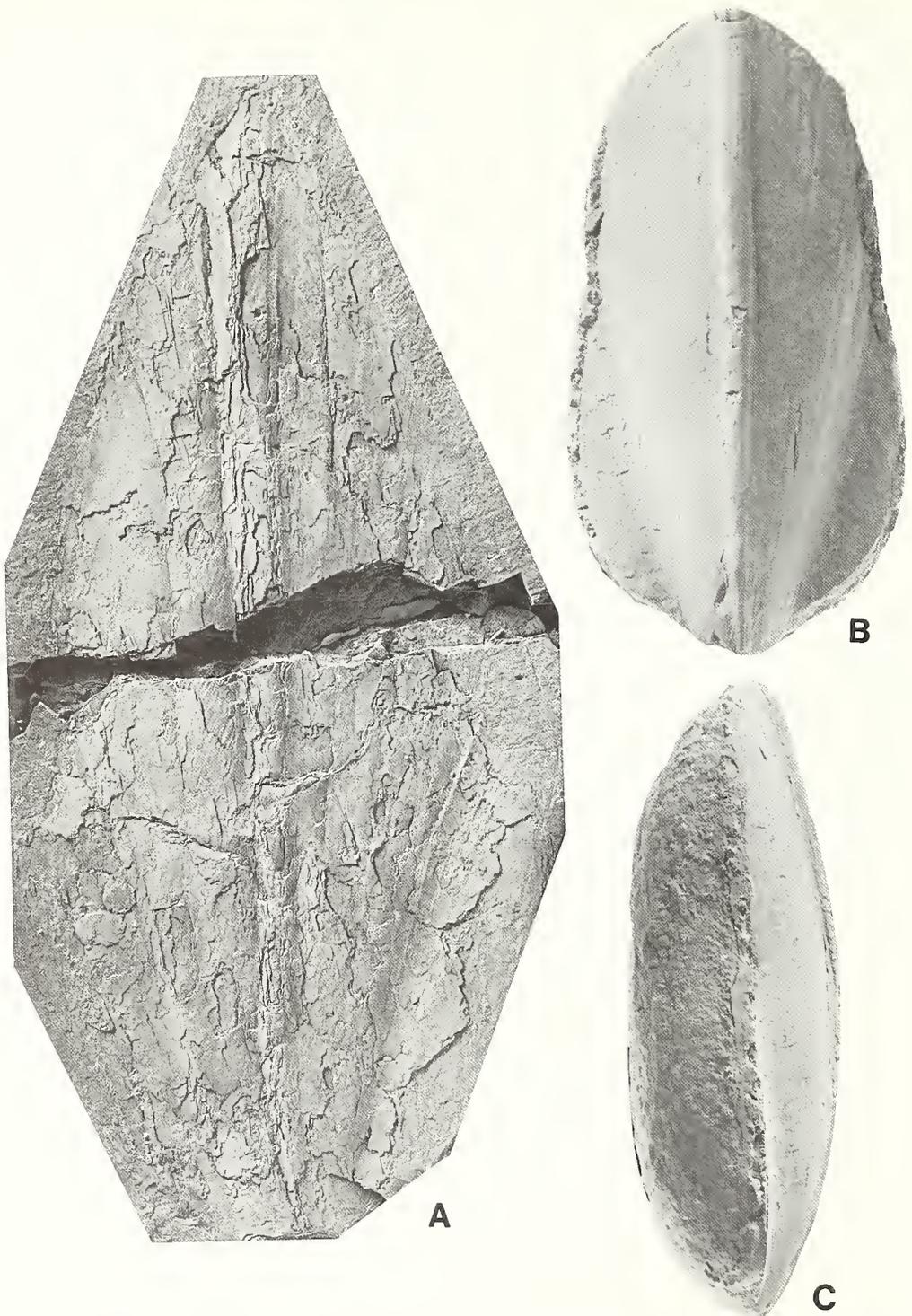
The smaller specimen (SM J.35012), has a similar morphology to the larger specimen, and is obviously a juvenile of the same species. It is preserved in three dimensions, with the hyperbolic zones falling as the



TEXT-FIG. 4. A, *Teudopsis schuebleri* (Quenstedt), WM 4, $\times 1$. Ventral view, posterior part missing. Lectotype of *Sepia cuspidata* Simpson. B, *Saurorhynchus brevisrostris* (Woodward), WM 682, $\times 1$. View of skull in same orientation as 4A. This specimen was labelled *Sepia cuspidata* in the WM catalogue. C, *Teudopsis schuebleri* (Quenstedt), SM J.35013, $\times 1$. Ventral view.

curvature between the laterally extended wings and the main body of the gladius (text-fig. 5B). The median keel has a relief of 2 mm above the rest of the gladius (text-fig. 5C). The leading edges of the anterior extension of this specimen are curved giving a spatulate appearance. This obviously misled Blake (*in* Tate and Blake 1876), who used this specimen as holotype of his new species *Beloteuthis leckenbyi*. However, that this spatulate form is an artifact of the preservation is indicated by the growth lines on the surface of the gladius which reveal the typical rhomboid form of *Teudopsis subcostata* (text-fig. 5B).

Remarks. This species is very clearly distinguished from both *Teudopsis bunelii* Deslongchamps and *Teudopsis schuebleri* (Quenstedt) by its larger size and regular rhomboid form (text-fig. 1).



TEXT-FIG.5. *Teudopsis subcostata* (Münster), A, BMNH C.12056, $\times 0.75$. Ventral view. B, C, SM J.35012, holotype of *Beloteuthis leckenbyi* Blake, $\times 1$. B, ventral view. C, left lateral view.

INTER-REGIONAL COMPARISONS

Inter-regional comparisons of fossil teuthid faunas are difficult because of their fragility and hence scarcity in the fossil record. Preservation of such delicate features as ink-sacs requires immediate burial (see Lyell 1878, p. 350) and/or a lack of scavengers. Thus, many teuthid finds are from deposits renowned for their exceptionally preserved faunas (fossil Lagerstätten; see Seilacher *et al.* 1985 for a review).

Fortunately, the Toarcian was a period of widespread anoxia in the shelf-seas of Europe (e.g. Riegraf *et al.* 1984) and elsewhere. Close similarities exist between the Yorkshire and southern England teuthids and those of Normandy and southern Germany (e.g. Deslongchamps 1835; d'Orbigny 1842, 1845; Quenstedt 1846–49; Riegraf *et al.* 1984, p. 36) in these adjacent shelf seas. Local differences do occur however, with, for example, the apparent absence of *Teudopsis bunelii* from Yorkshire, and similarly the absence of *Jeletzkyteuthis agassizi* from southern England. However, these are most probably artifactual differences, a result of the imperfect teuthid record. Nagy (1958) described a specimen of *Teudopsis* from the Lower Jurassic of Hungary which Engeser (1988) subsequently referred to *T. bunelii*. However, Nagy's figures illustrate a specimen too poorly preserved to be reliably identified to specific level.

In addition to the species described above, Riegraf *et al.* (1984) listed *Lioteuthis problematica* Naef (unknown outside Germany), *Geopeltis emarginata* (Voltz) and *Parabelopeltis flexuosa* (Münster). None of these species are known to occur in Britain. Riegraf *et al.* (1984) also listed the pliesioteuthids *Paraplesioteuthis sagitata* (Münster) and *P. hastata* (Münster). Again, neither of these teuthids are known in Britain, but Hall (1985) has recorded the latter species from the Toarcian bituminous shales of Alberta, Canada. This is the only Lower Jurassic squid recorded outside Europe.

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Note added in proof. Hall and Neuman (1989) have recorded a new species of *Teudopsis*, close to *T. schuebleri*, from the lower Jurassic (*falciferum* Zone) of Alberta, Canada, suggesting close faunal links with Europe.

HALL, R. L. and NEUMAN, A. G. 1989. *Teudopsis cadominensis*, a new teuthid squid from the Toarcian (Lower Jurassic) of Alberta. *Journal of Paleontology*, **63**, 324–327.

CLUSTER ANALYSIS OF PREVIOUSLY DESCRIBED COMMUNITIES FROM THE LUDLOW OF THE WELSH BORDERLAND

by PIERRE J. LESPÉRANCE

ABSTRACT. Previously described communities ('associations') from the Ludlow of the Welsh Borderland were subjected to cluster analysis on a PC microcomputer. Miscellaneous absence–presence data sets derived from the published information were analysed using different combinations of clustering algorithms, distance and similarity measurements, with and without Jaccard's coefficient of association. Variations in order of data entry produced major differences (chaotic behaviour) in clustering using unmodified data. With unmodified data, only the single linkage method showed no clustering differences with the three distance and similarity measurements applied to the whole of the data. The raw data, modified with Jaccard's coefficient, showed major improvement in clustering upon variation of order of data entry. Such improvement in non-chaotic behaviour is interpreted as the result of the lesser, finite raw data consisting of zeros and ones, as compared with the more infinite numbers generated using a coefficient of association. Nearly equally good results are obtained, however, when the unmodified data are analysed using the *cosine θ* measurement. The UPGMA, single and complete linkage methods, with *cosine θ* , are recommended as quickly and routinely applicable to unmodified data for, at least, first approximations in community analysis. Dendrograms so generated should nonetheless be submitted to variation in order of data entry to test for chaotic behaviour.

WITH the advent of microcomputers and powerful programs adapted to this specific hardware, treatment of data previously available only on mainframe computers is now possible within each scientist's office or home. The purpose of this contribution is to explore the use of cluster analysis on a microcomputer well within its practical limits, but in a situation typical of most palaeoecological studies.

Cluster analysis is a non-parametric statistical technique, that is, it is not based on the familiar Gaussian, or probability, bell-shaped curve. It classifies data and produces, if desired, dendrograms (i.e. tree-shaped diagrams), which are visually instructive and, hopefully, of easy interpretation of the classified data. The practical limits of the microcomputers previously alluded to, refer to the available memory. More specifically, the internal memory to hold data, or matrices, places an upper limit to these data in better equipped standard IBM-type personal microcomputers (PC) in the neighbourhood of 4.6 Mb (mega bytes) (of which 4 Mb is expanded memory), at least with the software here employed. About three-quarters of this memory is needed, in a study like this one, if a coefficient of association is calculated on a spreadsheet contained in a single file (note 1, appendix gives more details). Data storage is also a problem, but hard disks of 30 Mb are readily available, and those ten times that amount equally available, but expensive.

The description of the Ludlow communities of part of the Welsh Borderland, a portion of the world standard of the upper Silurian, was first outlined by Calef and Hancock (1974), criticized by Lawson (1975), reinvestigated by Watkins (1979) and partly extended to a regional scale by Cherns (1988). Watkins (1979) is a comprehensive study of many aspects of synecology of the whole of the Ludlow in the Welsh Borderland. Although more restricted in area than Cherns (1988), published faunal lists, community tabulations, and stratigraphical coverage are more extensive in Watkins (1979) and better suited to the aims of this study. Although he named the resultant communities 'associations', this term was used interchangeably with 'communities' (Watkins 1979, p. 210), which the writer prefers (but then, discussion persists as to whether these 'associations' are

communities: Cherns 1988, p. 488). Other aspects of Ludlow palaeoecology are treated in Watkins (1978), Watkins and Aithie (1980), Hewitt and Watkins (1980), and Mikulic and Watkins (1981), but these contributions do not present data as complete as in Watkins (1979), nor do they specifically modify the 1979 tabulations. Consequently, Watkins (1979) will be used exclusively here.

Stratigraphic nomenclature of the Welsh Borderland dates back, of course, to R. I. Murchison, but modern usage rests on Holland *et al.* (1963), subsequently very slightly modified by Holland *et al.* (1980), Holland (1980) and Antia (1980). As Watkins's (1979) distributional data rest on Holland *et al.* (1963), their stratigraphic nomenclature is followed.

This contribution proposes to use Watkin's (1979) data as a test case for isolating specific methods and procedures of cluster analysis. As these communities were described using 'classical' methods (i.e. communities are recurrent associations defined on the basis of abundance of specific taxa, with consideration commonly given to the spatial continuity of the associations and the absence of specific taxa), comparison of clustering efficiency and correctness can be assessed and judgments expressed. Clustering algorithms are numerous and their respective merits and disadvantages under specific circumstances are not obvious to the applied researcher (some theoretical aspects are covered in Milligan (1980) and Milligan and Isaac (1980)). Furthermore, many distinct coefficients of association between samples have been suggested (binary (absence–presence) ones are surveyed in Cheetham and Hazel 1979; a comprehensive survey is given in Legendre and Legendre 1983), but their respective advantages and disadvantages, again in specific circumstances, are equally far from obvious. In fact, one of the aims of this investigation was to question the necessity of the use of coefficients of association, following results and methodological uncertainties inherent to these results, previously obtained by Lespérance and Sheehan (1988). In view of these uncertainties, a pragmatic approach was best indicated; this is detailed in the following pages.

METHODS

Hardware

Calculations were performed on an IBM-compatible PC, equipped with an 8088 chip and mathematical coprocessor (8087). Mainboard memory was 640 Kb, with an expanded memory card of 1.5 Mb (only used by the Symphony software). The PC had a 30 Mb hard disk, with a tape backup of 60 Mb. An EGA card (Extended Graphics Adapter) or better, with its consequent monitor, are a requisite to produce the text-figures as presented. Mainboard memory was always sufficient, and matrices 2.4 times the size of the data here treated, requiring 188 K of RAM, have been analysed without memory shortage, although in this last case processing time increases dramatically to about $\frac{1}{2}$ hour.

Software

Statistical calculations were done using the SPSS/PC+ statistical package (version 2.0). Cluster analysis is available in the advanced statistics package; the optional data entry package facilitated the entry of the unmodified data from Watkins (1979), subsequent modification in a spreadsheet, and/or direct entry in the statistical programs. Jaccard's coefficient of association (note 1, appendix) was calculated on a spreadsheet; Symphony, version 1.2, was used (Lotus 1-2-3 is equivalent). A file compression utility (SQZ! plus) was invaluable to manage the matrices generated to calculate Jaccard's coefficient.

Data sets

The justification for the analysis of different data sets, all derived from Watkins (1979), will be presented in subsequent sections. Only a brief summary of the relations between the major data sets is presented here.

Tables 15 to 20 of Watkins (1979) give detailed faunal lists of the six communities, and intermediates or variants, recognized in the Ludlow of the Welsh Borderland. The communities are

not detailed in the same fashion; as a first step, the 48 different faunal lists were included in one data set. Only taxa identified to the specific or generic level were retained for analysis. A few pelagic taxa were singled out by Watkins (1979); these were included, if only because they provide some sort of information on the physico-chemical conditions in the water column above the level-bottom communities, if indeed all the taxa so identified were pelagic (as, for instance, the case of the brachiopod *Aegiria grayi*: Cherns 1988, p. 486). A total of 112 taxa was consequently retained and, unfortunately, the *Atrypa reticularis*-coral community does not contain a generically determined coral with this procedure. The order of data entry was as presented successively in Watkins's (1979) tables 15 to 20, except that three of the six cumulative faunas, of medium to high diversity from table 15, were arbitrarily entered as the last three faunas. The first data set is referred to as data set 48A. Data set 48B is identical to 48A except that five faunal lists, chosen at random (with the Symphony function of the same name) were removed and reinserted as the last five faunal lists.

Data set 46A was derived from 48A by the deletion of two cumulative faunas from Watkins' (1979) table 15: the *Go2* (*Glossia obovata*) fauna in the mudstone facies is detailed in table 17 and the *M1* (*Mesopholidostrophia laevigata*) fauna in table 18, and hence repetitive in the data set. Data set 46B was derived from 48B, with the deletion of the same two cumulative faunas.

Table 16 of Watkins (1979) lists six cumulative faunas of two taphonomic categories: disturbed neighbourhood assemblages, and transported assemblages, as recognized in three different communities. The faunal content of these three communities, from specific localities and samples, is presented in subsequent tables. Hence, these six faunal lists are also repetitive in the data sets, and they were deleted to produce data set 40. Data set 40A was derived from 46A, and 40B from 46B. Data set 40C is data set 40B, with five faunal lists chosen at random, deleted, and reinserted as the last five entries. As selected faunal lists were deleted, so were the taxa occurring only in the deleted faunal lists.

The raw, unmodified data were coded 0 and 1 (absent and present respectively) and used as such directly in the clustering. These data were subsequently used for Jaccard's coefficient, and the same order of data entry retained (e.g. data set 46A, modified or not by Jaccard's coefficient, has the same sequential order of entry). Justification of the use of absence–presence data is found in most discussions of cluster analysis, and need not be repeated here. The writer believes it is particularly appropriate to regional palaeoecological syntheses, to nullify local effects of species abundances.

THE COMMUNITIES

Watkins (1979) investigated the Ludlow of part of the Welsh Borderland, but excluded the basal part (the Lower Elton Beds) and the overlying brackish water Ludlow Bone Bed. Within this sequence, he recognized six communities which are, in ascending order, the *Glossia obovata* (*Go*) community, a succeeding transitional (*tr*) fauna with the one above, the *Mesopholidostrophia laevigata* (*M1*) community, a lower phase of the *Sphaerirhynchia wilsoni* (*lwSw*) community, an *Atrypa reticularis*-coral (*AC*) community, the preceding two communities locally absent below the upper phase of the *Sphaerirhynchia wilsoni* (*upSw*) community, the *Shaleria ornatella* (*So*) community and, uppermost, the *Protochonetes hudloviensis* (*PI*) community (table 1). These communities were defined using 'classical' methods and, more specifically, by a graphical method known as the transect method (Watkins 1979, p. 208) on a spatial basis.

Appendix 3 of Watkins (1979, tables 15–20, pp. 262–274) presents a formidable amount of distributional data, comprising but a small part of his unpublished data in the Library of the British Museum (Natural History). Visual examination of these data does not obviously reveal the community relationships, and hence its intended use as a test case for cluster analyses.

Tables 15 and 16 of Watkins (1979) give 12 cumulative faunas, while tables 17–20 give examples (from specific localities and collections) from five communities, the *Go* fauna in the laminated shale facies, the *lpSw* and the *AC* faunas being known only by cumulative faunas. Diversity (*d*) and average diversity (\bar{d}) within the miscellaneous faunal lists vary widely. Cumulative faunas have $d = 22$ to 75. Average diversity in tables 17–20 of Watkins (1979) decreases to about half its value

TABLE 1. Stratigraphic relations of the benthic communities discussed within the Ludlow (modified from Watkins 1979)

WHITCLIFFE	<i>Pl</i>	<i>Protochonetes ludloviensis</i>
LEINTWARDINE	<i>So</i>	<i>Shalera ornatella</i>
	<i>upSw</i>	upper phase <i>Sphaerirhynchia wilsoni</i>
BRINGEWOOD	<i>AC</i>	<i>Atrypa reticularis</i> -coral
	<i>lpSw</i>	lower phase <i>Sphaerirhynchia wilsoni</i>
	<i>Ml</i>	<i>Mesopholidostrophia laevigata</i>
ELTON	<i>tr</i>	transitional fauna
	<i>Go</i>	<i>Glassia obovata</i>

from the lower to the upper part of the Ludlow: from $\bar{d} = 18.9$ in the *Go* fauna, to $\bar{d} = 15.7$ in the *Ml* and *Sw* faunas, to $\bar{d} = 8.8$ in the *Sw* fauna and $\bar{d} = 7.3$ in the *Pl* fauna.

Distributional data are seldom available for sequences of communities, and Watkins's (1979) readily available publication mitigates against using his more complete unpublished data. Admittedly, these data are almost a worst case situation with such widely varying diversities (the *Pl*2C2 locality has but four taxa!) and unequal tabulation of cumulative faunas and individual localities. Nonetheless, results obtained were encouraging (see below).

CLUSTERING BEHAVIOUR: CHAOTIC?

Reproducibility is assuredly a prime requisite of any analytical method. It is thus particularly disturbing that, following F. Vogel, Bayer (1985, p. 98) has shown, at least geometrically, and with specific data sets, that cluster analysis is subject to chaotic processes (i.e. stochastic, random, aleatory processes, and hence the results are unreproducible) during the formation of clusters. This chaotic behaviour depends, to a great extent, on the sequence of input of the data. This serious defect of cluster analysis needs clarification before any palaeoecological application can confidently be pursued.

Data sets 48, 46, and 40 were used as a means of judging this suspected chaotic behaviour. Each set was used in its unmodified form, and its modified form using Jaccard's coefficient of association, and subjected to various clustering algorithms and distance, or similarity measurements.

Cluster techniques

Cluster analysis is described to varying extents by the following authors, amongst others, to which the reader may refer for fuller treatment than presented here: Sneath and Sokal (1973), Anderberg (1973), Everitt (1980), Legendre and Legendre (1983), Romesburg (1984), and Jones (1988). Q-mode analysis (between samples) and hierarchical clustering are used exclusively in this contribution.

Clustering algorithms. Seven clustering algorithms (methods for combining clusters) are available in the SPSS/PC + package. These are: (1) average linkage within groups method (WPGMA: weighted pair-group method using arithmetic averages), (2) average linkage between groups method (UPGMA: unweighted pair-group method using arithmetic averages), (3) single linkage method, (4) complete linkage method, (5) centroid method (UPGMC: unweighted pair-group centroid method), (6) median method (WPGMC: weighted pair-group centroid method), and (7) Ward's method. Much mistrust has been expressed relative to the single linkage method (discussed in Milligan 1980; rejected by Legendre *et al.* 1985, p. 275 in succession studies), although it has a natural logic, while UPGMA is generally considered to be the best method (and used exclusively, for instance, by Baarli 1987). Ward's method is popular (and used exclusively, for instance, by Lespérance and Sheehan 1988); it produces, probably, the most visually appealing (and interpretable?) dendrograms (see also discussion by Romesburg 1984, pp. 134–135).

Distance and angular measurements. Before combining clusters, an assessment of the distance between the items to be clustered is calculated. Either euclidian distances, or squared euclidian distances, can be used in the clustered hyperspace. Euclidian distances obey the familiar pythagorean relations of the hypotenuse in a triangle, while squared euclidian distances do not. Squared euclidian distance is consequently referred to as a pseudometric or a semimetric measure (Sneath and Sokal 1973, p. 121; Legendre and Legendre 1983, p. 194). Ward's method (Ward 1963) explicitly requires squared euclidian distances, while this same measure is preferable with the centroid and median methods (discussion in Sneath and Sokal 1973, p. 235). Reversals in cluster formation occur when euclidian distances are used with the centroid and median methods (Sneath and Sokal 1973, p. 235), but also occur with squared euclidian distances and the centroid method (Boyce 1969, p. 15). These reversals in clustering values (the agglomeration schedule printouts are available with the SPSS/PC+ package) occur in both the raw and modified data, and have been observed with the three distance and similarity measures used with the centroid and median methods. Additional complications arise with the use of euclidian distances with the centroid and median methods in that the dendrograms, with unmodified data, are step-wise and very difficult to interpret. This was not observed with modified data, using euclidian distances, but was present in a few cases with the centroid method using unmodified data and the proper squared euclidian distances. Dendrograms produced using the *cosine* θ measure and Ward's method give results where the majority of the clusters combine at the lowest level of similarity, and hence are meaningless. Nonetheless, it takes little effort to try all distance or similarity measurements on the algorithms to see what happens, much as Jones (1988, p.16) suggests, even though the mathematics may not be rigorously adhered to, and some of the resultant dendrograms may be of limited use.

A third measure, allied to distance measurements, is a similarity measure known as *cosine* θ (or as *cos* η , or the *cosine* measure, either considered a shape measure or a pattern similarity measure: note 2, appendix). Imbrie and Purdy (1962) have used it in their study of bahamian carbonates and faunas. Zhang and Hofmann (1982) employed it in their study of lamina shape of Precambrian stromatolites. Ward (1985) has used the *cosine* θ measure to compare disjunct variables in Cretaceous communities in Canada; other references are given by Romesburg (1984, p. 109). An *a priori* assumption in this study was that this measure could possibly help in grouping similar faunas differing only in diversity, but this was not borne out.

Coefficients of association. Jaccard's coefficient of association was used as representative of the numerous coefficients of association that have been suggested. It may be noted here that it can only be used on absence–presence data, and it does not take into account the absence of a taxon in both collections being compared. Furthermore, this coefficient has long been used in ecology (Sneath and Sokal 1973, p.131), is assuredly one of the best known, and most widely used of its class (Lespérance and Sheehan 1988), although its shortcomings have previously been pointed out (Raup and Crick 1979). Archer and Maples (1987) have also questioned the utility of Jaccard's coefficient, based on a probabilistic (gaussian) approach (Anderberg 1973, p. 91 discusses only briefly this aspect). In any event, the use of Jaccard's coefficient is meant as a test of raw versus modified data.

Input order and clustering

Even though some methods of clustering require specific measurements of distance, all data sets 48, 46 and 40 were sequentially submitted to the seven clustering algorithms, with all three distance-similarity measures taken in turn. Both the raw and modified data were submitted to the same cluster techniques, and dendrograms of the results generated.

In order to judge if indeed clustering is chaotic, subjective criteria had to be devised. An obvious result of the great majority of the dendrograms generated was that the nine localities of the *MI* Community (Watkins 1979, table 18), as well as the nine localities of the *Go* Community (Watkins 1979, table 17), with commonly the addition of the *Gol* (*Glassia obovata* fauna in the laminated shale facies, table 15), were correctly clustered together, at various levels of similarity depending on the measure used. The level of similarity defining each individual community was found, and the

TABLE 2. Comparison of clusters produced upon varying order of data entry on unmodified and modified absence–presence data

	ds	WPGMA U/M	UPGMA U/M	Single U/M	Complete U/M	Centroid U/M	Median U/M	Ward U/M
EUCLID	48	–/I	–/–	I/I	–/I	–/I	–/I	–/–
	46	–/I	–/–	I/I	–/I	I/I	I/I	–/–
	40	I/I	I/I	I/I	I/I	–/I	I/–	I/I
SEUCLID	48	I/I	–/–	I/I	–/I	–/I	I/I	–/–
	46	I/–	–/–	I/I	–/I	–/I	I/I	–/I
	40	–/I	I/I	I/I	I/I	I/I	–/I	I/I
COS θ	48	I/I	I/I	I/I	I/I	–/I	I/–	NA/NA
	46	–/I	I/I	I/I	I/I	–/I	–/I	NA/NA
	40	I/I	I/I	I/I	I/I	I/I	I/I	NA/NA

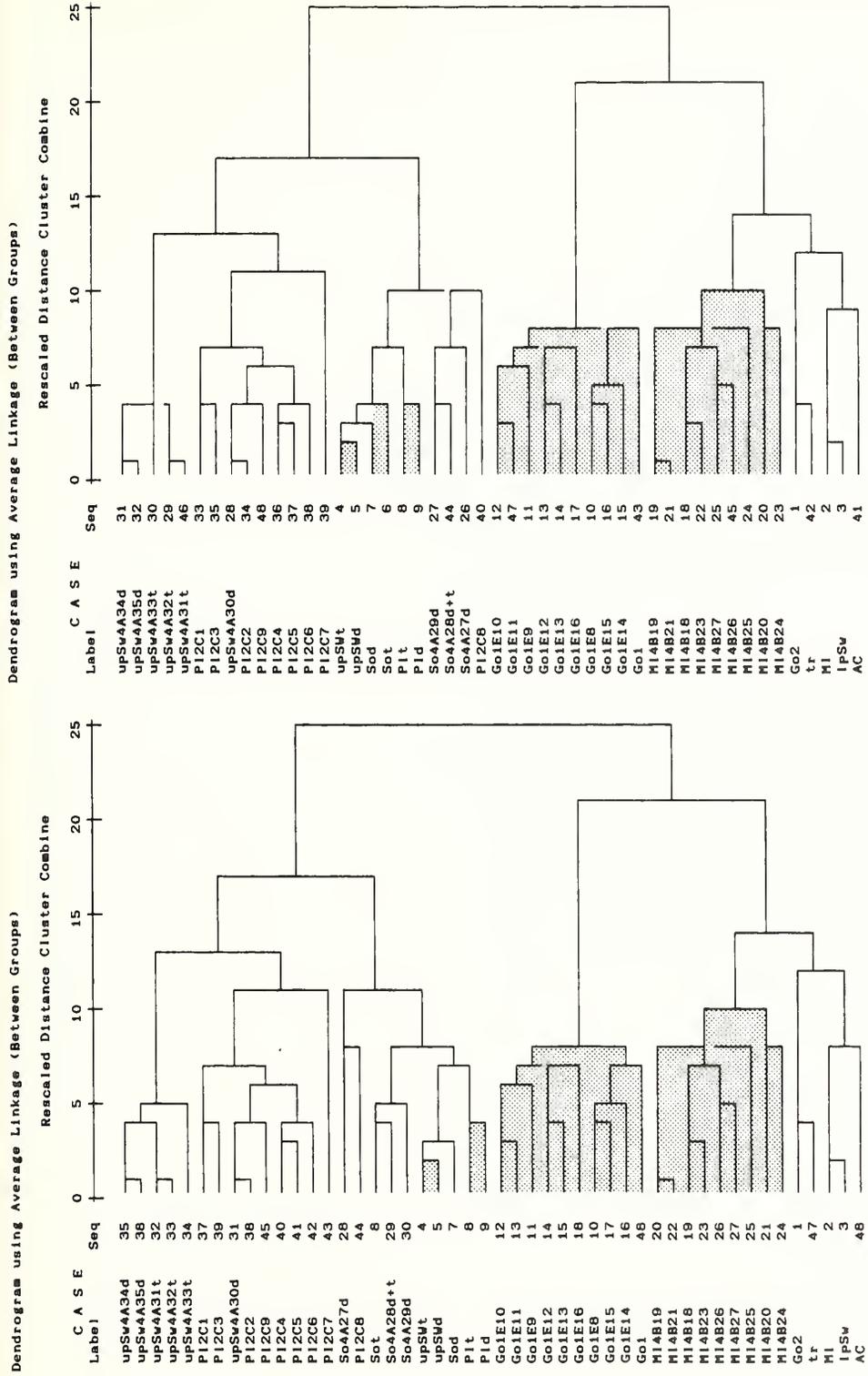
I: clusters identical; – clusters do not contain the same collections or faunas; NA: not applicable (clusters meaningless); ds: data set; U: unmodified data; M: data modified with Jaccard's coefficient; EUCLID: euclidian distance measurements; SEUCLID: squared euclidian distance measurements; COS θ : cosine θ similarity measure. Successive data sets derived from the preceding by the deletion of cumulative faunas (*Go2* and *M1* from data set 48 to obtain data set 46; and deletion of disturbed and transported assemblages *upSw*, *So*, and *Pl* from data set 46 to obtain data set 40).

average between the two noted. This average was projected throughout the dendrogram (i.e. a phenon line was plotted) and used to assess if clusters of the data using different orders of entry were identical. All major clusters with identical or slightly higher levels of similarity than this phenon line were compared. Those that contained the same faunas (or collections) were judged to be clustered identically. In cases where the dendrograms obtained were step-wise (chaining of Jones 1988, p. 16), judgement was less structured but followed the same general principles.

Table 2 presents the results obtained upon varying the order of data entry on the raw and modified data. Obviously, chaotic clustering behaviour occurs, and is a significant characteristic to be reckoned with (text-fig. 1 is typical of the results obtained). This chaotic behaviour was not detected when using the single linkage method, but occurs with all other methods. It occurs equally abundantly whether euclidian or squared euclidian distance measurements are used, but less so when the cosine θ similarity measure is employed. Furthermore, the modified data clearly are less prone to chaotic behaviour than the raw data. Viewed somewhat differently, the centroid, median and Ward's methods perform no better with their mandatory squared euclidian distances.

A coefficient of association is thus useful, if only to decrease chaotic behaviour, contradicting one of the first assumptions of this study. The cosine θ similarity measure also appears almost ideal when compared to either of the other two distance measurements, particularly if the centroid, median and Ward's methods are restricted to their proper squared euclidian distance measurements. This improvement in non-chaotic behaviour is interpreted to be the result of the lesser, finite raw data consisting of zeros and ones, as compared with the more infinite numbers generated using a coefficient of association. Ten decimals were used to compute Jaccard's coefficient, thus greatly decreasing the chance of two points in hyperspace having the same coordinates (even though only a single quadrant, of 0 to 90°, is considered with the cosine θ measure), thus decreasing chaotic behaviour as described by Bayer (1985).

The most noteworthy results of table 2 are (a) the poor performance of the UPGMA method with euclidian and squared euclidian distances and the equally poor performance of Ward's method with all three distance-similarity measures, (b) the excellent performance of the single linkage method with all three distance-similarity measures, and (c) the equally excellent performance of the cosine θ similarity measure with unmodified and modified data with Jaccard's coefficient.



A Dendrogram using Average Linkage (Between Groups) Rescaled Distance Cluster Combine

B Dendrogram using Average Linkage (Between Groups) Rescaled Distance Cluster Combine

TEXT-FIG. 1. Unretouched computer printouts of dendrograms demonstrating chaotic clustering behaviour. Printouts obtained with a 9-pin dot-matrix printer employing emphasized combined with overstrike printing (a Citizen 120-D printer was used). Missing ascenders and descenders at the junction of some vertical and horizontal lines presumably due to the failure of the statistical program to use ASCII codes 169 and 170. 'Case labels' are identical to Watkins's (1979) association or sample numbers in his tables 15-20. 'Case seq' gives the input sequence of the data. Shading added to clusters reproducing Watkins's (1979) communities or his three cumulative disturbed-transported assemblages, *A*, using data set 48A, modified with Jaccard's coefficient of association, euclidian distances and the UPGMA algorithm. *B*, as *A*, but using data set 48B.

CLUSTERING EFFICIENCY

Again, subjective criteria of clustering efficiency (in relation to the previously described communities) must be devised to judge cluster analyses against Watkins's (1979) communities. The make-up of the various data sets, as well as an overview of the communities, have been previously given, but additional considerations are essential to understand the criteria used.

Data set 48 presents an unrealistic situation of cluster analysis in which cumulative faunas and, partly, their constituent parts are considered in a single data set. Nevertheless, it does offer extremes in diversity and an opportunity of testing chaotic behaviour in cluster analysis. Efficiency of clustering was extended to this data set for the sake of completeness.

Data set 46 contains the results of a major conclusion submitted by Watkins (1979). He has submitted that transported assemblages are similar in content of epifaunal species to adjacent disturbed neighbourhood assemblages, that the basic community integrity of the transported assemblages is maintained (Watkins 1979, pp. 207–208), and that there was no significant difference between the two.

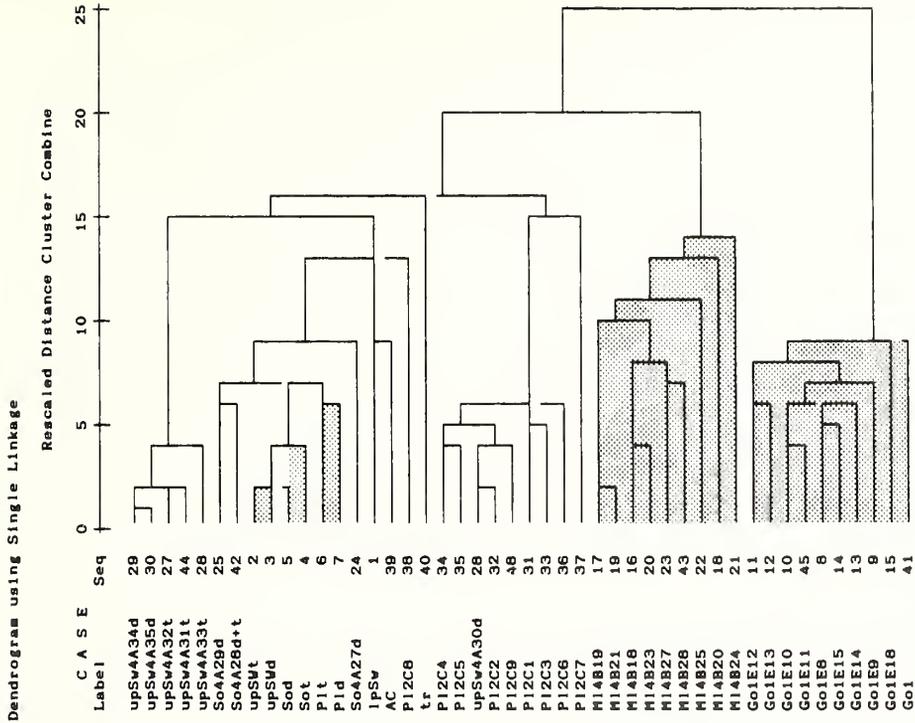
Data set 46 is more realistic than 48, but nonetheless suffers from the improbability of including cumulative taphonomic assemblages with individual collections and, partly, their cumulative faunas. Even so, the taphonomically separated cumulative faunas (Watkins 1979, table 16) do give more comprehensive cumulative faunas than the sum of the individual collections cited in succeeding tables. Data set 40 excludes these taphonomically separated faunas and is, with data set 46, not ideal as some sort of standard. Data sets 46 and 40 must consequently be used, at least as data for tests of clustering efficiency with sets of differing diversity.

TABLE 3. Clustering efficiency as judged from comparison with previously described communities or faunas of Watkins (1979)

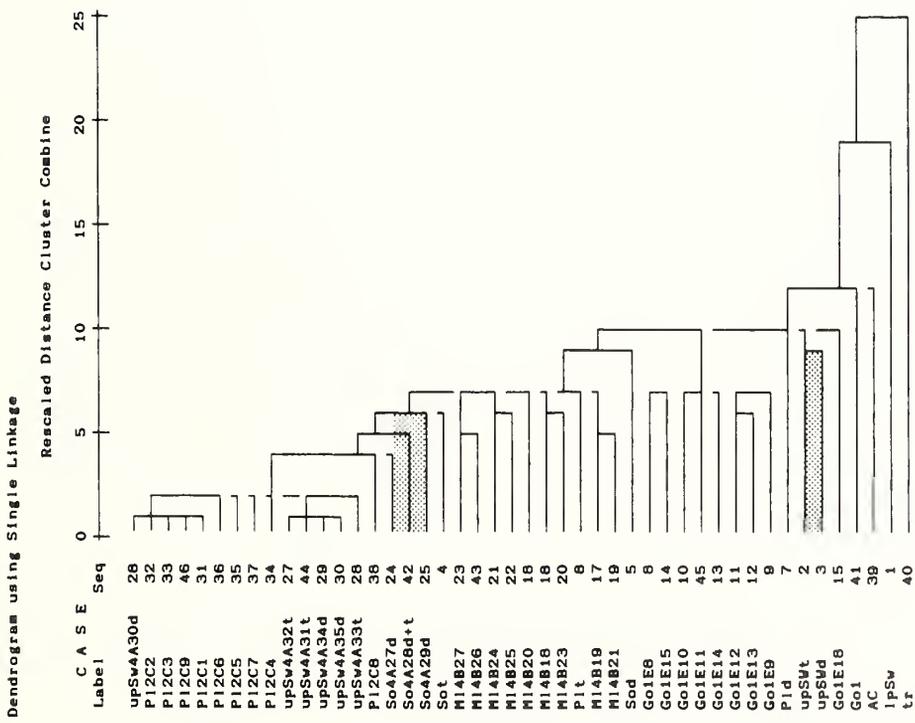
	ds	WPGMA U/M	UPGMA U/M	Single U/M	Complete U/M	Centroid U/M	Median U/M	Ward U/M
EUCLID	48A	NC/8	NC/NC	1/6	NC/8	NC/6	NC/NC	NC/NC
	46B	NC/8	NC/NC	1/6	NC/6	NC/6	NC/NC	NC/NC
	40A	NC/5	NC/NC	1/5	NC/5	NC/5	NC/NC	NC/NC
SEUCLID	48A	NC/NC	NC/NC	1/6	NC/8	NC/8	NC/8	NC/NC
	46B	NC/NC	NC/NC	2/7	NC/7	NC/7	NC/7	NC/NC
	40A	NC/NC	NC/NC	1/5	NC/5	NC/5	NC/5	NC/NC
COS θ	48A	NC/8	7/6	4/6	7/9	NC/7	NC/NC	NA/NA
	46B	NC/7	6/8	6/7	8/8	NC/6	NC/NC	NA/NA
	40A	NC/5	4/5	4/5	4/5	NC/4	NC/NC	NA/NA

NA: not applicable (clusters meaningless); NC: not considered; ds: data set, maximum possible scores on 48A = 12, 46B = 11 and 40A = 8; U: score on unmodified data; M: score on data modified with Jaccard's coefficient; EUCLID: euclidian distance measurements; SEUCLID: squared euclidian distance measurements; COS θ : cosine θ similarity measure. See table 2 for explanation of the derivation of the data sets, and the text for explanation of A and B suffixes.

Keeping in mind the nature of the clustered data, and the fact that high diversity collections will cluster together before clustering with their constituent parts, or other low diversity collections (notes 3 and 4, appendix), it is possible to define *a priori* clustering results. A total of 12 sets of circumstances applicable to data set 48 can be envisioned (11 on data set 46 and 8 on data set 40); these are numbered (1) to (12) below. Clustering efficiency can be judged with the **requirement** that individual collections from specific localities assigned to specific communities (Watkins 1979, tables 17–20) be individually recognized; these are (1) the *Go* medium diversity community, (2) the *M*/low

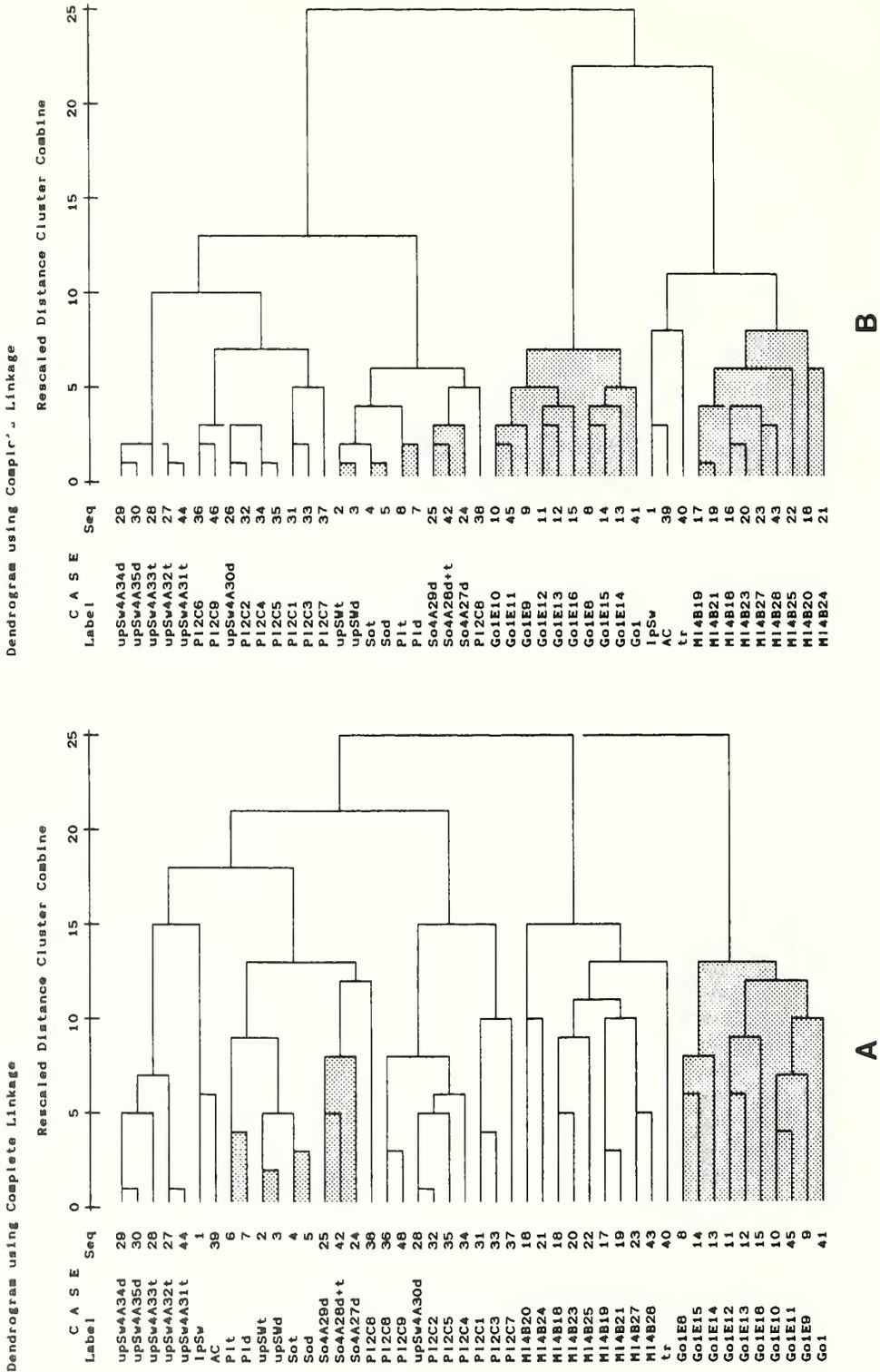


B

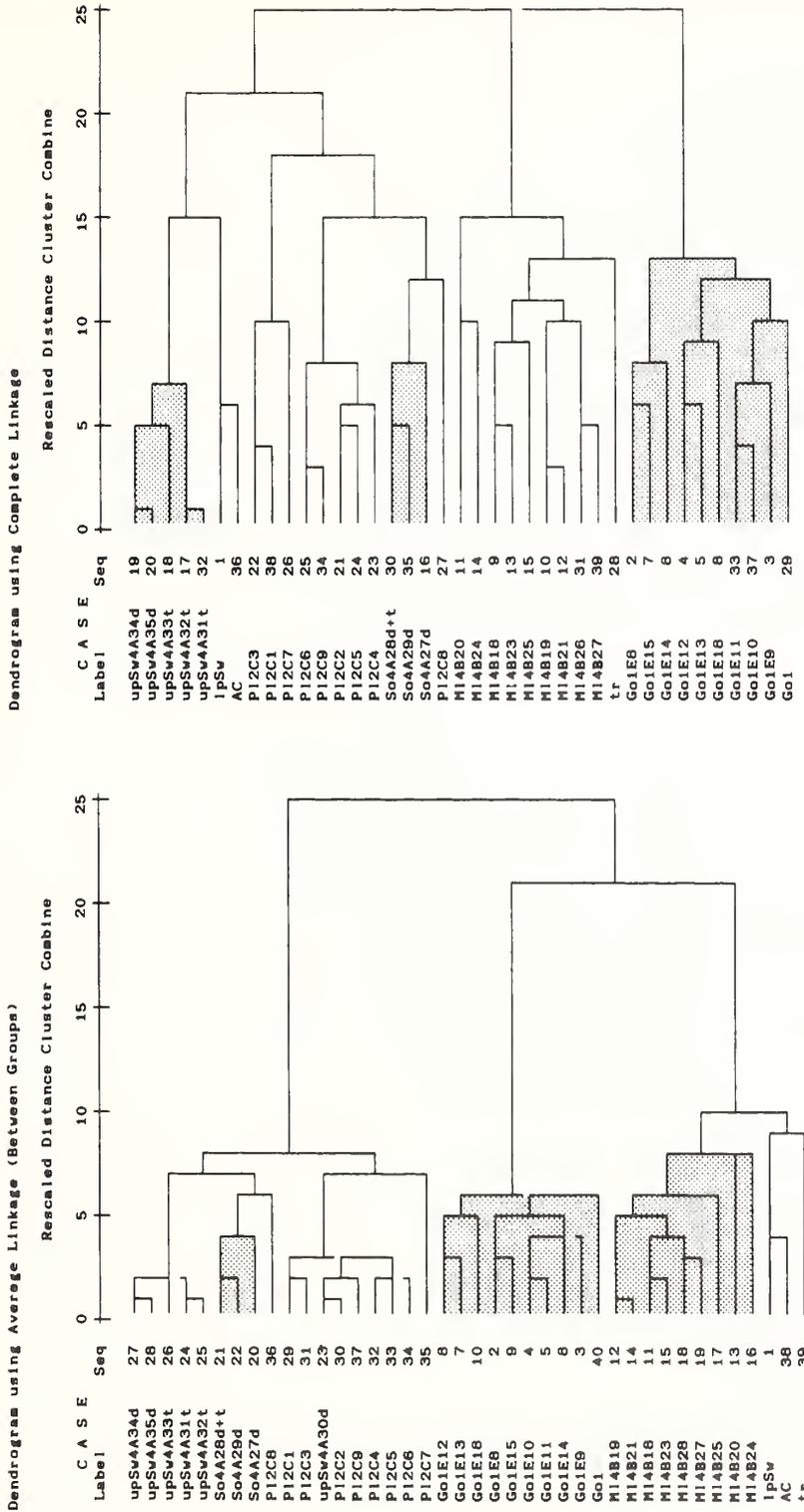


A

TEXT-FIG. 2. Unretouched computer printouts demonstrating increase in clustering efficiency with data modified with Jaccard's coefficient, otherwise as text-fig. 1. A, using unmodified absence-presence data, data set 46B, squared euclidian distances and the single linkage algorithm. B, same as A, but data set modified with Jaccard's coefficient.



TEXT-FIG. 3. Unretouched computer printouts demonstrating equally good clustering efficiency using the cosine θ similarity measure on unmodified and modified data, otherwise as text-fig. 1. A, using unmodified data set 46B and the complete linkage algorithm; position of transitional fauna (*tr*) and lower phase of *Sphaerirhynchia wilsoni* (*IpSw*) fauna are notable. B, as A, but with data set 46B modified with Jaccard's coefficient.



TEXT-FIG. 4. Unretouched computer printouts demonstrating typical clustering results and increasing efficiency in clustering, otherwise as text-fig. 1. A, typical results on data modified with Jaccard's coefficient, using data set 40A, the cosine θ measure and the UPGMA clustering algorithm. B, better clustering of Watkins's (1979) communities, using unmodified data set 39C, cosine θ and the complete linkage algorithm.

to medium diversity community, (3) the *So* medium diversity community, (4) the *upSw* low diversity community and (5) the *Pl* low diversity community; **expectation** that the cumulative faunas of the disturbed neighbourhood assemblages and transported assemblages of the same communities be clustered together at very high levels of similarity, and ideally, should form binary clusters; such should be (6) *upSw*-*upSw*d, (7) *Sot*-*Sod* and (8) *Pl*-*Pl*d; and **hope** (because of the significant differences in diversity) that the four medium to high diversity cumulative faunas retained from table 15 of Watkins (1979) cluster with their respective counterparts given by specific collections and localities; such should be (9) *Go*1 with the *Go* community, (10) *lpSw* with *upSw*, (11) *MI* with *MI* individual collections and (12) the *tr* fauna with either the *Go* or *MI* communities or, ideally, in an intermediate position. The *AC* community has been considered anomalous (Watkins 1979, p. 231) and should not, *a priori*, cluster with any particular community.

The same dendrograms generated for testing chaotic behaviour were used to test these assumptions of efficiency. Because of the chaotic behaviour of some algorithms with specific distance-similarity measures, only those cases exhibiting no chaotic behaviour were considered (e.g. WPGMA with euclidian distance measurements was considered only with modified data).

Table 3 presents the scores obtained from the previous 8 to 12 assumptions, depending on the data set. These results are subjective judgments, and should be viewed as such. Interpretation of table 3 must consider which type of data is used for clustering. In the case of unmodified absence–presence data, clustering efficiency is very poor if euclidian or squared euclidian distance measurements are used and, in fact, best not employed. *Cosine θ* similarity measurements give greatly improved results in efficiency (text-fig. 2).

The choice of measures and methods increases greatly with data modified with Jaccard's coefficient, and all are approximately equally efficient when chaotic behaviour does not occur. A most surprising conclusion, however, resides in the fact that *cosine θ* measures with raw or modified data give nearly equally good results (text-fig. 3). Routinely applicable combinations are *cosine θ* with UPGMA, single and complete methods, with raw or modified data. Such a combination with unmodified data is particularly well suited to obtain quick results and is recommended as ideally suited, at least, for first approximations in community analyses (text-fig. 4A is typical).

Nonetheless, even the highest scores of table 3 do not reach the maximum permissible ones. A serious deficiency of the cluster analysis is the failure to recognize, in all the dendrograms generated, the low diversity *upSw* and *Pl* communities. The *upSw*4A30d collection always clustered with the *Pl* series. The fauna of the *upSw*4A30d locality has $d = 6$, the lowest of the *upSw* localities, and five of its constituent taxa are present in an average of 74% of the *Pl* collections. It is consequently far from surprising that this locality clusters with the *Pl* series; it is logically part of the *Pl* community, even though it lies immediately below the *So* community. It was a simple matter to exclude the *upSw*4A30d locality from sets 40A and 40C, to form data set 39 (39A and 39C), which was submitted to cluster analysis using the single linkage algorithm with euclidian, squared euclidian and the *cosine θ* measure; this last measure was also used with the UPGMA and complete linkage algorithms. Chaotic behaviour was not detected, and clustering was most efficient, again, with the *cosine θ* measure; complete linkage yielded the best results (text-fig. 4B). Text-figures 3A and 4B both contain the correct positioning of the *lpSw* fauna, near *upSw*, and the transitional fauna (*tr*) occurs close to the *MI* fauna (by definition, the *tr* fauna is intermediate between the *MI* and *Go* faunas), and, in fact, it destroys the *MI* cluster.

In a study which pretends to be objective, the procedure outlined above to obtain data set 39 is not without serious reservations (i.e. the procedure is subjective); additional speculation appears unwarranted (but see note 5 of the appendix).

DISCUSSION

The pragmatic approach utilized here to test chaotic behaviour and clustering efficiency of previously described communities from part of the Welsh Borderland is probably the most realistic method of unravelling the intricacies and uncertainties associated with cluster analysis as presently

understood. Some specific methods are judged to be safe and do show positive results, *with the specific data set employed*. Additional testing is necessary to extend their applicability. It would appear, for instance, that unmodified presence-absence data, combined with the median method and squared euclidan distances employed by Lespérance and Sheehan (1988, appendix 2) to recognize previously defined communities by them is a spurious result, in view of tables 2 and 3. Nonetheless, chaotic behaviour occurs in cluster analysis, even if some specific algorithms and distance-similarity measurements appear preferable to others. Future investigators should therefore check the trustworthiness of their dendrograms by varying their order of data entry to test if chaotic behaviour occurs with their specific data.

Lespérance and Sheehan (1988) have contrasted the methodologies employed during 'classical' community definition, non-parametric cluster analysis and parametric statistical methods (as discriminant analysis); this is pertinent to this contribution, but need not be repeated here. Results obtained in the present study could be interpreted to mean that the 'classical' community approach is vindicated by cluster analysis. On the other hand, the same results could also indicate that cluster analysis is more rigorous, gives reproducible results, and is as precise as the 'classical' approach.

The data set employed here is typical of 'middle' Palaeozoic data, and of such magnitude as to be representative of situations when cluster analysis is envisioned, i.e. when visual examination does not reveal the underlying structure of the data. Communities are recurring associations of taxa and cluster analysis is a statistical method specifically construed to group samples, and hence recognize communities. It is consequently worthy of more extended usage. Presently available PCs and software greatly facilitate this.

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APPENDIX – NOTES

1. *Jaccard's coefficient*. This is defined as the number of taxa in common between any two collection p and q , divided by the number of taxa not shared by the two collections. This can be expressed as

$$\frac{c}{a+b}$$

where c is the number of taxa in common between collections p and q , a the number of taxa restricted to collection p , and b the number of taxa restricted to collection q . As the total number of taxa is more readily

available from the raw data than taxa restricted to either collection, it is more convenient to calculate Jaccard's coefficient as

$$\frac{c}{d+e-c}$$

where d is the total number of taxa in collection p , and e the total number of taxa in collection q .

As each and every collection must be individually compared, Jaccard's coefficient consequently requires, where n = number of collections,

$$(n-1)(n/2)$$

times the calculation of the formula (Imbric and Purdy 1962, p. 258), that is, number of rows within a spreadsheet. As a first step in calculating the coefficient, the number of taxa common between each and every collection was isolated. With the spreadsheet used, the following formula (in 'Symphonese') was employed, assuming that each collection (1, 2, ... n) is in a row, that collection p is in a row 2, q is in row 3, that labels of the taxa within the data set to be analysed are in cells A1, B1, ..., and absence–presence data (0 or 1) are in rows 2, 3, ... $n+1$:

$$@IF((A2+A3) = 2, 1, 0) + @IF((B2+B3) = 2, 1, 0) + \dots$$

which reads: if the sum of cells A2 and A3 is 2, return 1, otherwise return 0, plus This is the most time-consuming process of calculating the coefficient and, furthermore, is the one which consumes the greatest amount of memory. To calculate the 48 collections and 112 taxa of data set 48A or 48B within a single file would require, approximately, 3.5 Mb of mainboard and expanded memory; it was easier to split the calculations into three distinct files of almost 1.4 Mb each. Jaccard's coefficient was finalized in another file, after extracting and combining the values obtained from the previous three files.

2. *The cos θ (cosine theta) similarity measure.* The origin of this angular measure of similarity is uncertain. Boyce (1969, p. 3) traces it back to 1946 and attributes it to A. Bhattacharyya. Imbric and Purdy (1962, p. 257) introduced vector notation in their study and used the following angular measure of similarity:

$$\frac{\sum_{i=1}^n x_{ip} x_{iq}}{\sqrt{\sum_{i=1}^n x_{ip}^2 \sum_{i=1}^n x_{iq}^2}}$$

where n are rock properties (here considered as absence–presence data), p and q are any pair of samples, and a generalized observation x_{ij} on the i 'th property of the j 'th sample ($i = 1, 2, \dots, n; j = 1, 2, \dots, N$ samples). This measure of similarity replaces euclidian, or squared euclidian distances (or other distance or similarity measures) in cluster analysis. The *cos θ* measure is not discussed in some standard texts. Anderberg (1973, p. 71) presents perhaps the most extensive discussion. The SPSS/PC+ statistical package offers it as a choice within the clustering module.

Boyce (1969) uses the formula above to define his *cosine of angle*, considers it a measure of resemblance and, more specifically, a measure of similarity in shape. Sneath and Sokal (1973, p. 172) define *cos η* with the same formula quoted above, and follow Boyce (1969). Anderberg (1973) uses the same formula, names the result the cosine of the angle between the vectors, and views it as a measure of similarity between two vectors. The SPSS/PC+Advanced Statistics manual (Norusis 1988, p. B-86) again uses the same formula, names the cosine measure the *cosine of vectors of variables*, and considers it a pattern similarity measure.

3. *Clustering truism 1.* Diversity directly affects clustering, e.g. low diversity collections will cluster together, while high diversity ones will do likewise, before clustering with the low diversity ones.

Consider the worst case situation in which four collections a, \dots, d with, respectively, diversities of 8, 10, 44 and 55, where the ratios of $a:b$ are as $c:d$. Furthermore, assume that any smaller collection is totally included in any larger collections. These data, modified with Jaccard's coefficient of association produce the following symmetrical matrix:

	a	b	c	d
a	1.0			
b	0.800000	1.0		
c	0.181818	0.227273	1.0	
d	0.145455	0.181818	0.800000	1.0

It is obvious from above that collections $a-b$ and $c-d$ will cluster together before any other collection.

4. *Clustering truism 2*. Parts of a whole will cluster together before they cluster with the whole, e.g. individual collections of a community will cluster together before clustering with the cumulative fauna of the community.

This is but a special case of the preceding. Consider that collections *a*, *b* are collections within the cumulative fauna *c*, and that fauna *d* is a cumulative fauna from another community. Collections *a*, *b* are obviously contained in *c*, but if fauna *d* is from another community, it should have less than 50% taxa in common with *c*, say in the worst case, 45% (= 25 taxa). Assuming that *a*, *b* are also contained within *d*, these data produce:

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
<i>a</i>	1.0			
<i>b</i>	0.80000	1.0		
<i>c</i>	0.181818	0.227273	1.0	
<i>d</i>	0.145455	0.181818	0.337838	1.0

It is clear that collections *a*–*b* will cluster first, followed by *c*–*d* at lower levels of similarity. In fact, with the above matrix, a dendrogram of the clustering (using all the measures and methods outlined in the main text) shows that the *c*–*d* cluster joining the *a*–*b* cluster only at the lowest level of similarity.

5. *Use of the Manhattan (city-block) distance measure*. Use of the infrequently employed Manhattan, or city-block, distance measurement (instead of euclidian or squared euclidian distances; see Legendre and Legendre 1983, p. 198), in conjunction with unmodified data in sets 40A, 40C, 39A and 39C, with complete linkage and Ward's algorithms, gave increasingly better clustering. Perfect clustering was obtained when localities *PL2C7* and *PL2C8* were deleted from data set 39, again using complete linkage and Ward's methods with unmodified data. Chaotic behaviour did not occur with any of the three data sets, in the specific circumstances described above, but occurred with unmodified data sets 48 and 46.

LATEST CRETACEOUS WOODS OF THE CENTRAL NORTH SLOPE, ALASKA

by ROBERT A. SPICER *and* JUDITH TOTMAN PARRISH

ABSTRACT. Coniferous woods from the Kogosukruk Tongue of the Prince Creek Formation (Campanian-Maastrichtian), central North Slope, Alaska (U.S.A.) have narrow growth rings, abundant false rings, and high ratios of late wood to early wood. These characteristics are the same across several taxa, and suggest that summers were cool and growing conditions variable. When compared with woods from the middle Cretaceous Nanushuk Group of the North Slope, the growth-ring characteristics of the Kogosukruk Tongue support conclusions that climate deteriorated substantially on the North Slope during the Late Cretaceous.

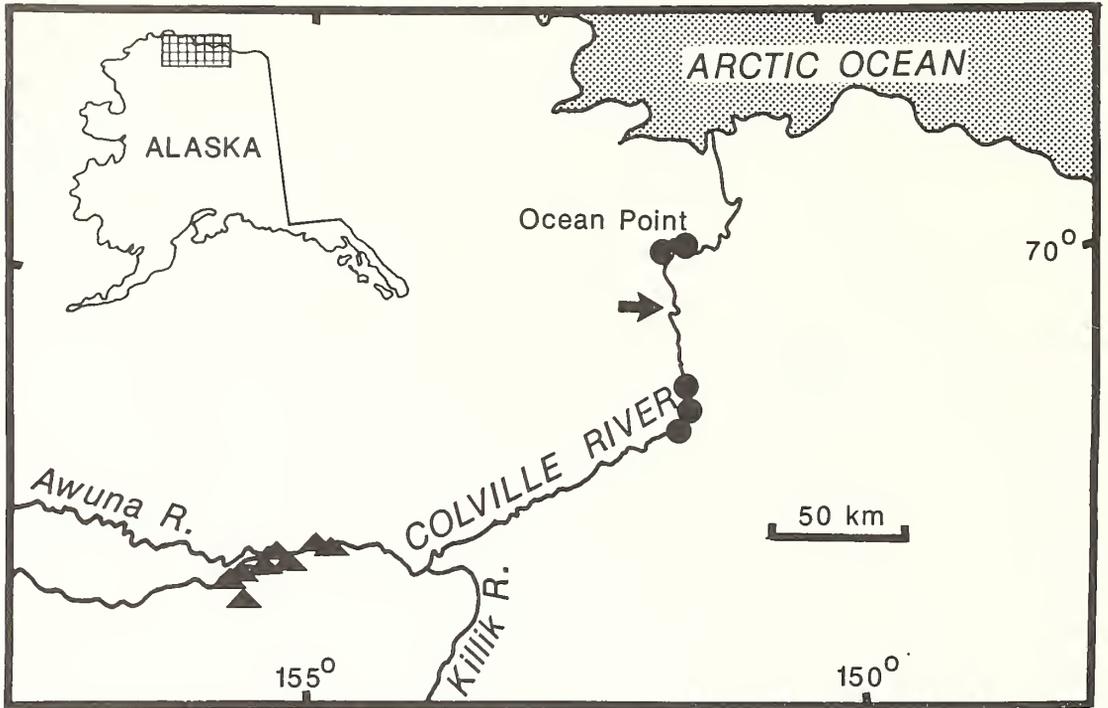
ALTHOUGH the total data set is still small, the analysis of growth rings in ancient (pre-Quaternary) woods is proving to be of considerable use in interpreting palaeoclimate, particularly when used in conjunction with other data. Analyses to date include those of Creber (1977), Jefferson (1982), Francis (1984, 1986), Creber and Chaloner (1984, 1985, 1987), and Parrish and Spicer (1988*a*). All of these workers used standard techniques of growth-ring analysis (Fritts 1976; Creber 1977). These techniques were originally established for dendrochronological, as well as palaeoclimatic, studies of Holocene and Quaternary woods (Fritts 1976). However, they are proving useful for understanding more ancient palaeoclimates, particularly when used in conjunction with other data, such as vegetational physiognomic analysis (Spicer and Parrish 1986; Parrish and Spicer 1988*b*).

The purpose of this paper is to present new data on growth-ring characteristics of fifteen specimens of well-preserved fossil wood collected from the upper part of the Kogosukruk Tongue of the Prince Creek Formation, which crops out along the Colville River, North Slope, Alaska (text-fig. 1). The trees were small, rarely exceeding 20 cm in diameter; the largest was 50 cm in diameter (Spicer and Parrish 1987). The specimens comprise six taxa (Table 1), including *Xenoxylon latiporosum* (Cramer) Gothan, which is widespread at northern high latitudes (Arnold 1952) and also is found in Cenomanian-age rocks of the North Slope (Parrish and Spicer 1988*a*). This taxon occurs in the upper part of the section, from probable Maastrichtian-age rocks. The remaining taxa are from the Campanian part of the section (see below). To our knowledge, the remaining five taxa have not yet been described. We do not attempt to name them in this paper, although we provide brief descriptions and illustrations.

GEOLOGY AND DEPOSITIONAL ENVIRONMENTS

The Kogosukruk Tongue (Gryc *et al.* 1951) is the upper member of the Prince Creek Formation, which is the terrestrial portion of the Late Cretaceous (Turonian to Maastrichtian) Colville Group (see also Molenaar *et al.* 1987; text-fig. 2). In the northeastern portion of the lower Colville River region, the unit is divided into two parts by the marine Sentinel Hill Member of the Schrader Bluff Formation, which is marine and partly equivalent to the Prince Creek Formation. The lower part of the Kogosukruk Tongue is conglomeratic and very thin along the Colville River, and did not yield any useful plant megafossils, although the unit contains thin coal beds, and wood and plant fragments are abundant (Brosgé and Whittington 1966; this study).

The upper part of the Kogosukruk Tongue is a fluvio-deltaic unit, dated Campanian to Maastrichtian on the basis of marine fossils from over- and underlying beds (Brosgé and Whittington 1966; Marinovich *et al.* 1985; McDougall 1986), pollen (Frederiksen 1986; Frederiksen *et al.* 1986), and ostracodes (Brouwers 1988). The unit includes thin coal beds that decrease in thickness and rank toward the top (Spicer *et al.* 1988). The coals also become less woody toward the top, which may reflect a decrease in the proportion of trees in the



TEXT-FIG. 1. Map showing fossil wood localities. Triangles: Nanushuk Group (Parrish and Spicer 1988*a*). Circles: Kogosukruk Tongue (this paper). Arrow indicates position of the Campanian-Maastrichtian boundary (at Sentinel Hill) with Campanian rocks occurring southward of this point.

mire environment (Spicer and Parrish 1987). Plant megafossils generally are found in the overbank mudstones and lacustrine (pond) claystones, although the wood specimens were collected from channel sandstones and levée deposits as well. None of the wood was found in life position.

On the basis of pollen, Frederiksen (1986) provisionally drew the Campanian-Maastrichtian boundary within the Kogosukruk Tongue just north of Sentinel Hill. Thus, thirteen of our wood specimens (7-1 to 80-5; Table 1) are probably Late? Campanian age whereas the remaining two (272-1 and 336-1) are Maastrichtian age.

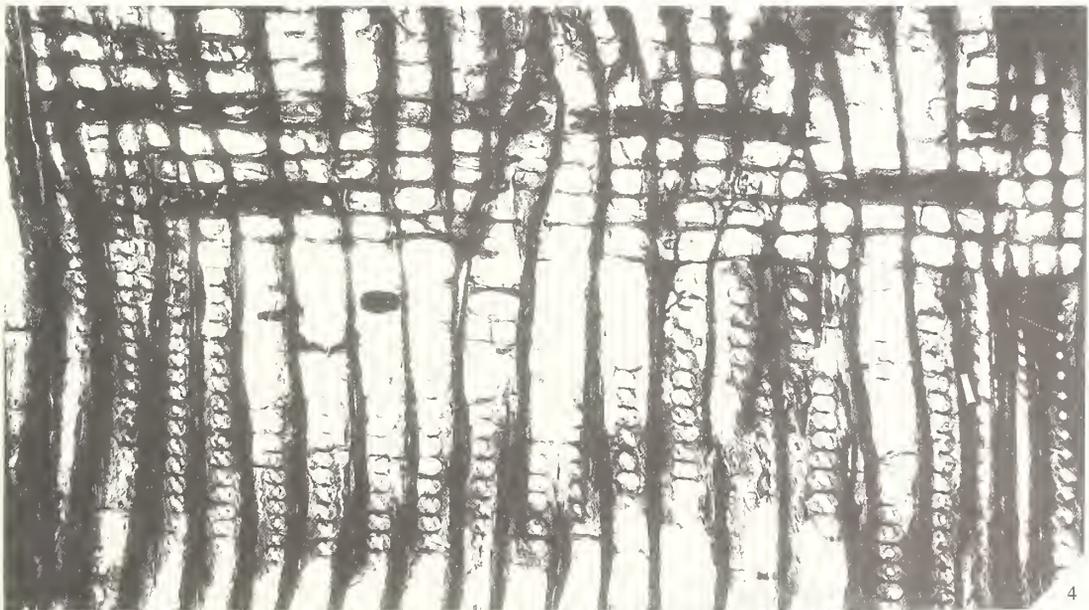
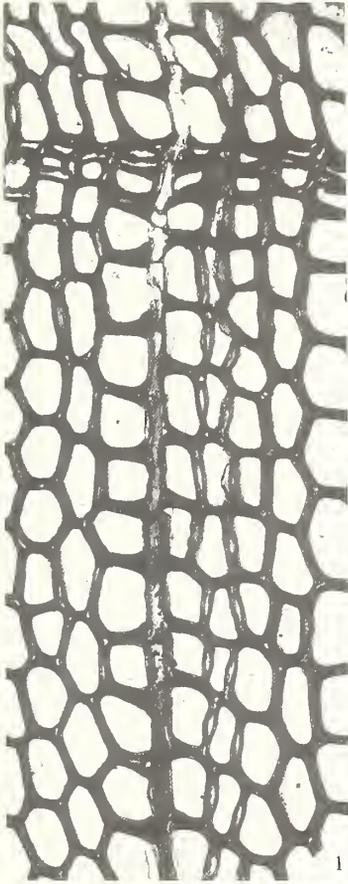
PREVIOUS WORK

We recently reported an analysis of growth rings in woods from middle Cretaceous rocks of the Nanushuk Group (Chandler Formation) of the North Slope of Alaska (U.S.A.; Parrish and Spicer 1988*a*). These rings showed the following: (1) moderate to high variability in ring width, suggesting variable growth conditions from year to year; (2) wide growth rings with rare false rings, suggesting favourable conditions during the growing seasons; and (3) very narrow late wood, suggesting abrupt cessation of otherwise rapid growth. We interpreted these data to mean the following:

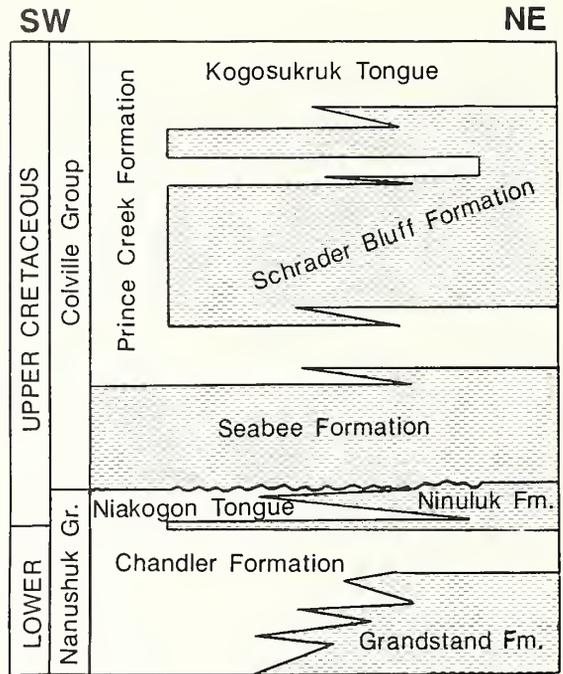
1. The Nanushuk Group trees grew in a shifting sedimentological and hydrological environment. This conclusion is consistent with the fluvial setting interpreted from the rocks.

EXPLANATION OF PLATE I

Figs. 1-4. *Xenoxylon latiporosum*. 1, specimen 272-1, transverse section, $\times 177$. 2, specimen 272-1, tangential longitudinal section, $\times 177$. 3, specimen 336-1, tangential longitudinal section, $\times 177$. 4, specimen 336-1, radial longitudinal section, $\times 177$.



TEXT-FIG. 2. Generalized Cretaceous stratigraphy of the Colville River region (modified from Brosgé and Whittington 1966). Shading: marine units.



2. Conditions during each growing season were favourable for rapid and continuous growth. This is consistent with equable climate during the growing season. The high-latitude positions of northern Alaska during the Late Cretaceous (77° – 85° N; Smith *et al.* 1981; Ziegler *et al.* 1983) would have resulted in continuous daylight during the summer, and the fossil leaf flora supports the interpretation that climate was relatively warm (Spicer and Parrish 1986).

3. Growth ceased abruptly at the end of the growing season, consistent with the rapid change in photoperiod at high latitudes. Seasonality of light also is supported by the leaves (Spicer and Parrish 1986), which show that all plants were deciduous (angiosperms, taxodiaceous conifers, cycadophytes, ginkgophytes), could die back every winter (sphenophytes, ferns), or could become dormant (cupressaceous conifer).

DESCRIPTION OF THE WOODS

Xenoxylon latiporosum (Cramer) Gothan (Pl. 1, figs. 1–4; Pl. 5, fig. 3)

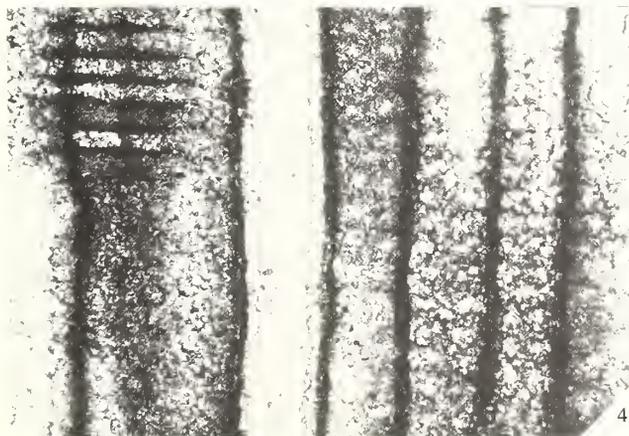
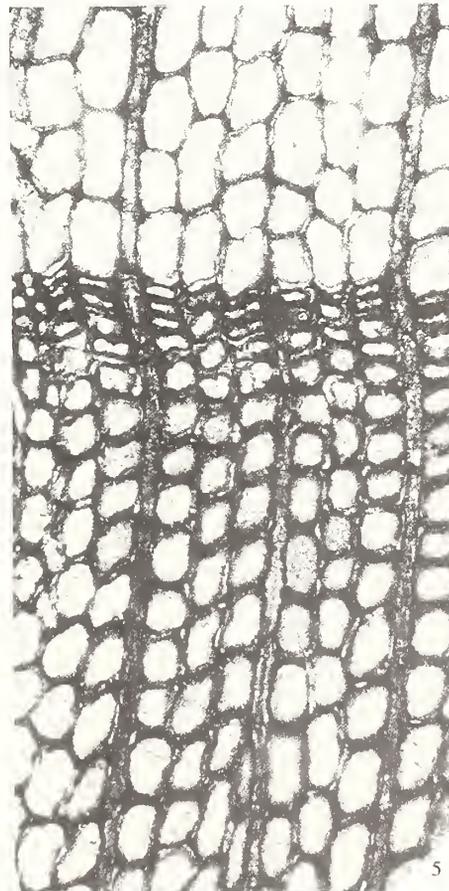
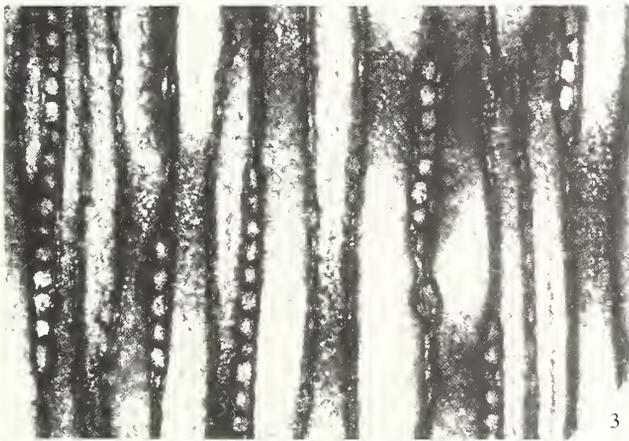
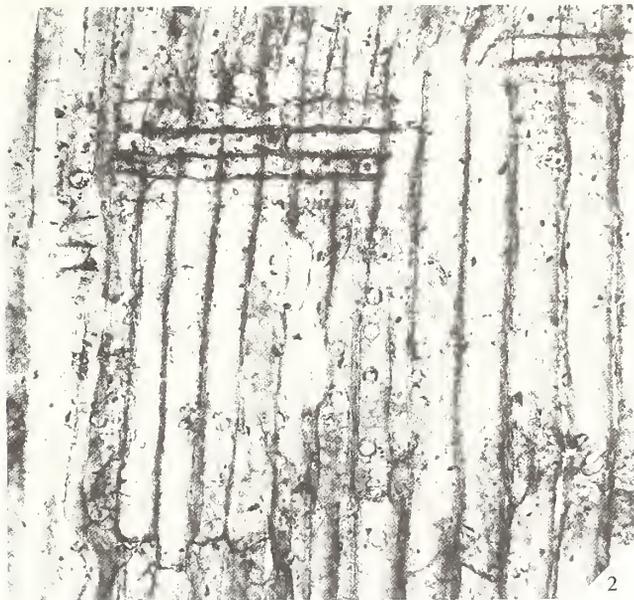
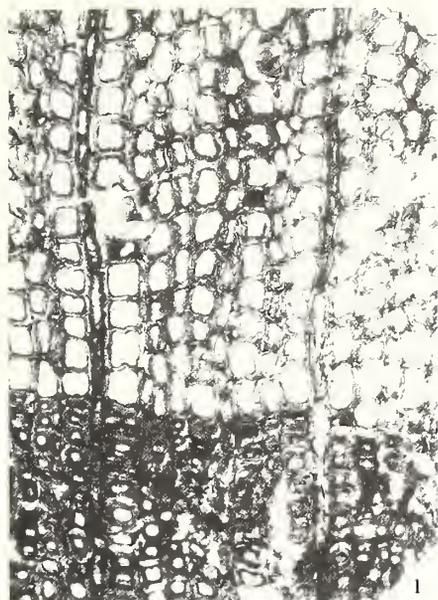
Transverse section. Secondary wood consists of tracheids. Early wood tracheid lumina typically are $900 \mu\text{m}^2$ in cross-sectional area. Resin canals apparently are absent.

Radial longitudinal section. Bordered pits are uniseriate, contiguous, oval, and $25 \mu\text{m}$ wide by 15 – $18 \mu\text{m}$ high, with apertures $5 \times 7.5 \mu\text{m}$. Tracheids have numerous septa (resin plates?), typically 13 – $25 \mu\text{m}$ apart. Cross-field pits are fenestriform. Ray cells are $25 \mu\text{m}$ high.

EXPLANATION OF PLATE 2

Figs. 1 and 2. Taxon A. 1, specimen 7·1, transverse section, $\times 177$. 2, specimen 7·1, radial longitudinal section, $\times 177$.

Figs. 3–5. Taxon B. 3, specimen 46·1, tangential longitudinal section, $\times 177$. 4, specimen 46·1, radial longitudinal section, $\times 177$. 5, specimen 80·1, transverse section, $\times 177$.



Transverse longitudinal section. Rays are uniseriate, very rarely biseriata, and generally short (usually less than 22 cells high) and 15 μm wide.

Taxon A (Pl. 2, figs. 1 and 2)

Transverse section. Secondary wood consists of tracheids and parenchymatous rays only. Resin canals are absent. Cross-sectional area of early wood tracheid lumina is typically 550 μm^2 .

Radial longitudinal section. Axial tracheids only are present; no axial parenchyma is visible. Bordered pits are irregularly uni- and biseriata, not always contiguous, and typically 12 μm in diameter, with apertures 3–4 μm diameter. Cross-field pits are 6–8 μm in diameter. Ray cells are 20–24 μm wide in a vertical direction and 70–190 μm long, with mostly vertical or sometimes oblique walls.

Transverse longitudinal section. Rays are uniseriate, typically 5–20 cells high. Areas of ray cell lumina typically measure 400 μm^2 in vertical section.

Taxon B (Pl. 2, figs. 3–5)

Transverse section. Secondary wood consists of tracheids and parenchymatous rays only. Resin canals are absent. Early wood tracheid cell lumina typically are 2000–2300 μm^2 in cross-section area; overall cell dimensions are 20–25 μm diameter.

Radial longitudinal section. Tracheid bordered pits are biseriata, opposite, contiguous, and 20 μm in diameter. Cross-field pits are circular, 2 per cross-field area, and 10 μm in diameter. Ray tracheid walls are oblique. Ray cell height is typically 15 μm .

Transverse longitudinal section. Rays are uniseriate, typically 2–30 cells high. Ray cells are typically 10–12 μm broad.

Taxon C (Pl. 3, figs. 1–4)

Transverse section. Secondary wood consists of tracheids and ray cells only. Early wood tracheids typically are 2000 μm^2 in cross-sectional area. Resin canals and axial parenchyma apparently are absent.

Radial longitudinal section. Tracheid bordered pits are uniseriate, not necessarily contiguous and often irregularly distributed. Cross-field areas are not preserved.

Transverse longitudinal section. Rays are uniseriate, with cells in long files (> 20 is common). Ray cells are 12–15 μm wide. Highly multiseriate areas occur rarely.

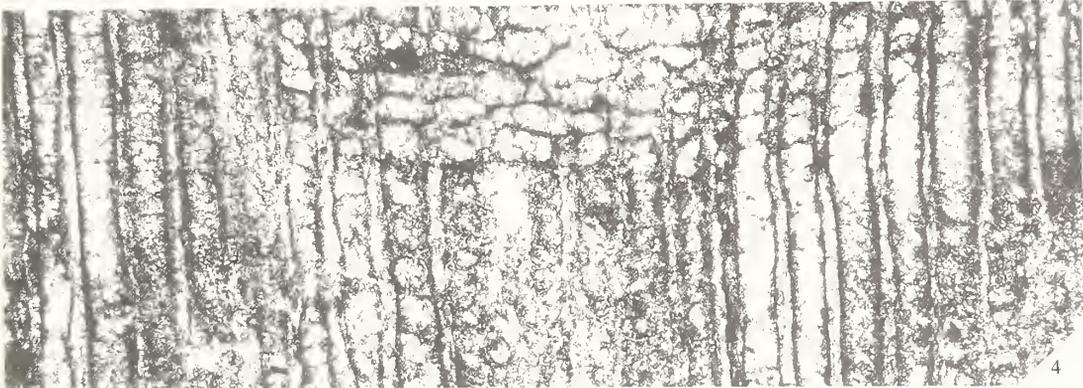
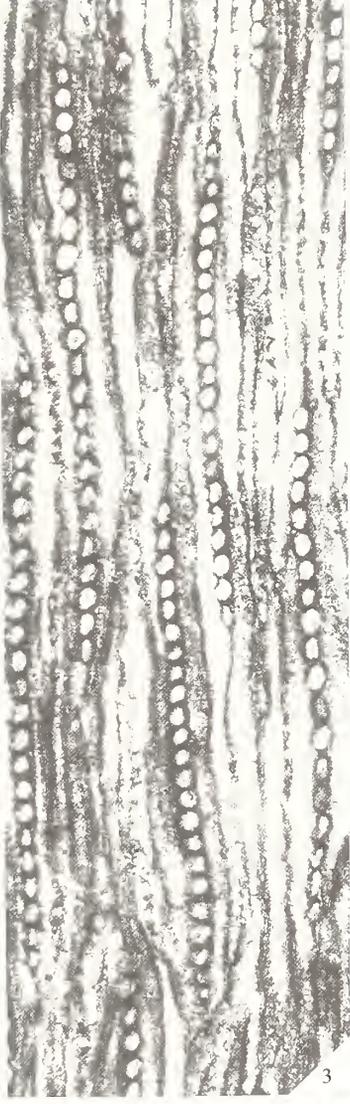
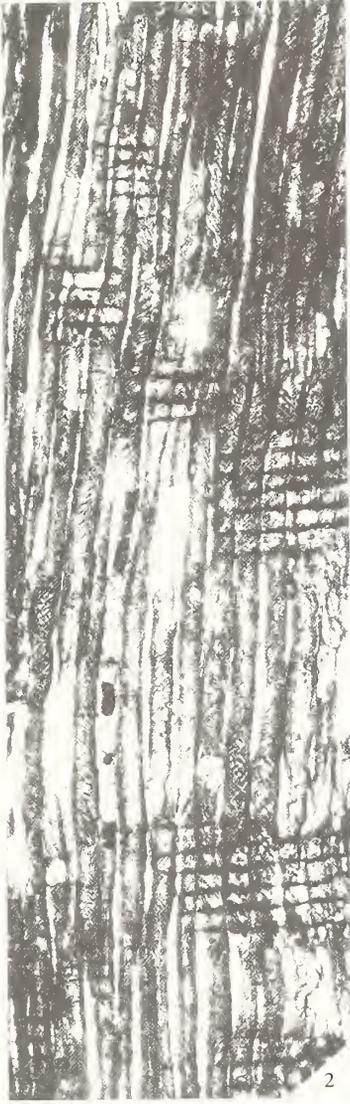
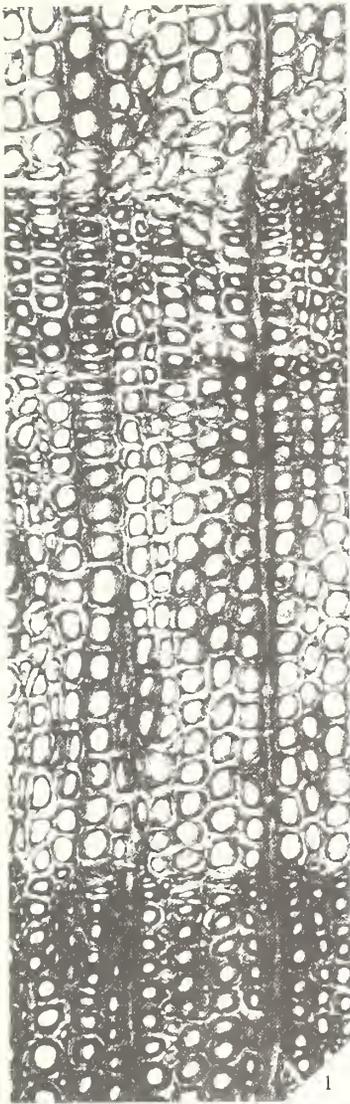
Taxon D (Pl. 4, figs. 1–5)

Transverse section. Secondary wood consists of tracheids; resin canals and parenchyma apparently are lacking. Early wood tracheid cross-sectional areas are variable, between 750 μm^2 and 2900 μm^2 , but usually about 2300 μm^2 .

Radial longitudinal section. Bordered pits are small, 12–18 μm in diameter, with apertures 4–6 μm in diameter, and are numerous, irregularly distributed, and often isolated. Cross-field pits are poorly preserved, and may be circular, with several per cross-field area. Ray cells are approximately 20 μm high.

EXPLANATION OF PLATE 3

Figs. 1–4. *Taxon C*. 1, specimen 46.8, transverse section showing false ring in early wood $\times 177$. 2, specimen 46.8, radial longitudinal section, $\times 177$. 3, specimen 46.2, tangential longitudinal section, $\times 177$. 4, specimen 80.5, radial longitudinal section, $\times 177$.



Transverse longitudinal section. Rays are mostly uniseriate, but may be bi- or multiseriate in places, 5–30 cells high, 15 μm wide.

Taxon E (Pl. 5, figs. 1 and 2)

Transverse section. Secondary wood is composed of tracheids and ray parenchyma only. Resin canals apparently are absent. Early wood tracheid lumina are typically 1500–2000 μm^2 in cross-sectional area.

Radial longitudinal section. Bordered pits are uniseriate and contiguous, with borders typically 15 μm in diameter and apertures 5 μm in diameter. Cross-field pits are not preserved. Ray parenchyma cells are typically 25 μm high. Ray tracheids are 20 μm high. Axial parenchyma is abundant and associated with the rays.

Transverse longitudinal section. Rays are uniseriate, typically 30 μm wide. Axial parenchyma cells are typically 100 $\mu\text{m} \times 45 \mu\text{m}$.

METHODS

Methods of growth-ring analysis have been explained in detail elsewhere (Fritts 1976; Creber 1977; Parrish and Spicer 1988a), so only a brief summary will be included here. Characteristics of growth rings that are useful for studying the climatic signal in pre-Quaternary woods are (1) ring width, (2) interannual variability in ring width, (3) proportion of late wood to early wood, and (4) presence or absence of false rings.

Growth rings wider than about 0.5 cm are regarded as indicative of favourable conditions during the growing season, that is, enough light, water and warmth to permit rapid and continuous growth. However, because ring width is also dependent on other factors, such as genetics, no quantitative climatic information may be drawn from this parameter, and it is most useful for comparing woods from different times and/or localities.

Interannual variability in ring width is termed 'mean sensitivity' and quantified using the equation

$$\text{M.S.} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|,$$

where x_t is width of ring t and x_{t+1} is the width of the adjacent younger ring. Woods with mean sensitivities less than 0.3 are termed 'complacement' and are interpreted to have grown under conditions that were stable from year to year. Woods with mean sensitivities greater than 0.3 are termed 'sensitive', suggesting variable conditions from year to year. Sensitive trees of a particular taxon live at the edges of the range of that taxon (e.g. LaMarche 1974; Kay 1978), and the sensitivity is generally linked to climatic effects, although other factors, such as waterlogging of roots, also can affect sensitivity (Fritts 1976).

The proportion of late wood to early wood which, like ring width, is qualitative and most useful in a comparative sense, can reflect the nature of seasonality. A high proportion of late wood to early wood is typical of temperate-forest trees, where growing conditions gradually become less favourable as the summer wanes. Narrow late wood, on the other hand, is suggestive of rapid cessation of growth owing to abrupt change in growing conditions such as light (Parrish and Spicer 1988a) or water (Francis 1984).

False rings are formed during temporary slowing or cessation of growth during the growing season. False rings indicate that the tree grew under conditions that became temporarily inimical, owing, for example, to fire, drought, freezing or insect attack. The climatic significance of false rings, must, therefore, be supported with other, such as sedimentological, evidence.

Preservation of the woods was generally good. Only one specimen, 80.3, showed crushing of the growth rings during compaction. Interestingly, the crushing was not in the early wood, as observed by Jefferson (1982) and

EXPLANATION OF PLATE 4

Figs. 1–5. Taxon D. 1, specimen 80.4, radial longitudinal section, $\times 177$. 2, specimen 46.9, radial longitudinal section, $\times 177$. 3, specimen 80.4, tangential longitudinal section, $\times 177$. 4, specimen 46.9, transverse section, $\times 177$. 5, specimen 46.5, transverse section, $\times 177$.

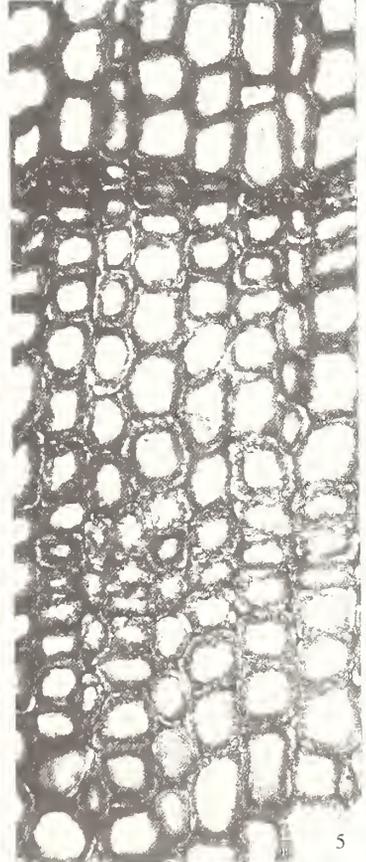
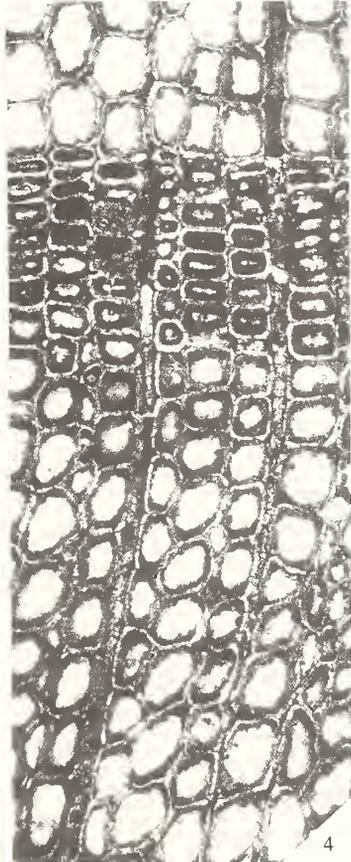
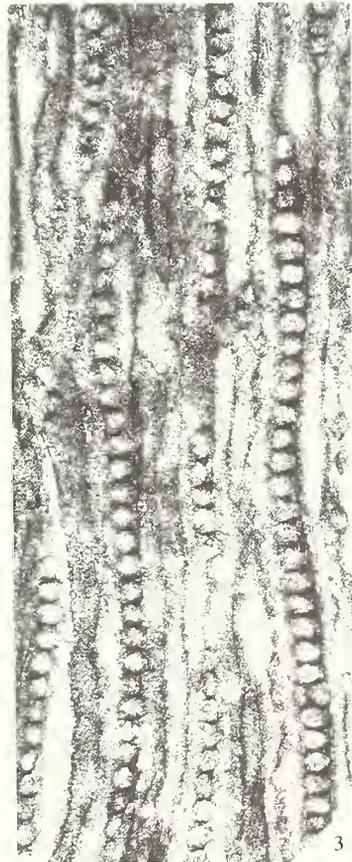
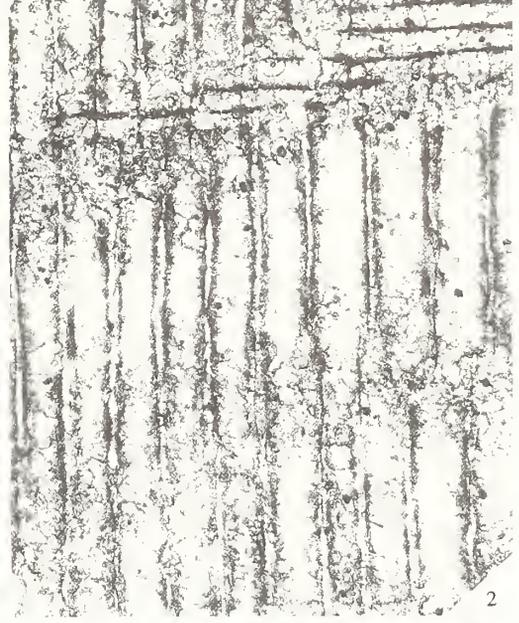
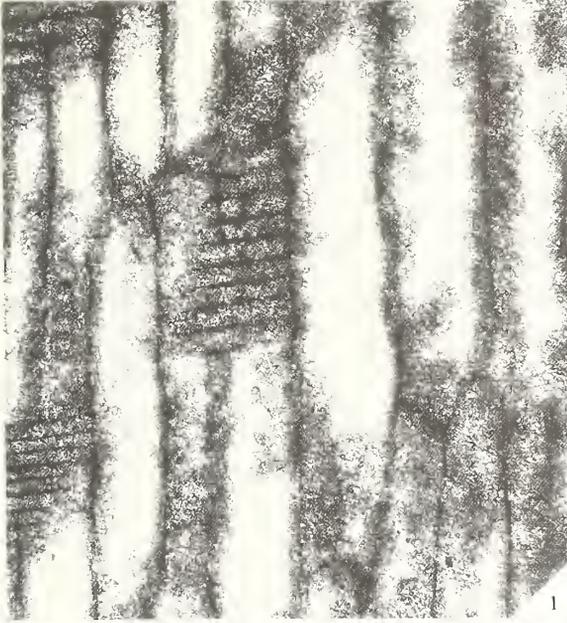


TABLE 1. Wood samples providing data on growth rings and thickness of late wood.

Sample number	Name	Thickness of late wood—number of cells or percentage of total ring width
272-1	<i>Xenoxylon latiporosum</i>	2-4 cells
336-1	<i>Xenoxylon latiporosum</i>	1-5 cells
7-1	Taxon A	5-12 cells
46-1	Taxon B	2-4 cells
80-1	Taxon B	3-9 cells
46-2	Taxon C	2-5 cells
46-8	Taxon C	6-26 cells
80-3	Taxon C	not measured (see text)
80-5	Taxon C	not measured (see text)
46-5	Taxon D	1-10
46-9	Taxon D	up to 34 %; 6-23 cells
80-4	Taxon D	5-8 cells
46-7	Taxon E	up to 58 %
46-13	Taxon E	1-8 cells
46-4	unident., branch (see text)	up to 77 %

Parrish and Spicer (1988a), but in the late wood, making measurement of the late wood impossible (Table 1). However, overall the average diminution of ring width in this specimen was only about 10 %; corrected values were used in the statistics (Tables 2 and 3).

RESULTS

Growth rings in fifteen specimens were measured from thin sections and/or polished blocks (Table 2). The blocks provide longer ring sequences on which to perform the statistics, so in the discussion below and in Table 3, we use measurements taken from polished blocks in preference to those taken from thin sections. However, both data sets for the relevant samples are presented in Table 2. The longest ring-width series, one from each taxon, are presented in text-figs. 3 and 4. Raw measurements are available from J.T.P. on request; the material is lodged with R.A.S. at Oxford University Museum. All of the growth-ring characteristics reported below were observed in woods collected from widely separated localities.

Mean ring widths in woods from the Kogosukruk Group ranged from 0.39 mm to 3.67 mm, with a mean of 1.76 mm. The narrowest ring measured was 0.14 mm (specimen 46.4). The widest 'normal' growth ring measured was 5.88 mm (specimen 46.5). This was the innermost ring of the specimen. Ring width normally decreases as the tree ages, although it should be noted that, in this particular specimen, the adjacent and all subsequent rings were much narrower. A growth ring 13.6 mm wide was measured in specimen 46.1, and was the first ring in a five-year sequence of wood generated in response to injury. The injury is apparent as a longitudinal scar in the trunk, around which the rings grew. The response, as indicated by the contrast with the normal rings, was dramatic (Table 4), but typical. Mean sensitivities of the Kogosukruk woods were 0.10-0.77, with a mean of 0.40.

EXPLANATION OF PLATE 5

Figs. 1 and 2. Taxon E. 1, specimen 46.7, radial longitudinal section, $\times 177$. 2, specimen 46.7, tangential longitudinal section, $\times 177$.

Fig. 3. *Xenoxylon latiporosum*, specimen 272.1, radial longitudinal section, $\times 177$.

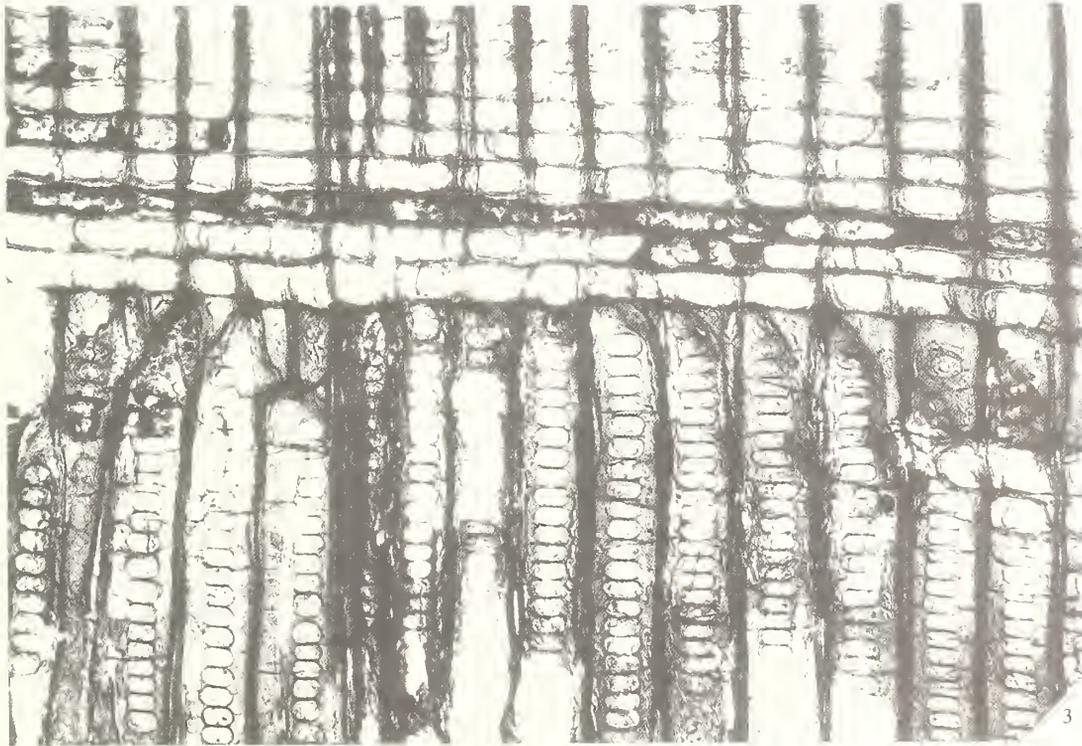
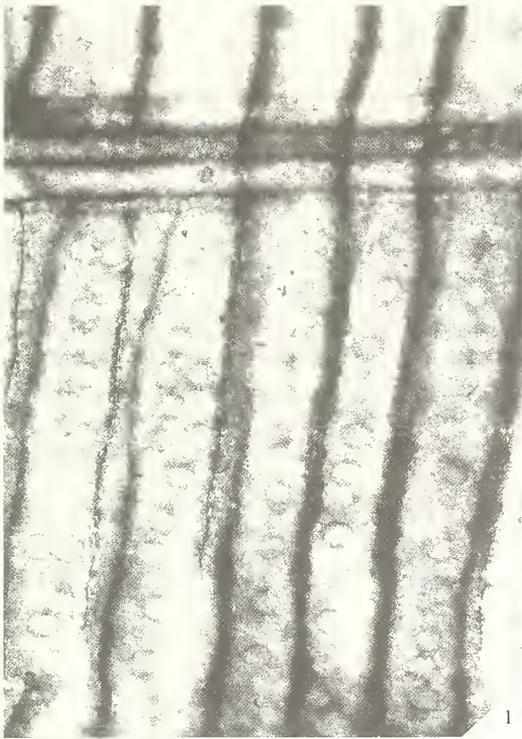


TABLE 2. Data on growth-ring characteristics of woods from the Kogosukruk Tongue of the Prince Creek Formation. Samples are in order by taxon (see Table 1).

Sample	Number of rings	Mean ring width (mm)	Variance	Mean sensitivity
272-1	15	2.23	1.00	0.52
336-1	31	1.46	1.31	0.53
7-1	7	1.94	0.87	0.77
46-1	20	0.87	0.03	0.12
46-1*	30	0.77	0.02	0.15
80-1†	46	1.14 (1.02)	0.24	0.41
46-2	13	3.04	0.82	0.10
46-8	6	1.18	0.31	0.49
80-3†	6	3.67 (3.51)	0.75	0.32
80-5	47	0.53	0.18	0.42
46-5:	transect 1**			
	9	1.35	0.99	0.66
	transect 2, (2 thin sections)			
	17	1.86	1.62	0.48
46-9	14	2.87	1.30	0.39
46-9*	15	3.32	1.56	0.34
80-4	6	3.94	0.29	0.17
80-4*	16	2.96	0.41	0.25
46-7	13	0.97	0.25	0.48
46-13	10	0.98	0.23	0.39
46-4	35	0.39	0.03	0.32

* Measured from block

** This portion sustained injury during growth; the measurements are provided for information only and not included in statistics.

† Number in parentheses is uncorrected for crushing (see text).

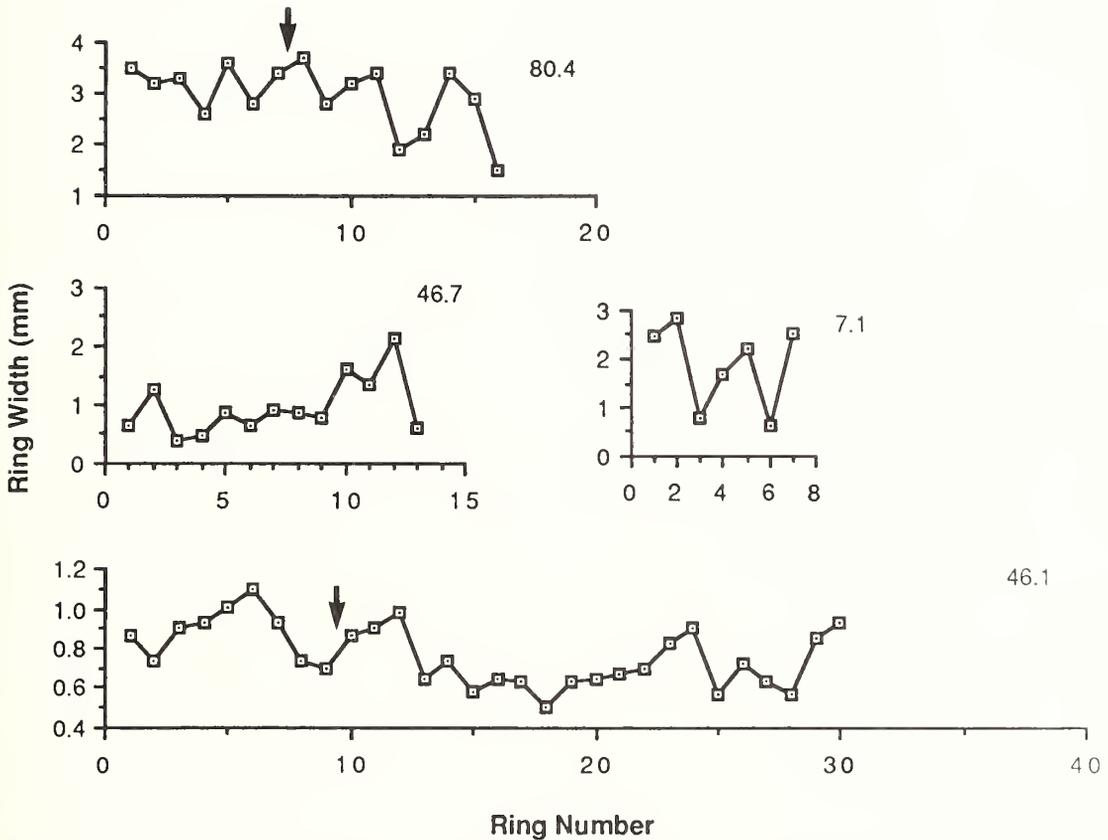
TABLE 3. Comparison of growth-ring characteristics of woods from the Kogosukruk Tongue and the Nanushuk Group. For samples measured from blocks and thin sections, the measurements from the blocks are used in the combined statistics.

	Kogosukruk woods	Nanushuk woods
Ring width (mm)		
Range	0.14-5.88	0.4-12.9
Range of means	0.39-3.67	1.1-4.9
Means of means	1.76	2.81
Mean sensitivity		
Range	0.10-0.77	0.28-0.76
Mean	0.40	0.44
Late wood		
Number of cells	1- > 30	1-15
Ratio to early wood	max. 0.83	max. 0.30
False rings	abundant multiple false rings per growth ring	rare (1 sample), 1 false ring per growth ring

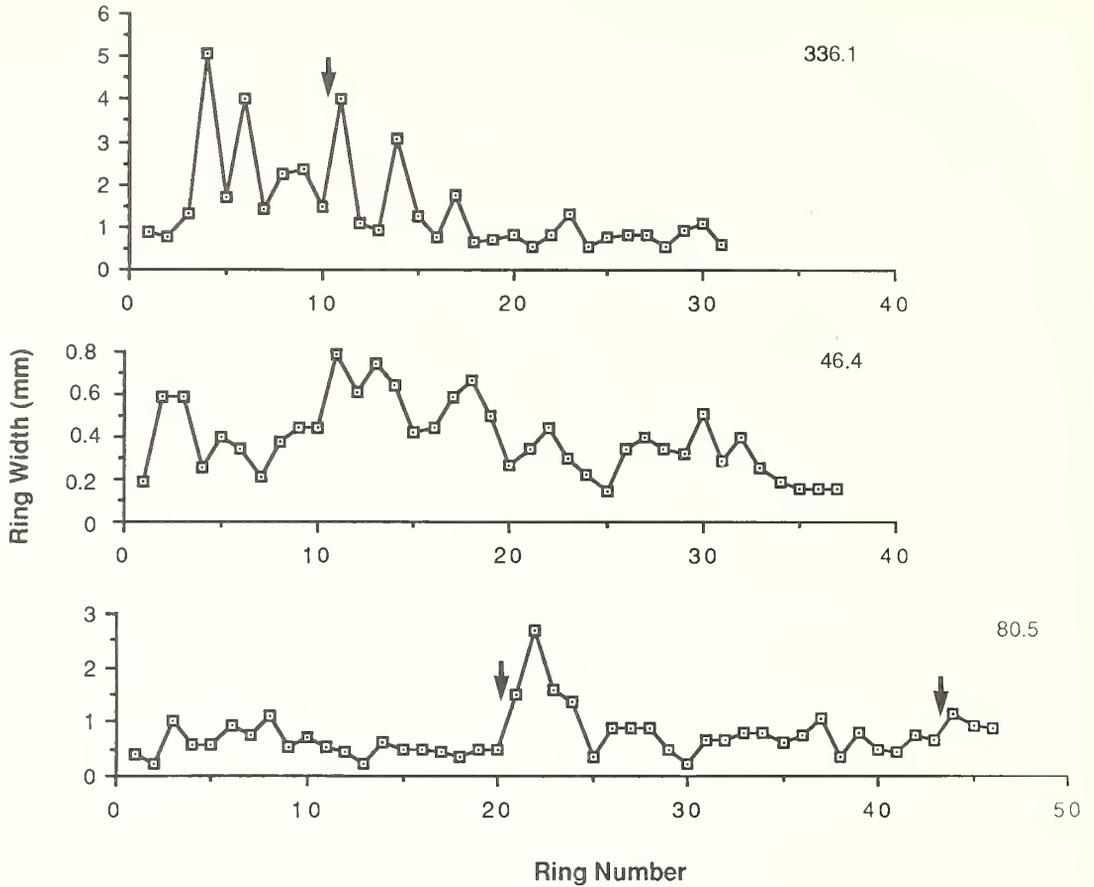
TABLE 4. Growth response to injury in specimen 46-1. Only the last few normal rings of a 31-ring sequence are listed.

Ring type	Ring width (mm)
normal	0.9
normal	1.0
normal	0.8
normal	0.7
response	
1st year	13.6
2nd year	11.1*
3rd year	11.6*
4th year	6.6
5th year	5.2
bark	

* False ring present.



TEXT-FIG. 3. Ring-width series for specimens 7-1, 46-1 (block), 46-7, and 80-4 (block). Locations in the series where rings were unmeasurable are marked by arrows. Note that vertical scales are not equivalent.



TEXT-FIG. 4. Ring-width series for specimens 46.4, 80.5, and 336.1. Locations in the series where rings were unmeasurable are marked by arrows. Note that vertical scales are not equivalent.

Late wood in growth rings from woods of the Kogosukruk Tongue was rarely narrower than three cells and, where counted, ranged as high as twenty-six cells (Table 1). In many rings, counting late wood cells was not possible because the cells diminished in size gradually over a substantial width of the ring; all the late wood in specimen 80.5 was of this nature. Where a distinct zone of late wood was present, its width was as much as 83% of the total ring width. The thickness of late wood was independent of the total width of the ring.

False rings were observed in nine of the specimens of wood from the Kogosukruk Tongue (specimens 7.1, 46.4, 46.5, 46.7, 46.9, 80.1, 80.5, 272.1, 336.1). As many as four false rings were observed in a single growth ring (specimen 46.5); two false rings per growth ring were common (specimens 7.1, 46.5, 46.7, 80.5, 336.1).

No difference in growth-ring characteristics exists between *Xenoxylon latiporosum*, which occurred in the Maastrichtian part of the section, and the other taxa, which occurred in the Campanian part.

INTERPRETATION AND COMPARISON WITH WOODS FROM THE NANUSHUK GROUP

Ring width and mean sensitivity

Growth-ring characteristics of woods of the Kogosukruk Tongue are compared with those of the Nanushuk Group in Table 3. Growth rings in woods from the Nanushuk Group were wider, with means ranging 1.1–4.9 mm, against 0.39–3.67 mm in woods from the Kogosukruk Tongue. This difference is statistically significant at $P \leq 0.01$. The narrowest ring measured from Nanushuk woods was 0.4 mm, versus 0.14 mm in the Kogosukruk woods, and the widest rings were 12.9 mm versus 5.88 mm.

Woods from both the Nanushuk Group and Kogosukruk Tongue were sensitive (Table 3). Mean sensitivities in woods from the Nanushuk Group were 0.28–0.76 with a mean of 0.44, against 0.10–0.77 and a mean of 0.40 in woods of the Kogosukruk Tongue. This difference in means is statistically significant at $P \leq 0.05$.

Although climate is most important in determining mean sensitivity, it is not the only factor, and we (Parrish and Spicer 1988a) interpreted the sensitivity of the Nanushuk woods to a shifting sedimentological and hydrological environment, rather than to climate. The woods generally lacked other characteristics, such as significant late wood and false rings, that would have indicated a stronger climatic effect on the growth of the trees. The sensitivity of most of the Kogosukruk woods also could be due to variations in sedimentology and hydrology, as the Kogosukruk Tongue and Chandler Formations (the unit of the Nanushuk Group from which the woods were collected) were deposited in similar environments. However, the Kogosukruk woods exhibit additional characteristics that indicate a somewhat severer climate than that encountered by the woods from the Nanushuk Group. Nevertheless, many of the woods in the Kogosukruk Tongue were complacent, suggesting that, although climate might have been severer overall, the interannual variability was not great.

Late wood and false rings

The major difference between the two sets of woods was in the amount of late wood and the number of false rings. Late wood in woods from the Nanushuk Group was rarely wider than three cells, with a maximum of fifteen cells in one ring. By contrast, late wood in woods from the Kogosukruk Tongue was usually wider than three cells and, because the rings were narrower, constituted a substantially higher proportion of the wood than in woods from the Nanushuk Group. Growth of the Kogosukruk trees did not cease abruptly, as it did in the Nanushuk trees, but rather slowed during the latter part of each growing season, much as occurs in temperate-region trees today. Thus, the cessation of growth in the Kogosukruk woods was not due just to light, as we interpreted from the Nanushuk woods, but also was influenced by temperature.

The resiliency lent to the Kogosukruk woods by the high proportion of late wood is probably partially responsible for the generally good preservation; about half the samples collected were well enough preserved to be useful for analysis. Crushing was much more prevalent in woods from the Nanushuk Group and, indeed, only a fraction of the samples collected from the Nanushuk (seven of forty-five) were sufficiently well preserved to permit growth-ring analysis (Parrish and Spicer 1988a).

False rings were abundant in the woods from the Kogosukruk Tongue, whereas only one specimen of wood from the Nanushuk Group had false rings. Multiple false rings within a single growth ring were not observed in woods from the Nanushuk Group. We tentatively rule out insect attack as the cause of false rings in the Kogosukruk woods because we found no evidence for insect attack in either the woods or the leaves, and because many growth rings have more than one false ring. Insects in seasonal climates tend to have rigid life cycles and attacks on trees by a given species of insect will occur during a relatively constrained time period. Thus, if the false rings were formed during the stress of insect attack, several species of insects would have to have been involved. No evidence for even temporary drought has been found in Kogosukruk sediments; indeed, the system

was very wet (Phillips 1987). Fire and freezing both are plausible explanations for growth disruption in Kogosukruk woods. Charcoal is abundant in Kogosukruk Tongue (indeed, the presence or absence of charcoal can be useful in distinguishing these rocks in core; J. T. Parrish and R. A. Spicer, unpublished data). However, freezing is an equally likely explanation, given the low temperatures suggested by the thick late wood and the vegetational physiognomy (Parrish and Spicer 1988b).

Vegetation

The fossil leaf flora changed dramatically between the Nanushuk Group and the Kogosukruk Tongue (Spicer and Parrish 1987; Parrish and Spicer 1988b). The flora of the Nanushuk Group is very diverse, including sixty-seven forms of angiosperm leaves; several taxa each of ferns and conifer leaves and cones; and ginkgophytes, sphenophytes and cycadophytes (Spicer and Parrish 1986). By Kogosukruk time, total diversity of megafossils other than wood was ten forms, including the sphenophyte *Equisetites*, two ferns, two conifer leaf forms, a fruit, two angiosperm leaf forms and two types of small seed (Spicer and Parrish 1987; Parrish and Spicer 1988b). Quantitative estimates of mean annual temperature, derived from angiosperm leaf-margin analysis (Wolfe 1979), were 10°C for the latest Albian and Cenomanian and 13°C for the Coniacian (Parrish and Spicer 1988b). The angiosperm megaflora was too depauperate in the Kogosukruk Tongue for leaf-margin analysis, but we interpreted the drastic drop in diversity as indicative of cooling. Based on the overall physiognomy of the flora, we estimated the mean annual temperature to be 2–6°C. In such a climate, cold snaps seem likely (Parrish *et al.* 1987).

Frederiksen *et al.* (1988) reported a relatively high diversity of angiosperm pollen from the Kogosukruk Tongue. The discrepancy between the diversity of the megaflora and that of the palynoflora would appear to indicate that the angiosperm component of the vegetation was principally herbaceous. This is consistent with the cooler and more variable climate indicated by the woods. Such a climate would favour opportunistic taxa with annual life cycles.

The question of whether freezing occurred is critical to understanding the presence of dinosaurs in the Kogosukruk Tongue (Clemens 1985; Brouwers *et al.* 1987; Parrish *et al.* 1987; Paul 1988). The palaeobotanical data suggest that winter temperatures were likely to have been close to freezing. In addition, the presence of glendonites, which form in seawater near freezing, in older and younger marine sediments of the North Slope (Kemper 1987) suggests that the Arctic Ocean was likely to have been cool throughout the Cretaceous.

Although the vegetation suggests cool temperatures, the morphology of the tracheids in the woods may provide evidence against prolonged freezing. Tracheid cross-sectional areas are related to exposure to water stress. Where water stress is experienced, thick tracheid walls (and therefore small lumina) are necessary to prevent tracheid collapse as tension builds up in the water column. Conversely thin-walled tracheids and large lumina are correlated with stress-free environments. Although some Kogosukruk early wood tracheid cross-sectional areas are as small as 550 μm^2 (specimen 7.1) most are greater than 2000 μm^2 . This figure is comparable to modern conifers growing in highly mesic environments where water stress is never experienced (Carlquist 1975). Thus, it is unlikely that the Kogosukruk trees experienced freezing of the root zone, which could have induced severe water stress, particularly during the early spring growth. It appears that periglacial conditions were not experienced at sea level, even at northern latitudes greater than 80° N.

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ORIENTATION OF CEPHALOPOD SHELLS IN ILLUSTRATIONS

by SVEN STRIDSBERG

ABSTRACT. Most drawings and photographs of fossil cephalopods show the shell upside down in respect to the animal's living position. As there is no advantage in this way of making illustrations, presumably based on tradition, the author suggests that fossil as well as living cephalopods should be illustrated in life position. This is particularly important today, as functional morphology is of vital interest to cephalopod workers. To facilitate understanding of the behaviour of fossil cephalopods, the first step must be to see them orientated in the same way as they saw each other.

ILLUSTRATIONS have always played an important role in palaeontological publications and it is of vital importance that they present material in a proper way. This applies to drawings as well as to photographs. All palaeontologists will agree with the above, but unfortunately we are, in some cases, still trapped in the traditional way of presenting illustrations.

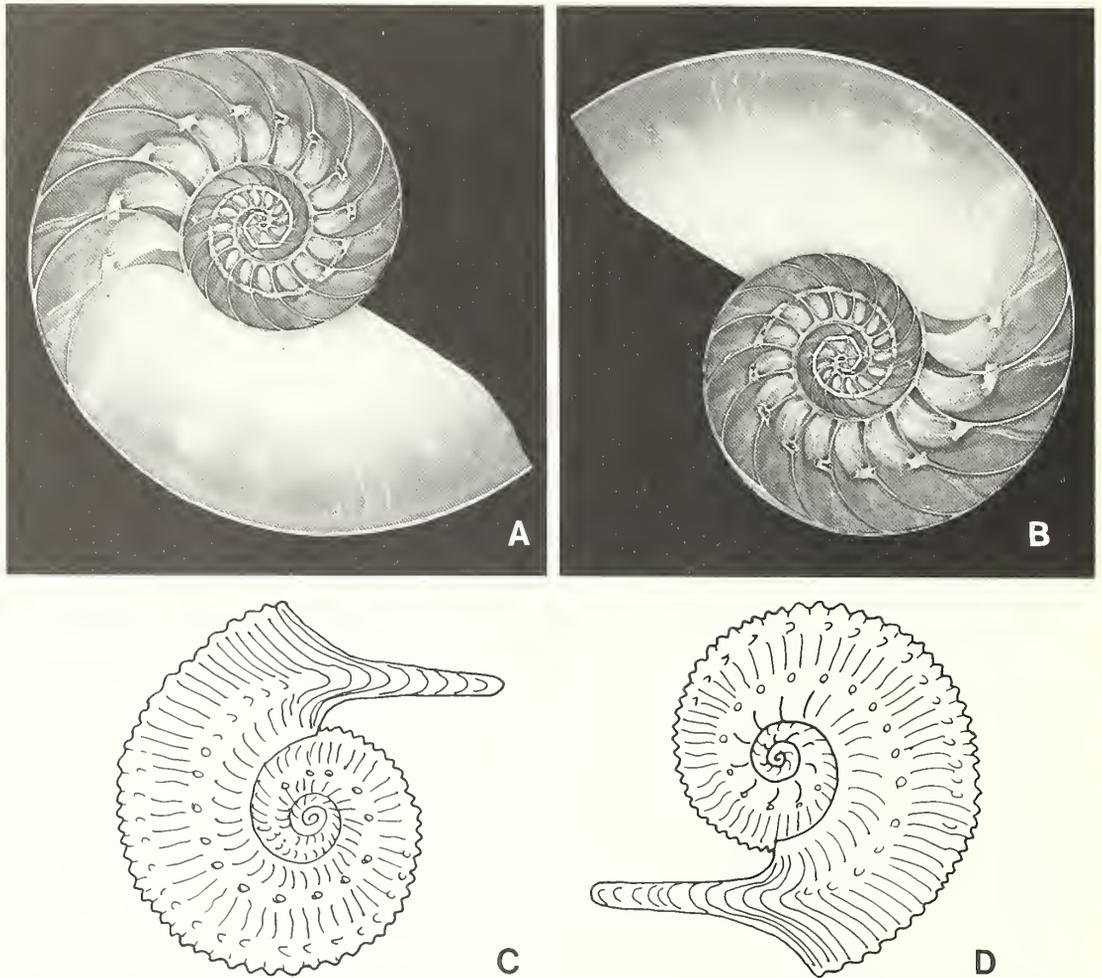
In the last century when fossils were scientifically illustrated for the first time, it seems that aesthetics dictated their orientation. Regarding the cephalopods, evolute and involute specimens were normally illustrated with the body chamber on top of the shell in all lateral views. This might perhaps have been artistically satisfying, but it is definitely misleading for one trying to reconstruct the animal or study its functional morphology.

The tradition of presenting illustrations of cephalopods upside down, in respect to the living animal, is firmly established among palaeontologists. In many publications illustrating, for example, various forms of ammonites, it is fairly common for complementary drawings to be included to show the supposed living position of the animal. A very good example of such convention is the number of articles concerning the extant nautiloid, *Nautilus*, where the complete animal is photographed in living position whilst the cut shell, showing all the chambers, is shown upside down. Even I have been accused by an old friend of having illustrated *Nautilus* upside down (Stridsberg 1981, fig. 2), after he had studied the literature on the subject. All illustrations of *Nautilus* he could find showed the shell with the body chamber at the top of the shell. Now I find myself asking the same question (text-fig. 1) as he did: 'Why do they put it upside down?'

The literature to which my friend referred was not only the popular variety but also palaeontology text-books and the *Treatise*. In the chapter 'Living *Nautilus*' in the latter (Stenzel 1964, pp. K59–K93) *Nautilus* is nicely illustrated in living position with soft parts (fig. 43) and upside down without soft parts (figs. 54–56). In all it is figured in ten pictures, five in living position and five upside down. I have asked before (Stridsberg 1985, p. 10) and I do so again. Who would dream of illustrating an *Australopithecus* upside down?

It must be in the interests of cephalopod workers to facilitate the understanding of all their readers, laymen as well as professionals, of the results they achieve, and not to use misleading methods. If anyone is in the position to interpret the correct living position it is the palaeontologist, and therefore we have a great responsibility to other readers.

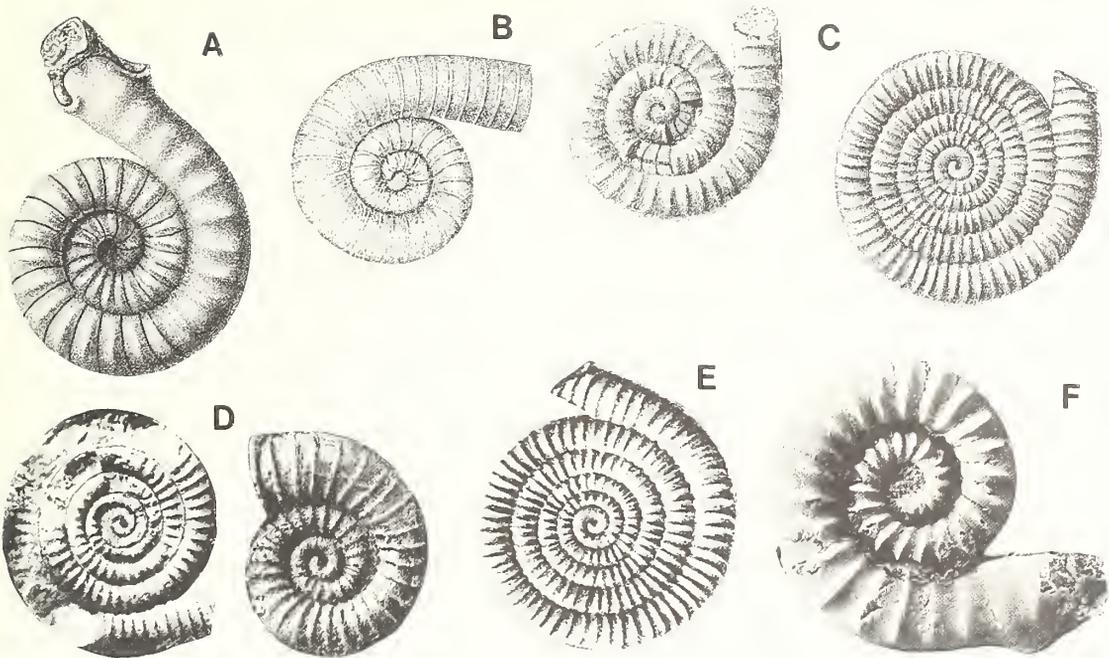
Naturally it would be a break with tradition for many palaeontologists to see their material illustrated 'upside down' (in the old sense), but I strongly urge cephalopod workers to use common sense rather than to continue to follow old conventions. It might be confusing for those adhering to the 'old system' but I consider the present situation to be more confusing with all its possible combinations (text-fig. 2).



TEXT-FIG. 1. A, *Nautilus* shell in living position. B, *Nautilus* upside down. What makes B look more attractive than A? C and D, the ammonite *Kosmoceras* in common publication mode (C) and in living position (D).

However, there is a problem in reconstructing the living position in incomplete involute or evolute cephalopods as the only indicator of up-and-down is the position of the body chamber. In ammonites where there is good reason to believe that only the body chamber is missing due to the lack of the reinforcements the septa make to the phragmocone, the end of the whorl might as well be orientated at the lower part of the shell as at the upper. This suggestion is based on the fact that the body chamber in ammonites often occupies roughly a whole whorl of the shell. In similarly shaped nautiloids with missing body chamber, variation is great between various taxa. In *Ophioceras* for example the body chamber will occupy almost a whole whorl, while *Nautilus* has a body chamber occupying only about a third of a whorl. Nevertheless the seeker of perfection must always try to reconstruct the orientation of the specimen under consideration. Naturally due to lack of information incomplete specimens might be incorrectly orientated in the future but that is not an argument for ignoring the problem.

An advanced and accurate method on how to reconstruct the life orientation of fossil cephalopods is demonstrated by Okamoto (1988), who investigated some heteromorph ammonoids.

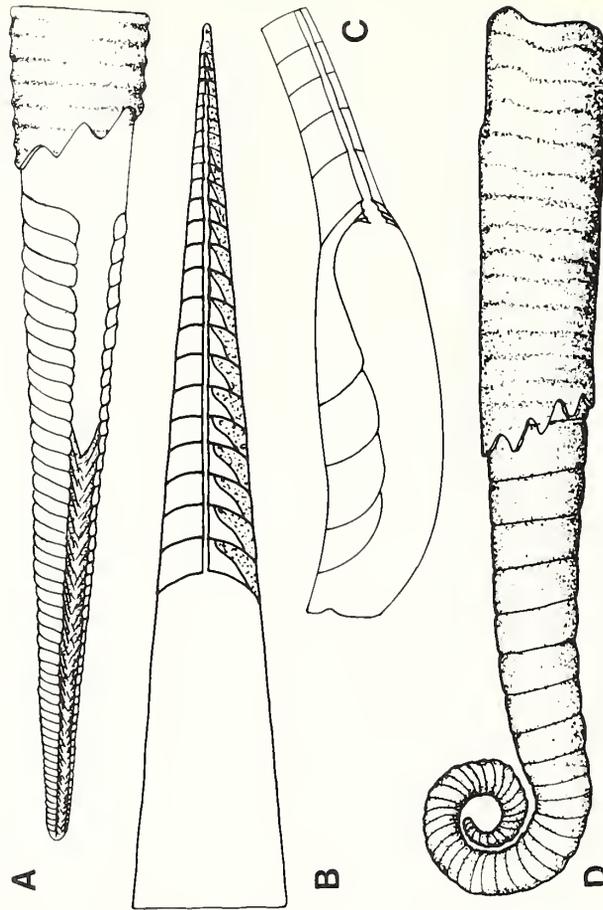


TEXT-FIG. 2. Illustrations of *Ophidioceras* from six publications demonstrating various orientations: A, *Ophidioceras simplex* Barrande 1865, as figured by Barrande (1865, pl. 97, fig. 2). B, *Ophidioceras reticulatum* Angelin 1880, as figured by Angelin and Lindström 1880, tab. 16, fig. 1). C, *Ophidioceras reticulatum* Angelin 1880 and *Ophidioceras rota* Lindström 1890 as figured by Lindström (1890, pl. 7, figs. 29 and 34). D, *Ophidioceras welleri* Foerste 1930 and *Ophidioceras winningtonense* Foerste 1925 as figured by Foerste (1930, pl. 25, figs. 5 and 6). E, *Ophidioceras reticulatum* (Angelin 1880), the same illustration as in C but figured in the Treatise in the same position as Barrande's *O. simplex* (A) (Furnish *et al.* 1964b, fig. 270: 1b). F, *Ophidioceras simplex* Barrande 1865 as figured by Turek (1972, fig. 3). Apart from one of Foerste's figures (D (5)) this is the only illustration figuring a specimen of *Ophidioceras* (*Ophidioceras*) in living position.

The shells from these animals are extremely difficult to orientate due to their highly irregular shape. Assisted by a computer, Okamoto managed to reconstruct extremely well not only the life orientation of adult animals but also changes in life orientation during their ontogeny (Okamoto 1988, text-fig. 6). Naturally this computer method is also available for other cephalopods and similar investigations with symmetric shells will be less complicated. Hopefully there will soon be more investigations employing computer orientations, and this will increase the demand for standardization of cephalopod illustrations.

Unfortunately it is not only evolute or involute cephalopods which are treated in an unfair way, but also many of the orthocones. In a palaeoecological paper, Flower (1957; pp. 829–852) discussed the horizontal floating position of various kinds. He (Flower 1957, figs. 2–6) demonstrated from the disposition of internal deposits the resulting floating orientations of the animals. Three of his illustrations (Flower 1957, figs. 4–6) have become classical and have been republished several times as they show very clearly the orthocone floating mechanism (see also Flower 1955, p. 246).

The deposits found in orthocones are located in the apical chambers, in the siphuncle, or in both areas. They do not completely fill the apical chambers but are concentrated on the ventral side of the shell to help the animal maintain stability. Strictly speaking they served more or less as ballast, to keep longitudinal as well as rotational stability. In those genera where the deposits were concentrated in the siphuncle, this was not situated in the centre of the shell but was ventral, or ventrally to the centre, to obtain the same result, viz. maintenance of stability.



TEXT-FIG. 3. This text-fig intentionally illustrates four longicones in vertical orientation in a full page figure, as if they were too long to be illustrated horizontally. All specimens have a defined floating position and have their dorsal side towards the left. A, *Endoceras* with siphuncular deposits, indicating what is dorsal and ventral. B, *Orthoceras* with ventral deposits in the closed chambers. C, in this nearly mature *Glossoceras* the dorsally located gas chambers serve to keep the shell in balance. D, the gas-filled apical end of *Lituites* keeps the dorsal side of the shell upwards.

As orthocones with cameral or siphuncular deposits, have a defined living position, there is no reason to illustrate these shells with the ventral side upwards. As soon as we can decide what is dorsal and what is ventral, there should be no hesitation in showing this in illustrations (text-fig. 3).

In some groups of more or less straight cephalopods with a horizontal living position, stability was not accomplished by ventral deposits, but by dorsally located gas chambers. In *Lituites* the coiled apical end of the shell served as a stabilizer (text-fig. 3D) and in *Glossoceras* the dorsally located gas chambers in the mature animal kept the shell in balance (Furnish *et al.* 1964a, fig. 190C).

Regarding the orthocones and other long shells, it is sometimes not practically possible to print lateral views in a proper way as the length of the shell favours a vertical reproduction. 'By tradition' the apical end has been located mostly to the top of the page. Again, however, it must be emphasized that all lateral views of orthocones, orientated along the page, should be figured with the dorsal side in the same direction, here suggested to the left, regardless of whether the apical end will be located

at the top or the bottom of the page. This will facilitate the reader to understand the illustration when turning the figure to place the orthocones horizontally.

A good example of illustrating a cephalopod in a proper way is the reconstruction of the ascocerid, *Glossoceras lindstroemi* Miller in the *Treatise* (Furnish *et al.* 1964a, figs. 190–191). However, in the following figures in the chapter the authors have chosen to place all specimens with the apical end in the same direction, and thus some specimens are illustrated with the dorsal side to the right and some with the dorsal side to the left (e.g. fig. 196: 1b and 2b respectively). The authors have been consistent in making their illustrations and all shells have the same orientation, although some shells are not placed correctly based on functional morphology. If all shells had been orientated with the dorsal side up, or at least to the left, it would have facilitated comparison of different specimens.

The brevicone nautiloids comprise another group carefully illustrated upside down. As the cameral part of the shell acted as the lifting device and the body chamber the sinking device, I can see no reason for figuring these shells with the apical end downwards. In this case it is probably a heritage from Barrande, who made numerous illustrations of rich material (Barrande 1865, 1866). As some of these groups had interesting apertural openings, the material was reproduced upside down several times, just as in Barrande's work. I recommend that in the future such specimens ought to be figured with the apical end upwards. I have illustrated brevicone nautiloids (Stridsberg 1985, 1988a and b), in what I believe is the living position and one comment in a review was 'it will be normal if you turn the page over'.

I believe it would be better for us to overturn the old way of making cephalopod illustrations, rather than to leave it to future readers. In summary I strongly recommend that cephalopods are illustrated according to inferred life position, and I hope that this paper will stimulate fruitful discussion on this topic among cephalopod workers.

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A NEW EOCCRINOID FROM THE LOWER CAMBRIAN OF SPAIN

by G. UBAGHS and D. VIZCAÍNO

ABSTRACT. An eocrinoid similar to *Gogia*, but having single or partitioned epispires with dome-shaped calcite cover, is described as *Gogia (Alaniscystis) andalusiae* subg. et sp. nov. It is from the Lower Cambrian (Marianian stage) of Alanis (Seville), Andalusia, Spain, and it is the second species of *Gogia* from the Lower Cambrian.

THE eocrinoids comprise a heterogeneous assemblage of primitive pelmatozoans, which probably contains the ancestors of all other cystoids s.l. or blastozoan echinoderms (see Smith 1984; Paul 1988). Yet the term 'eocrinoid' remains convenient to designate those Cambrian and Ordovician pelmatozoans which, at this time, cannot be referred to any of the currently accepted classes.

Only three genera and three species of eocrinoids (including lepidocystoids) are known from the Lower Cambrian, all of them from North America (Sprinkle 1973; Durham 1978). They are *Kinzercystis durhami* Sprinkle, *Lepidocystis wanneri* Foerste and *Gogia ojenai* Durham. In addition, isolated plates from the Lower Cambrian of California (Sprinkle 1973), England (Donovan and Paul 1982) and south-east Iran (Wolfart 1974) have been described as possible or probable eocrinoid remains.

Among the species just referred to, only one has been assigned to the genus *Gogia*: *G. ojenai* from the late Lower Cambrian Latham Shale of California (Durham 1978). A second, but somewhat older species, was discovered a few years ago by one of us (D.V.) in south-western Spain (Andalusia) near Alanis (Province of Seville). This new species, described below, is of special interest because of its epispires as well as being the oldest recorded representative of the genus.

The presence of echinoderm plates in the Lower Cambrian of Alanis has been previously reported by R. and E. Richter (1940) and G. Henningsmoen (1958). According to the latter, the plates resemble those of *Gogia prolifica* Walcott from the Mt Whyte Formation, lower Middle Cambrian, British Columbia, Canada.

LOCATION AND AGE

The fossils dealt with herein were collected near Alanis, about 75 km north-north-east of Seville, in the Sierra Morena Oriental, from an outcrop on a pathway going from Alanis station to Hornillo-Viejo farm, some twenty metres after the crossing of the Benalija River (the position of this outcrop is indicated (2) in fig. 1 of Gil Cid 1972).

The layer that yielded the echinoderm remains belongs to the upper part of the Marianian stage (Lower Cambrian; Sdzuy 1971), correlated with beds of Botomian age of the Siberian sequence (Sdzuy 1972). The trilobite fauna of Alanis, as revised by Gil Cid (1975), comprises the following species: *Saukianda andalusiae* R. and E. Richter, *Perrector perrectus* R. and E. Richter, *Eops eo* R. and E. Richter, *Strenueva sampelayoi* R. and E. Richter, *Strenueva melendezi* Gil Cid and *Alanisia guillermoi* R. and E. Richter.

SYSTEMATIC PALAEOLOGY

'Class' Eocrinoidea Jaekel, 1918

Family Eocrinidae Jaekel, 1918

Genus GOGIA Walcott, 1917

Subgenus ALANISICYSTIS subg. nov.

Etymology. From Alanis (Seville), Spain, type locality.

Type species. *Gogia (Alaniscystis) andalusiae* sp. nov.

Diagnosis A subgenus of *Gogia*, characterized by single or partitioned epispires provided with external dome-like stereomic cover.

Discussion. *Alaniscystis* conforms with the diagnoses proposed by Sprinkle (1973) for the family Eocrinidae and the genus *Gogia*, except for the peculiar morphology of its epispires. While those of *Gogia* are single pore-like sutural openings surrounded by a prominent raised rim, those of *Alaniscystis* are commonly divided into two funnel-shaped hollows leading to a single or to paired internal pores and protected by an external dome-like stereomic cover or a pair of such covers.

Epithecal covering on epispires is known in several eocrinoids but none appears to be the same as that observed in *Alaniscystis*. In the type specimen of the Middle Cambrian *Acanthocystites briareus*, a thin lid – possibly on the plate interior (Sprinkle 1973) – with pores at opposite ends closes off the central part of each epispire (Ubaghs 1967), but other specimens assigned to this species by Fatka and Kordule (1984) do not show this feature (Fatka, personal communication). In the Lower Ordovician, *Rhopalocystis destombesi*, the existence of an external cover of minute plates over epispire pores has been reported (Ubaghs 1963). In other eocrinoids such as the Ordovician *Palaeocystites*, it is the plate epistereom itself that covers the epispires, which are therefore exposed only where the external plate surface has been eroded. But it is probably the calcitic cupolas protecting the humatipores of the diploporites *Holocystites* s.s. and *Pustulocystis* that the epispire covering of *Alaniscystis* most resembles, at least superficially.

Alaniscystis has an irregularly multiplated calyx and holdfast, more or less numerous epispires, spiralled brachioles (a feature found in some other species of *Gogia* but in no other echinoderms) attached separately or in groups to spout-like projections of modified calyx plates on the edge of the oral area, as well as an anal pyramid laterally located near the calyx summit. All these characters fit those of *Gogia*, indicating a close relationship with this genus. Still, with its peculiar and complex epispires, *Alaniscystis* stands apart from all known representatives of *Gogia*. It is unlikely that it could have evolved into one of them and probably represents an early offshoot from the main stock of *Gogia*. It is to mark at one and the same time its distinctiveness from, and its similarity to, *Gogia* that it is here considered as a subgenus of the latter.

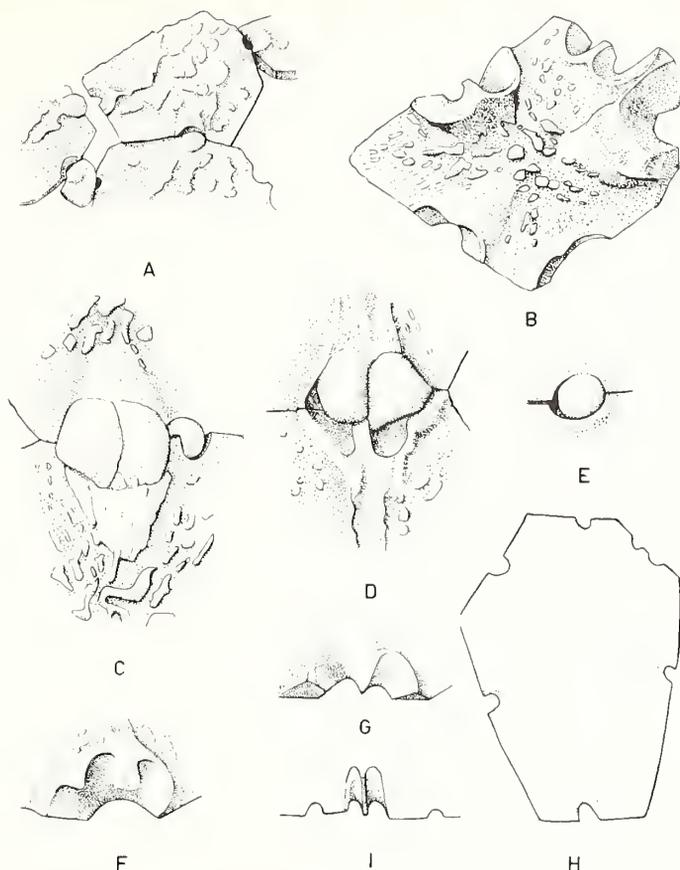
Gogia (Alaniscystis) andalusiae subg. et sp. nov.

Etymology. From Andalusia, a region of southern Spain, where this new species was discovered.

Holotype. Specimen VCE 24 (Pl. 1, fig. 7).

Diagnosis. A species of *Alaniscystis* with calyx probably globose; thecal plates relatively large and thick; showing pustulose and low ridged exterior ornament, epispires all over calyx or part of it, up to 12 per plate in large specimens; holdfast relatively short and distally inflated, composed of numerous small, unornamented plates; transition from calyx to holdfast abrupt; at least 6 or 7 brachioles, spiralled in right hand direction.

Material. Seven specimens (three with both part and counterpart) and isolated plates, all preserved as external moulds in a greenish shale and more or less distorted. Brachioles and holdfast still attached to the theca in three



TEXT-FIG. 1. Epispires of *Gogia (Alaniscystis) andalusiae* subg. et sp. nov., camera lucida drawings. A, VCE 11,1, thecal plates of a small specimen showing simple epispires (one cover missing). B-1, VCE 24; B, thecal plate with partitioned epispires, covers not preserved; C, paired covers and small simple (?incipient) epispire with cover on the right side; D, paired covers slightly displaced; E, small simple epispire with cover between two large plates; F and G, oblique view of epispires with partial and complete partition; H, smooth internal face of a plate, with slight markings associated with sutural openings (note the small size and feeble differentiation of these openings); I portion of internal edge of a plate, with simple and partitioned sutural openings. All figures approximately $\times 17.5$.

specimens, suggesting rapid burial at or near place of life. The specimens are numbered VCE 11,1-3, 23, 24, 25 and 26; they will be deposited in the collection of the Faculty of Sciences of the University of Madrid, Spain.

Description. Differences worthy of note may be observed between the smaller and the larger specimens. They mainly concern the shape of the theca, the relative size, complexity and distribution of the epispires, the ornamentation of the calyx plates and the aspect of the anal pyramid. They suggest the possibility of the existence of more than one species. Nevertheless, as the available material is small and variously preserved, it is dealt with below as representing a single taxon.

The specimens show a great diversity in size and thecal shape – the latter partly at least as a result of rock deformation. The calyces of the two smallest specimens (together on one slab and having the same orientation) are approximately twice as wide as high: VCE 11,1 (Pl. 1, fig. 1) is 6.6 mm wide and 3.9 mm high; VCE 11,2 (Pl. 1, fig. 4) is 6.1 mm wide and 2.9 mm high. The largest calyx (VCE 24; Pl. 1, fig. 7) is higher (11.2 mm) than wide (9.5 mm), but it is distorted. Its strong convexity suggests, however, that, like the calyx of the two smallest specimens, it was initially globose.

The calyx plates are relatively thick (up to 0.3 mm in larger specimens), polygonal, tessellated and irregularly arranged (Pl. 1, figs. 1, 4, 5). Their number per side is 18–25, suggesting an average of 35–50 plates for the whole calyx. The larger ones are located in the lower and middle portions of the theca (Pl. 1, figs. 1, 4, 7). In the smaller specimens, the calyx plates are slightly to moderately convex; in the larger ones, they have a slightly domed centre, but a few of the smaller plates are flat or even concave. They are rather coarsely ornamented. Those of the smaller specimens have irregular pustules, which become fainter towards the plate edges (Pl. 1, figs. 2 and 5), while those of the largest individual have vermiculate pustules concentrated on the upraised central area and passing to the periphery into low ridges which extend to the plate margins or meet the thickened apical portion of the prominent rim of the epispires (Pl. 1, fig. 9). Unlike the outer surface, the inner side of the calyx plates is smooth, but for faint markings associated with the sutural pores (text-fig. 1H).

The epispires are the most distinctive feature of the species. In the two smaller individuals, they are nearly or entirely lacking from one side of the theca (Pl. 1, figs. 4 and 5), while present on most plates of the other side, ranging from none to five per plate (Pl. 1, fig. 2; text-fig. 1A): most of them are 'U' shaped, small (0.2 mm wide), simple, with a raised rim thickened at the apex and provided with a hemispherical cap-like stereomic cover (not always preserved; text-fig. 1A). In the largest available specimen (VCE 24), the epispires seem to occur over the entire calyx, up to 12 per plate. They appear externally as conspicuous funnel-shaped sutural hollows, more than twice as large as those of the smaller specimens. They are surrounded by a powerful rim, with generally a prominent buttress-like thickening at the apex (text-fig. 1B–D). Their floor is rounded and smooth or it may comprise several shallow depressions (text-fig. 1B), but more commonly it is divided into two similar hollows by an internal partition which may be partial or complete. In the former case the epispire has a single internal pore (text-fig. 1F), in the latter case it has two contiguous internal openings (text-fig. 1G, I).

As stated above, each epispire has a conical or rounded cap-like cover, or a pair of such covers when the epispire comprises two separate compartments (Pl. 1, figs. 2, 7, 9; text-fig. 1C, D). These covers do not seem to be a mere continuation of the calyx plates, but rather distinct skeletal elements, apparently loosely connected to the calyx, for not infrequently they are displaced or altogether missing and, when missing, no trace of their attachment can be observed. They most certainly served to protect the presumed respiratory evaginations of the body wall that the epispires are said to have accommodated during life, but the question arises whether they could open and close, or whether they were permanently closed. In that case, gaseous exchange must have been effected through them, as it was through the calcified external surface of the tubercular humatipores of some diploporite cystoids (*Holocystites* s.s., *Pustulocystis*), which structures they somewhat resemble.

The partitioning of the epispires suggest that the soft organs they contained could branch, as do the papulae of some Recent asteroids. As to the internal pores, they are small and simple compared to the extended and complex external openings, though they generally show faint markings along their edges (text-fig. 1H). The occasional presence of small simple (?incipient) epispires in the largest plates, is noteworthy, and suggests that new epispires could still be added at a relatively late stage of plate development (text-fig. 1C, E).

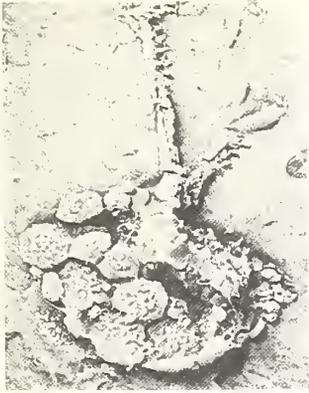
The transition from the calyx to the holdfast is abrupt. The best preserved holdfast (VCE 11,2) seems to be composed of a short (0.5 mm) and wide (1.6 mm) cylindrical proximal part, with about 10 plates across the width, and a distal expanded portion (2.9 mm largest diameter; Pl. 1, figs. 4 and 5). The holdfast is made of tiny unornamented, rounded plates (0.15–0.2 mm wide), slightly imbricating towards the distal end of the organ (Pl. 1, fig. 2).

The observed number of brachioles ranges from 5 (VCE 11,1) to 7 (VCE 24). None of these appendages is complete. The longest preserved one (VCE 24) is 27.5 mm, suggesting a brachiole:calyx length ratio equal or greater than to 2.5 to 3. The brachioles are spiralled in a clockwise direction: there are about 3 spirals in the longest observed brachiole; the spiralling in this, as in other brachioles of the same specimen, starts within

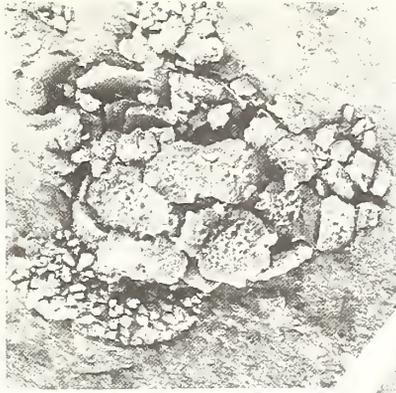
EXPLANATION OF PLATE I

Figs. 1–9. *Gogia* (*Alaniscystis*) *andalusiae* subg. et sp. nov. 1, 3 and 6, VCE 11,1, calyx and part of brachioles of a small specimen, $\times 6$; 3, anal pyramid (see text-fig. 3A), $\times 10$; 6, proximal portion of two brachioles, $\times 10$. 2, 4 and 5, VCE 11,2; 2, calyx and inflated distal portion of the holdfast (note presence of epispires on calyx plates) $\times 8$; 4 and 5, counterpart of the same small specimen and detail of calyx plates and holdfast (note absence of epispires on this calyx face), $\times 6$ and $\times 12$. 7, 8 and 9, VCE 24, holotype; 7, calyx (somewhat distorted) and brachioles (note spiralling of brachioles in clockwise direction; the arrow indicates the anal pyramid), $\times 4$; 8, portion of two brachioles (see text-fig. 2B), $\times 10$; 9, detail of calyx plates, $\times 8$.

All photographs are of latex casts whitened with ammonium chloride sublimate.



1



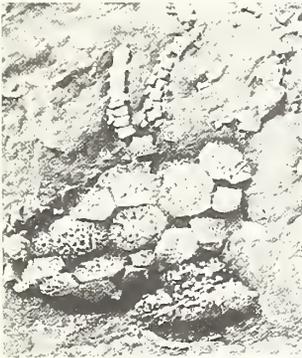
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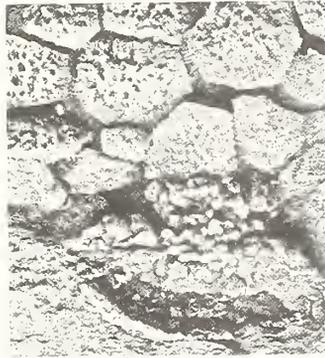
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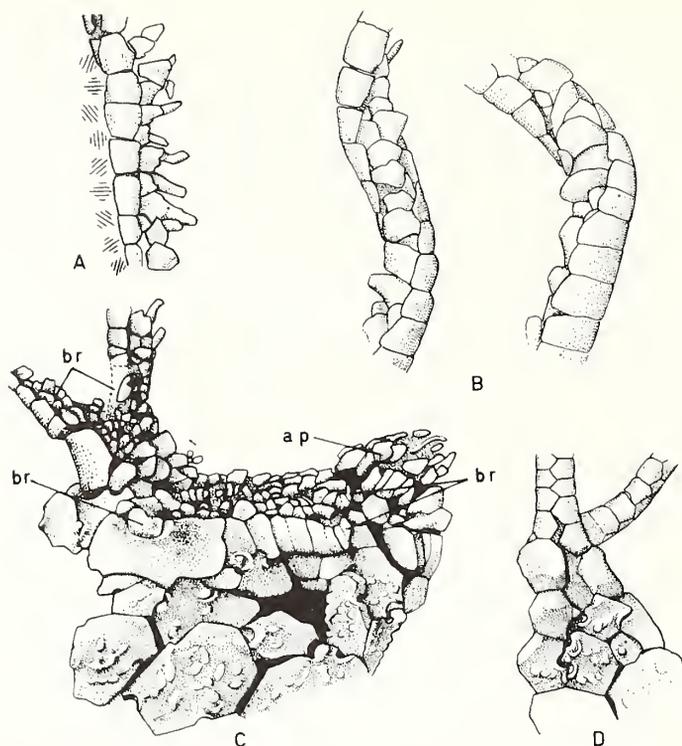


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9

UBAGHS AND VIZCAÏNO: *Gogia (Alanicystis) andalusiae* nov.

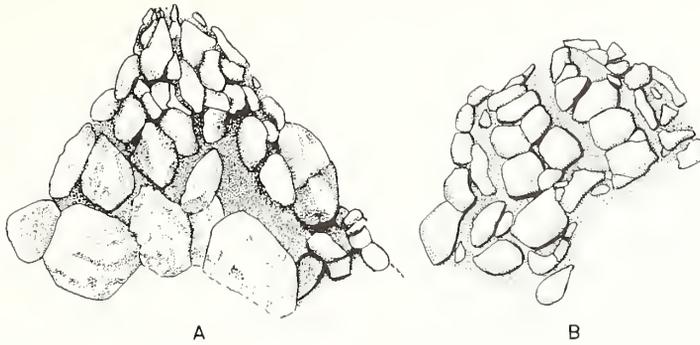


TEXT-FIG. 2. *Gogia (Alaniscystis) andalusiae* subg. et sp. nov., camera lucida drawings. A, VCE 11, *I*, portion of a brachiole, $\times 17.5$. B, VCE 24, portion of two brachioles (see Pl. 1, fig. 8) $\times 17.5$. C, VCE 11, *I*, calyx summit showing oral area, insertion and proximal portions of five brachioles (br) and anal pyramid (ap), $\times 12.5$. D, reverse view of the pair of brachioles on the left side of the preceding figure, $\times 12.5$.

2.3 mm of the calyx summit (Pl. 1, figs. 1, 6, 7). The brachioles taper very gradually. They are composed of unornamented brachiolar plates, about 15 on a side in 5 mm proximally and about 20 more distally (specimen VCE 24). Their ventral groove, as observed on the proximal portion of a brachiole, is wide and deep; it shows on its lateral walls an abrupt change of surface, possibly serving as the mounting area for cover plates. The latter are a little more numerous than the brachiolar plates, in a ratio of 7 or 8 to 5. There are apparently two sets of them, smaller ones alternating with larger ones (Pl. 1, figs. 6 and 8; text-fig. 2A, B). The latter, which slightly imbricate in distal direction, are as wide as the brachiolar groove, while the smaller ones cover only a part of it.

The brachioles are attached to unornamented spout-like calyx plates edging the relatively small oral area, either singly or in groups of 2 or 3 (Pl. 1, figs. 1 and 6; text-fig. 2C, D). Each brachiole is inserted on two thecal plates (text-fig. 2D), except possibly in the A ray (opposite the anus) where an apparently single large thecal plate bears only one attachment facet (text-fig. 2C). Neither the mouth nor the ambulacral grooves have been observed on the thecal summit, but the arrangement of brachioles around the oral area in specimen VCE 11, *I* – the only one to show this part of the calyx – suggests the existence of a single ambulacral groove in the A ray and of two lateral ones leading to a pair of brachioles on either side; such triradiate symmetry of the ambulacral system would certainly represent a very primitive condition.

The oral surface is paved with small (0.12–0.20 mm wide), unornamented irregular plates. On its very edge or slightly below it rises a relatively conspicuous anal pyramid. In the two smaller specimens (VCE 11, *I* and 2), the anal pyramid appears as a pointed structure (2.3 mm wide at base, 1.7 mm high in specimen VCE 11, *I*) made of rows of elongated convex plates of decreasing size towards the summit and ending in needle-shaped platelets (Pl. 1, fig. 3; text-fig. 3A). In the largest specimen (holotype), it looks like a truncated cone (1.7 mm wide at base, 1.5 mm high) composed of rows (6–7 on the exposed face) of subquadrate, convex plates converging towards the apex (possibly missing; Pl. 1, fig. 7; text-fig. 3B).



TEXT-FIG. 3. *Gogia* (*Alaniscystis*) *andalusiae* subg. et sp. nov., camera lucida drawings, anal pyramid. A, VCE 11,1, (see Pl. 1, fig. 3), $\times 17.5$. B, VCE 24 (see Pl. 1, fig. 7), $\times 17$.

Comparison. *Gogia* (*Alaniscystis*) *andalusiae* shows the same general organization as all known species of *Gogia*. In addition, it shares: 1. spiralling of brachioles (though in opposite direction) with *G. ojenai*, *G. spiralis*, *G. granulosa* and *G. guntheri*; 2. relative shortness and distal expansion of holdfast with *G. ojenai* and *G. goudi*; 3. abrupt transition of calyx to holdfast with *G. spiralis* and *G. radiata*; 4. coarseness of calyx plate ornamentation with *G. ojenai*, *G. granulosa* and some Poleta plates figured by Sprinkle (1973, pl. 25, figs. 9 and 19). On the whole, it is *G. ojenai* of late Lower Cambrian (Durham 1978), that it most resembles, for it has in common with this species characters 1, 2 and 4 just mentioned. It differs from *G. ojenai* by its complex and covered epispines, less sharply ridged calyx plate ornamentation, less numerous and clockwise (instead of anticlockwise) spiralled brachioles, and abrupt rather than gradational transition from calyx to holdfast. While assuredly a primitive echinoderm, *G. (Alaniscystis) andalusiae* has surprisingly sophisticated respiratory structures, suggesting an early appearance of advanced features among the cystoid pelmatozoans.

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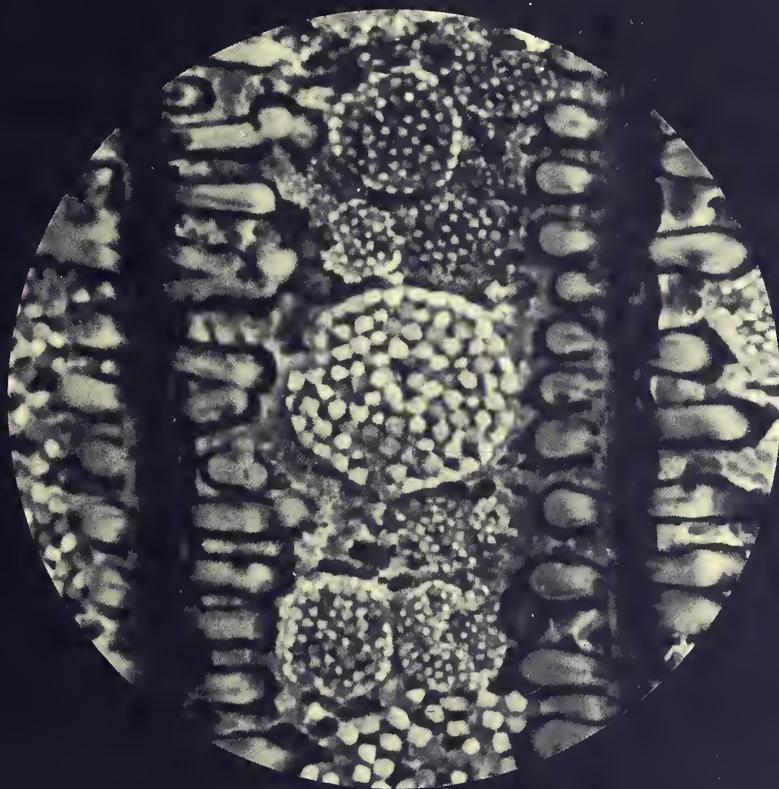
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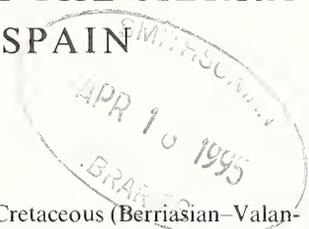
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LOWER CRETACEOUS SPIDERS FROM THE SIERRA DE MONTSECH, NORTH-EAST SPAIN

by PAUL A. SELDEN



ABSTRACT. Four new specimens of spiders (Chelicerata: Araneae), from Lower Cretaceous (Berriasian–Valanginian) lithographic limestones of the Sierra de Montsech, Lérida Province, north-east Spain, are described, as *Cretaraneus vilaltae* gen. et sp. nov., *Macryphantes cowdeni* gen. et sp. nov. (two specimens), and *Palaeouloborus lacasae* gen. et sp. nov. All belong to the infraorder Araneomorphae. *Palaeouloborus* is the oldest representative of the superfamily Deinopoidea, *Cretaraneus* is referred to the superfamily Araneoidea, and *Macryphantes* is the oldest record of the superfamily Araneoidea, family Tetragnathidae (metine–tetragnathine–nephiline group). All three spiders were web weavers; *Macryphantes* and *Palaeouloborus* wove orb webs, and may have used a wrap attack to prey on the abundant contemporaneous insect life preserved in the Montsech deposit.

SPIDERS are rare in rocks of Mesozoic age. Only two specimens, *Juraraneus rasnitsyni* Eskov, 1984, and *Jurarchaea zherikhini* Eskov, 1987, from the Jurassic of the USSR, have been adequately described. Three specimens from the Lower Cretaceous of New South Wales (Jell and Duncan 1986) and twelve from the Trias of France (Gall 1971) were not identified to a taxonomic rank below that of order. Spiders reported from Canadian Cretaceous amber (McAlpine and Martin 1969), the Jurassic and Cretaceous of Siberia and Mongolia (reported in Eskov 1984), and the Cretaceous of Botswana (Waters 1989) await description. The four specimens described here are sufficiently well preserved for their taxonomic affinities to be determined with some precision, and thus they represent only the third find of Mesozoic spiders to be described and named. The fossil spiders described here are placed in extant superfamilies or families, but closer assignation is considered unwise pending the outcome of current studies on living and fossil members of these groups.

GEOLOGICAL SETTING

Locality. The Sierra de Montsech lies in the foothills of the eastern Pyrenees, between Balaguer and Tremp in Lérida Province, north-east Spain (see Schairer and Janicke (1970) for details and location map). Three quarries in the vicinity of the abandoned village of Rúbies, in the eastern part of the sierra, yield remarkable fossils. ‘La Pedrera de Meià’ and ‘La Cabrúa’ have been worked for many years, and ‘El Reguer’ is currently under investigation.

Stratigraphy. The 50 m succession of limestones exposed in the quarries, the ‘Calcaires lithographiques à Plantes et Vertébrés de la Pedrera de Rúbies’, is a facies development of the 100 m ‘Calcaires à Charophytes du Montsech’ (Peybernes 1976). The deposit has been determined as late Berriasian to early Valanginian in age on the evidence of ostracodes (Peybernes and Oertli 1972; Brenner, Goldmacher and Schroeder 1974; Whalley and Jarzembowski 1985), a conclusion consistent with evidence from palynology (Barale *et al.* 1984; R. Porter, personal communication 1988).

Sedimentology. The Calcaires à Charophytes du Montsech is a sequence of mostly pale, fine-grained, thinly-bedded limestones. Sedimentary structures include laminations, fine grading, minor deformation, and roll marks; trace fossils include arthropod trackways (Schairer and Janicke 1970). The environment of deposition deduced from the sedimentological and palaeontological evidence

(see below) is that of coastal lagoons within a large area of algal flats separating marine conditions to the north from the Ebro continent to the south (Barale *et al.* 1984). The spider-bearing sequence, the Lithographic Limestones, represents a particularly tranquil lacustrine depositional episode (Lacasa and Martinez 1986).

History of the fauna and flora. The exceptionally preserved biota of the Montsech lithographic limestone has received attention from palaeontologists since the beginning of this century. In the last few years, renewed interest in the deposit has brought new material to light, including the specimens described here, and avian fossils of phylogenetic importance from a locality of similar age and lithology in the neighbouring province of Cuenca (Sanz *et al.* 1988). Lists of the fauna and flora were given by Barale *et al.* (1984), with the most recent summary, especially of the insects, provided by Lacasa and Martinez (1986). All the indigenous microflora is of terrestrial or non-marine aquatic provenance; the macroflora includes a wide range of gymnosperms, progymnosperms, a few ferns and horsetails, and other, unclassified, plants. Animals include ostracodes, few decapod crustaceans, larval and mature insects belonging to eight extant orders, a wide variety of fish, a few frogs and reptiles, and some bird remains. The spiders were first mentioned by Lacasa (1985, p. 228), and a preliminary report of the results presented here was given by Selden (1989).

MATERIAL AND METHODS

Preservation. The spiders are preserved on thin slabs of pale buff-grey limestone. Grains are not visible in the rock, and the hackly fracture and vitreous appearance under high-power microscopy suggest crystallization from a lime mud. Calcite-filled cracks cross some specimens. The spiders are preserved as pieces of cuticle on the bedding surface. The cuticle is brittle and brown: thicker parts are deep brown and the thinnest cuticle pale buff. The cuticle has not been chemically analysed; it is presumed still to be organic, but probably not of the original composition. The best-preserved parts are visible through a thin layer of translucent limestone, but their morphological details are hazy due to the presence of the overlying matrix. In such instances, 2–4% hydrochloric acid was used, sparingly and with care, to remove the matrix and thus to reveal fine structural details. The spiders are in varying states of original decay: for example in LC 1753 AP the podomeres, of leg 1 in particular, are crowded with subcircular objects along the central parts of the shaft. These objects are interpreted as the decayed remnants of muscles. LC 1754 AP is very poorly preserved: mainly a mould remains, and this is interpreted as a specimen in which decay has progressed further.

Both part and counterpart of specimens LC 1753 AP and LC 1754 AP are preserved, but only the part of specimens LC 1150 IEI and LP 1755 AP was collected. Specimens LC 1753 AP B, LC 1754 AP A, LC 1150 IEI, and LP 1755 AP represent lower slabs preserving mainly ventral features of the specimens; LC 1753 AP A and LC 1754 AP B are upper slabs with dorsal features. However, splitting of the rock has not resulted in perfect separation of dorsal and ventral, and due to the mode of preservation within the limestone (described above), most of both dorsal and ventral parts are preserved on LC 1753 AP B, and LC 1150 IEI. LC 1754 AP is mainly an external mould with little cuticle remaining, but on LP 1755 AP ventral parts of the body and both dorsal and ventral sides of the distal parts of the legs are preserved. On all specimens, the legs and abdomen (when present) are crushed flat. The carapace has sufficient convexity to produce relief in the fossils, so that on LP 1755 AP, for example, the carapace shape can be determined by the relief of the fossil, and the shapes of the sternum and coxae are outlined by setae and cuticle. The male palps of LC 1753 AP, LC 1754 AP, and LC 1150 IEI appear to occupy depressions in the matrix. This is probably because they were bulbous structures in life and therefore created a concavity in the sediment into which the palp collapsed during burial.

The spiders were studied under a Wild M7S stereomicroscope, with the specimens immersed in ethanol or glycerine to enhance their contrast against the pale rock background. Camera lucida drawings were made and photographs were taken under the same conditions. In addition, a Zeiss photomicroscope was used, in reflected light mode with oil immersion objectives, to view

and photograph details at higher magnifications. The computer program MacClade, version 2.1 (Maddison and Maddison 1987) proved very useful for exploring relationships.

Terminology. Setal terminology is somewhat problematical, since different authors have used the same terms in different ways. Furthermore, there is a complete gradation in size between setae (small, and may be short or long, thick or thin), bristles, and spines (large). Macroseta is a term used, for example by Opell (1979), to describe a large seta which could equally be called a small spine or bristle. The common hair-covering of *Cretaraneus* is the serrate seta, which is smooth apart from a few minute accessory spines which are no longer than the mean thickness of the seta (see Lehtinen 1967, fig. 10a; Kullmann 1972, fig. 7). Two fairly distinct setal types are commonly called plumose (e.g. by Forster and Wilton 1973; Forster and Blest 1979). The first, which is here called plumose, is generally thicker than the serrate seta, and has helical ridges bearing small accessory spines which are much shorter than the width of the seta (see Lehtinen 1967, fig. 8; Kullmann 1972, fig. 8). The second, which is here called feathery, is fine, smooth, and has long accessory branches which are much longer than the width of the seta (see Lehtinen 1967, fig. 9). Many other types of seta and spine exist; there may be complete gradations between them, and the extent of their phylogenetic importance is unknown.

Terminology of the sclerites of male palps differs between workers in different groups of spiders due to a lack of understanding of the homologies between the sclerites. Thus the task of recognizing palpal sclerites in fossil spiders is problematical. Useful descriptions of the constituent parts of male palpal organs are found in Comstock (1948), Levi (1961), Merrett (1963), and Millidge (1977).

In leg formulae (e.g. 1243), the leg lengths are ranked in order longest (first) to shortest (last). Abbreviations used in the text and text-figures are as follows:

ab	abdomen	l	labium	s	serrula
bo	book-lung operculum	lp	left palp	st	sternum
ca	cephalic area	m	maxilla	t	tegulum
cal	calamistrum	ma	median apophysis	ta	tarsus
ch	chelicera	mt	metatarsus	ti	tibia
cx	coxa	pa	patella	tia	tibial apophysis
e	embolus	pc	paracymbium	tr	trochanter
f	fovea	pe	pedicel		
fe	femur	rp	right palp		

Provenance and depository. Three of the fossil specimens, LC 1150 IEI, LC 1753 AP, and LC 1754 AP, come from the quarry of La Cabrúa, the fourth, LP 1755 AP, is from the locality of La Pedrera de Meià. Exact stratigraphical provenance is not known, but both of these localities are in the same 50 m sequence of lithographic limestones, the Calcaires lithographiques à Plantes et Vertébrés de la Pedrera de Rúbies, described above. The specimens are deposited in the Institut d'Estudis Ilerdencs, Lérida.

Preserved specimens of extant spiders were studied for comparative purposes, and in addition to those in the author's collection of mainly British species, the following specimens were examined. Uloboridae: *Hyptiotes flavidus*, female, Funchal, Madeira, M. J. Jones Collection No. 119, Manchester Museum; *Uloborus walckenaerius*, male and female, Chobham, Surrey, D. W. Mackie Collection No. G4999, Manchester Museum; *Philoponella* sp., male and female, Lake Naivasha, mature and immature males, Nairobi, Kenya, J. Murphy Collection Nos 1302, 1363. Deinopidae: *Deinopis guianensis*, female, British Guiana, British Museum (Natural History) (BM(NH)) No. 1939.3.24.228; *Deinopis stauntoni*, female, Durban, South Africa, BM(NH) No. 1903.8.20.1; *Deinopis* sp., female and immature, Kilifi, Kenya, J. Murphy Collection; *Menneus camelus*, females (types), Durban, South Africa, BM(NH) No. 1903.7.10.22; *Menneus* sp., male, Kitale, and female, Nairobi, Kenya, J. Murphy Collection; *Avella angulata*, female, Gayndah, Australia, BM(NH) No. 1919.9.18.5732; *Avella despiciens*, female, Sydney, Australia, BM(NH) No. 1919.9.18.5733.

Dictynidae: *Aebutina binotata*, immatures, Aguas Negras, near Tarapuy, Napo, Ecuador, British Museum (Natural History) Arachnid Collection.

SYSTEMATIC PALAEOLOGY

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder ARANEOMORPHAE Smith, 1902

Remarks. The phylogenetic scheme for the higher classification of spiders which is currently widely accepted originated with Pocock (1892). In this scheme, the Liphistiomorphae (Mesotheleae) is the sister group to the Opisthothelae (Mygalomorphae + Araneomorphae). The morphology of liphistiomorphs is distinctive (Platnick and Gertsch 1976, fig. 5). The fossil spiders described here differ markedly from this pattern, lacking one or more of the following liphistiomorph synapomorphies: posteromedian invaginations of the fourth coxae, seven or eight forwardly situated spinnerets, sclerite of the first abdominal segment (Platnick and Gertsch 1976), and labium as wide as or wider than the sternum (Raven 1985). Thus they are referred to the Opisthothelae.

Mygalomorph synapomorphies include the following external morphological features: cheliceral fang which operates in the sagittal plane (orthognathous), complete loss of expression of the anterior median spinnerets, three or four articles in the posterior lateral spinnerets (Platnick and Gertsch 1976), labial and maxillary cuspules, and reduced male palpal sclerites (Raven 1985). The alternative character states typify the Araneomorphae, and it is to this latter group that the Montsech spiders are referred. In particular, the chelicerae of *Cretaraneus* gen. nov. are labidognathous (i.e. they operate transversely); the male palp of *Macryphantes* gen. nov. is more complex than the mygalomorph palp; and *Palaeouloborus* gen. nov. possesses a calamistrum and a cribellum; the latter is a homologue of the anterior median spinnerets. Neither labial or maxillary cuspules nor three- or four-segmented posterior lateral spinnerets are known in any of the Montsech spiders, and each of them shows greater affinity to araneomorph families than to mygalomorphs.

Assignment of the Cretaceous spiders to lower taxonomic categories presents greater difficulty. A competent araneologist can place most living spiders seen in the field into a family with a high degree of certainty. Even in the absence of field characters, such as web type and habitat, spider familial keys are relatively straightforward, only requiring the use of a binocular microscope and normally no dissection. Spider families are diagnosed on unique combinations of morphological characters such as number and position of eyes, spinneret pattern, and number of tarsal claws. However, research has shown that many of the characters on which the families are based are plesiomorphic at higher taxonomic levels, convergent with other groups, or are 'loss' characters (Lehtinen 1978). A classic example of this is the recognition of the cribellum as a synapomorphy for Araneomorphae: its presence in lower categories is merely the expression of the plesiomorphic state, and its absence illustrates convergence of the apomorphy in many araneomorph families. Whilst unique combinations of plesiomorphies may work as familial descriptions in practice, they cannot reflect true relationships between families. Of necessity, therefore, recent cladistic analyses have sought new or previously overlooked characters as apomorphies. These characters are commonly behavioural or anatomical, and may be poorly known in groups outside those under particular study. More important in the present work, such characters are most unlikely to be preserved in the fossil record.

An additional concern encountered when working with rare fossils which have Recent relatives arises from the possibility that the fossils may be ancestors of Recent species. Should the fossils be classified in the same scheme as their Recent relatives, or in a separate scheme? Such problems have been discussed by Crowson (1970), Farris (1976), Wiley (1981) and others. A useful device for classifying fossils with their Recent relatives is the plesion (Patterson and Rosen 1977); this presupposes, however, that the Recent classification is soundly based on shared derived characters.

In spider systematics this is not yet true. In this paper, the new taxa are classified as close as possible to their presumed position in the Recent classification. Inevitably this entails placement within taxa yet to be defined by synapomorphies or defined on shared derived characters which cannot be seen easily in fossils. Because these are among the first Mesozoic spiders to be described, and because of the paucity of diagnostic features in the fossils, and the present lack of knowledge of synapomorphies in living families, the fossil spiders are assigned to superfamilies, and in one case to a family, but to no extant lower taxa. (Note that among Cretaceous insects, classification to modern genera is not unusual.) More specimens of Mesozoic spiders which are becoming available for study may help to elucidate further the taxonomic positions of the specimens described here, and assist in unravelling the complexities of spider phylogeny and evolution. The 'consensus' spider classification scheme given in Shear (1986b) is followed here in general, but with discussion concerning the status of groups assigned to the Araneidae following recent work by Coddington (1989a, b, 1990).

Superfamily DEINOPOIDEA Koch, 1851

Remarks. This superfamily consists of the two cribellate families Uloboridae and Deinopidae, which weave orb webs (most Uloboridae) or spin modified orb webs which are then thrown, *retiaris*-like, at their prey (Deinopidae). Much more is known about uloborids than deinopids, though work on the latter is currently in progress. Although these two families have been considered closely related for nearly a century (Simon 1892), Coddington (1986, p. 359), with reference to his cladogram (p. 358), remarked that: 'the monophyly of the uloborid-deinopid lineage is based on only three characters, primarily because so little is known about deinopids.' The three characters Coddington accepted as deinopoid synapomorphies are: puffed cribellate silk, pseudoserrate plumose hairs, and fourth-tarsal macrosetae; however, he qualified this by suggesting that the first two characters may actually be synapomorphies for all orb-web weavers (Deinopoidea and Araneoidea) (Coddington 1986, pp. 327, 359). Recent work by Coddington (1989a, b, 1990) has resolved the apparent trichotomy between Araneoidea, Uloboridae, and Deinopidae (reported in Platnick 1986); Deinopoidea and Araneoidea being seen as sister groups in a monophyletic group of orb-web weavers: the Orbiculariae Walckenaer, 1802.

Palaeouloborus gen. nov., described below, possesses three tarsal claws with accessory claws typical of web weavers and lacks the tarsal adaptations of the superfamilies Thomisoidea, Philodromoidea, Lycosoidea, Clubionoidea, Salticoidea, and Pholcoidea. The fossil genus also lacks the synapomorphies of Scytodoidea (Lehtinen 1986), Dysderoidea (Forster and Platnick 1985), Palpimanoidea (Forster and Platnick 1984), Hersilioidea, Hypochiloidea (Platnick 1977), Eresoidea, and Agelenoidea. Dictynoidea are cribellates, and the deinopoid families have, at one time or another, been referred to this superfamily, and to the family Dictynidae in particular. However, dictynids are generally small spiders, with short legs of approximately equal length, and lack femoral trichobothria (see below); thus they are quite unlike *Palaeouloborus*.

The characters which are most useful in placing *Palaeouloborus* are: femoral trichobothria on legs 2, 3, and 4, leg 1 more than five times the length of the carapace and more than twice the length of leg 3, all leg tarsi with large accessory claws and apparently non-pectinate paired claws, presence of calamistrum and cribellum, and presence of plumose hairs.

Femoral trichobothria occur in only two groups of araneomorph spiders: the metine-tetragnathine lineage of the superfamily Araneoidea, and the family Uloboridae (Opell 1979; Lehtinen 1980; Levi 1980, 1981). In both of these groups there is great disparity in length between the elongate anterior legs (1 and 2) and the short third pair (Pl. 2, fig. 9), a feature also found in some other Araneoidea (Argiopinae, Levi 1983). *Palaeouloborus* is cribellate, and since only the Deinopoidea, but not the Araneoidea, are cribellate, this genus must be referred to the former superfamily. The calamistrum of *Palaeouloborus* is situated in a curved depression on the superior surface of the fourth metatarsus. Such a curvature occurs in uloborids (Pl. 2, fig. 10), to a much lesser degree in deinopids (Shear 1986a), and also in *Aebutina*, a poorly known genus tentatively referred to the Dictynidae (only females and immatures of this genus are known). Additionally,

Palaeouloborus bears plumose setae, which are found in Deinopoidea but not Araneoidea. The characteristic tarsal macrosetae of deinopoids (see below) appear to be absent from *Palaeouloborus*.

Palaeouloborus is referred to the superfamily Deinopoidea, on the evidence given above. The fossil clearly resembles members of the family Uloboridae more closely than the Deinopidae; the latter family has many autapomorphies (e.g. forwardly directed, enlarged, posterior median eyes, elongate legs all of a similar length, web-throwing) and lacks the femoral trichobothria typical of the Uloboridae and the fossil genus.

The position of *Palaeouloborus* within the Deinopoidea is now discussed. In a recent revision of the Uloboridae, Opell (1979) gave the following characters as diagnostic of the family: (1) lack of poison glands, (2) cribellate orb-web weavers, (3) femoral trichobothria, and (4) row of macrosetae (short spines) on metatarsus and tarsus of leg 4. The tarsal spines cannot be a synapomorphy for the Uloboridae since they also occur in Deinopidae (see below). Coddington (1986) added characters of the silk-glands described by Kovoor (1977), and some behavioural traits, to the list of uloborid synapomorphies, but omitted femoral trichobothria. Coddington's cladograms (1986, p. 358; 1989b, fig. 108) show the metine-tetragnathines, which also have femoral trichobothria, far from the dichotomy of Araneoidea with Deinopoidea, which presumes that femoral trichobothria are a convergent phenomenon in uloborids and metines-tetragnathines. The alternative hypothesis (that they are a synapomorphy for all orb-web weavers) would require their loss in many separate lines.

The row of tarsal and metatarsal macrosetae of uloborids was considered to be a synapomorphy of the family by Opell (1979), but in a later paper, Opell (1982) mentioned finding a poorly developed row on leg 4 of deinopids as well. My own observations confirm that macrosetae are present on the inferior surfaces of the distal half of the metatarsus and the tarsus of leg 4, and to a lesser extent on leg 3, in the deinopids *Deinopis*, *Menneus*, and *Avella*. These macrosetae are rather similar to the comb of serrate bristles seen in the Theridiidae in a similar position on the legs. However, they differ from theridiid bristles in being plumose, not serrate. As in the theridiids, they may need to be searched for, since they blend into the general hirsuteness of the tarsus. The macrosetae are not greatly different from the curved bristles normally present on the inferior surface of the distal end of the tarsus. Also, as in theridiids, they are not strictly confined to mt4 and ta4, also being present on leg 3, and they vary from species to species. In all the deinopids I studied they were quite unlike the comb of short, upstanding spines of the uloborid *Zosis geniculatus* illustrated by Opell (1979, pl. 1, figs. A and C). Rather, they resemble the row of macrosetae of the uloborid *Hyptiotes cavatus* figured by Opell (1982, pl. 1, fig. C). The similarity between theridiids and deinopids in this feature is presumably due to convergence in their prey-wrapping strategies rather than synapomorphy. Clearly, a comb of macrosetae on the fourth leg is a derived character of uloborids and deinopids which is not present in *Palaeouloborus*.

The legs of uloborids bear fine feathery setae amongst the normal setae; neither deinopids nor *Palaeouloborus* bear them.

Palaeouloborus cannot be included in the family Uloboridae because it has neither feathery setae nor fourth tarsal macrosetae. The fossil lacks the many specializations of the deinopids, and in addition the fourth tarsal macrosetal comb is absent. Rather than redefining the family Uloboridae to accommodate the fossil genus, it is left here within the superfamily Deinopoidea, closer to the Uloboridae than the Deinopidae, but not placed in either family. This placement indicates that the loss of a fourth tarsal macrosetal comb is autapomorphic for the fossil genus.

Genus PALAEOULOBORUS gen. nov.

Derivation of name. Greek, *palaios*, old, and the living genus, *Uloborus*, which the fossil genus resembles.

Type and only known species. *Palaeouloborus lacasae* sp. nov.

Diagnosis. Deinopoid with ovate carapace bearing marked break of slope separating anterior of carapace from sloping posterior area; leg 1 more than five times length of carapace and more than twice length of leg 3; many trichobothria on superior ?retrolateral surface of femur of leg 2 and superior ?prolateral surfaces of femora of legs 3 and 4; paired tarsal claws small, without teeth, median claw long, without teeth, pair of large accessory claws; superior surface of metatarsus of leg 4 in gentle S-shape, proximally convex and then concave, straightening out about half-way along podomere, bearing calamistrum which becomes row of curved bristles towards distal end of podomere; plumose setae present. Row of macrosetae absent from fourth tarsus.

Palaeouloborus lacasae sp. nov.

Plate 1; Plate 2, figs. 1–5, 7, 8, 10; text-fig. 1

Derivation of name. After Antonio Lacasa-Ruiz, palaeontologist at the Institut d'Estudis Ilerdencs, Llérida, Spain.

Type specimen. Holotype LP 1755 AP, from the quarry of La Pedrera de Meià, Sierra de Montsec, north-east Spain, and held in the collections of the Institut d'Estudis Ilerdencs, Llérida, Spain.

Diagnosis. As for the genus.

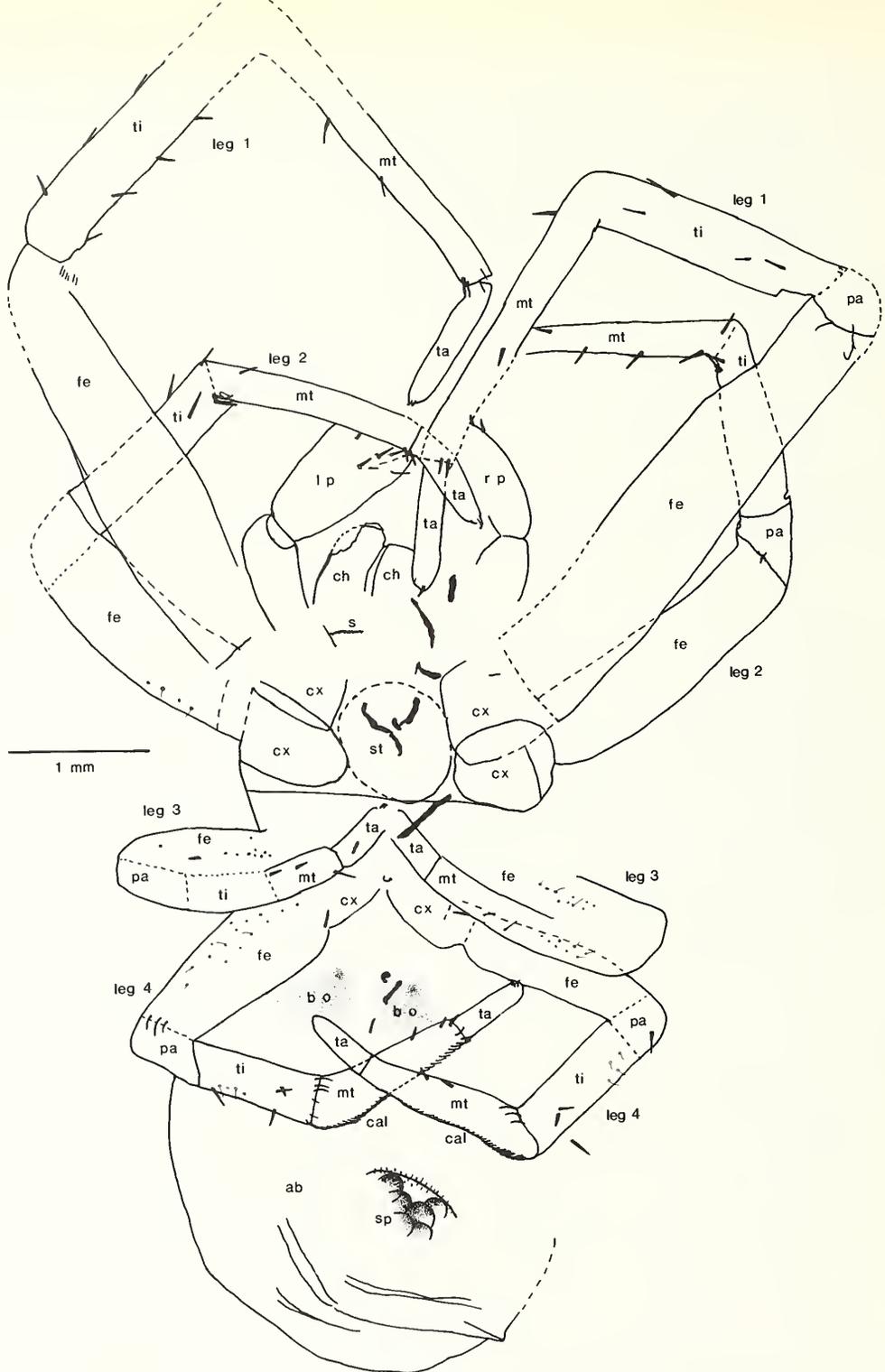
Description. The carapace shape is determined from fragments of cuticle and from the relief of the matrix. The scraps of cuticle preserved in the carapace region mainly represent coxae and sternum. However, on the left side between legs 2 and 3, cuticle of the carapace edge can be seen lying in a depression caused by pressure of the edge into the matrix. Faint traces of cuticle from the posterior edge of the carapace can also be discerned between the tarsi of legs 3. These cuticle remnants and the faint depression formed by the carapace margin suggests an ovate carapace with a truncated anterior margin. The carapace is 1.73 mm long, and 1.50 mm wide. It is widest just posterior to its midpoint. There does not appear to be a well defined cephalic area, nor an obvious fovea. There is a marked transverse break of slope just posterior to the widest part of the carapace and separating the raised foveal region from the backwardly sloping posterior part of the carapace. This slope is found in some living spiders (e.g. the uloborid *Philoponella*, Pl. 2, fig. 8), and accommodates an abdomen which extends forwards beyond the pedicel. Eyes not seen, no obvious tubercles.

The chelicerae are large, 0.67 mm long, and 0.33 mm wide, and somewhat forwardly directed, with parallel sides. The fangs cannot be seen, since the anterior edges of the chelicerae are obscured by overlying matrix.

The palps are clothed with setae, and short spines occur on the superior surface of the tarsus. The tarsus is oval, indicating that it was tumid in life. The distal end is not seen, so the presence of a claw cannot be confirmed. The specimen is therefore not a mature male, and could be an immature or a female. Very little of the basal parts of the palp can be seen, but superimposed on the anterior part of the carapace area is a dark line which, under high magnification, is seen to be serrate (Pl. 2, fig. 1). This is interpreted as the serrula of the left maxilla; cuticle is absent where the serrula of the right maxilla would have been preserved.

The leg formula is 1243. The coxae measure approximately 0.58 mm long, and the trochanters 0.18 mm. Lengths of the more distal podomeres, in mm, are as follows: leg 1: fe 3.27, pa 0.77, ti 1.64, mt 2.50, ta 0.96, total 9.14; leg 2: fe 2.11, pa 0.48, ti 1.35, mt 1.44, ta 0.77, total 6.15; leg 3: fe 1.35, pa 0.48, ti 1.06, mt 0.48, ta 0.48, total 3.85; leg 4: fe 1.64, pa 0.48, ti 0.87, mt 1.25, ta 0.52, total 4.76.

The legs are clothed with setae of the plumose type. Under high magnification, they are seen to bear a sculpture of striations arranged in a helical pattern, with abundant, minute serrae (Pl. 2, fig. 7). No feathery setae can be seen on the legs. The femora are only sparsely setose, setae and bristles becoming more abundant on distal parts of the legs. Groups of trichobothria are certainly present on the femora of legs 2–4, and on the tibia of leg 4. These trichobothria are not feathered (Pl. 2, fig. 2). Isolated trichobothria are more difficult to see, and their presence elsewhere on the legs cannot be confirmed. The leg spines are not large, and because only part of the specimen is preserved, the numbers of spines given below are not the maximum number which may be present on the legs. All tarsi are spineless, and bear two small, non-pectinate paired claws, a large median claw which appears to be non-pectinate or if pectinate then with only minute teeth, and two large accessory claws (Pl. 2, fig. 3). Fe1 bears few setae, mainly on the inferior surface (where they are curved) and on the superior surface, especially proximally and distally. Trichobothria may be present on fe1 (two possible trichobothrial bases can be seen on fe1 on the right side) but cannot be confirmed. Fe1 and pa1 are spineless.



TEXT-FIG. 1. *Palaeouloborus lacasae* gen. et sp. nov., holotype, LP 1755 AP. Explanatory drawing for Pl. 1. See Terminology for explanation of abbreviations.

EXPLANATION OF PLATE 1

Palaeouloborus lacasae gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain. LP 1755 AP, whole specimen, lower slab, under ethanol, $\times 21$. See text-fig. 1 for explanation.



SELDEN, *Palaeouloborus*

Ti1 bears four inferior spines and three superior spines along the shaft of the podomere, one proximal lateral spine, one lateral subdistal spine, and one superior subdistal spine. Mt1 bears three inferior and two lateral spines down the shaft of the podomere. Proximally, mt1 bears one superior, one lateral, and one inferior spine, and two inferior distal spines are present. Fe2 is spineless and bears few setae, principally on the inferior and superior surfaces. Both second femora are poorly preserved, but a few trichobothrial bases can be seen proximally, apparently on the retrolateral surface. Pa2 is spineless. Ti2 bears bristles proximally and along the inferior surface. Ti2 bears two inferior distal spines, one lateral subdistal spine, one superior subdistal spine, and one superior distal spine. More spines are probably present on ti2 but on both sides of the specimen this podomere is crossed by the large femur of leg 1, which obscures the mid-sections of ti2. Mt2 is very setose, and bears bristles, especially along the inferior surface. Mt2 bears superior and inferior proximal spines, two median inferior spines, and one lateral and two inferior distal spines. Fe3 bears few setae, one tiny spine laterally, and many trichobothria (probably 20–40 in life) over a large area of the ?prolateral surface. Pa3 is spineless. Ti3 is poorly preserved on both sides of the specimen, but bears many bristles. Mt3 bears two short inferior spines and one lateral distal spine. Fe4 is spineless, bears strong, curved bristles distally, and many trichobothria (as many as on fe3) over a large area of the superior, ?prolateral surface. Pa4 bears large bristles laterally. Ti4 bears one superior proximal spine, and prolateral, retrolateral and superior spines subdistally. Ti4 bears about four trichobothria on the proximal superior surface, and long, curved bristles distally. The superior surface of mt4 follows a gentle S-shape, proximally convex and then concave, before straightening out about half-way along the podomere. The superior surface of mt4 bears a calamistrum composed of curved setae, apparently in one row, running from the proximal end of the podomere for about two-thirds of its length, where it passes indistinctly into a row of curved bristles which continues to the distal end of the podomere (Pl. 2, figs. 5 and 8). Mt4 bears two short inferior median spines, at least two very short spines inferodistally, and large bristles distally.

The abdomen measures 3.67 mm long, and 2.89 mm wide. It is ovate, wrinkled posteriorly, and compressed to the right, indicating that it was globose in life. The abdomen is sparsely setose, the setae becoming thicker, but not longer, posteriorly, where they show their plumose structure under high magnification (Pl. 2, fig. 7). A pair of subtriangular areas of darker cuticle, each with a small dark patch anteriorly, is situated at the anterior end of the abdomen. These are interpreted as book-lung opercula. Three pairs of spinnerets are visible in the posterior half of the abdomen. They are compressed to the right. Their position indicates that they were not terminal, but ventral, in position in life. A recurved line immediately anterior to the anterior pair of spinnerets represents the cribellum. Little detail can be discerned because the cribellar plate is not preserved (this is presumably on the counterpart), only the fold of cuticle anterior to the plate. (In living spiders the cribellum is commonly invaginated into a fold in front of the spinnerets when not in use, see Pl. 2, fig. 6.) Along this fold there are numerous short, blunt setae of a type not seen elsewhere on the spider (Pl. 2, fig. 4).

Superfamily ARANEOIDEA Latreille, 1806

Remarks. *Cretaraneus* gen. nov. and *Macryphantes* gen. nov., described below, are assigned to this superfamily. Both genera lack a calamistrum and cribellum. This does not, by itself, exclude them

EXPLANATION OF PLATE 2

- Figs. 1–5, 7, 8. *Palaeouloborus lacasae* gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsec, Lérida Province, Spain, LP 1755 AP, oil immersion. 1, Serrula of left maxilla, bristle at left end, $\times 240$. 2, Femoral trichobothria, $\times 150$. 3, Claws on distal end of tarsus of left leg 4; note long median claw and accessory claws, $\times 100$. 4, Spinnerets: anterior pair (at top), median pair, and posterior pair (part); recurved line of short setae (seen at left) in front of anterior spinnerets mark approximate position of cribellum; compare with fig. 6, $\times 85$. 5, Proximal part of metatarsus of right leg 4, showing curvature of superior surface with calamistrum; note long, curved bristles at distal end of tibia (bottom left); compare with fig. 10, $\times 60$. 7, Plumose seta, $\times 625$. 8, Distal end of metatarsus of left leg 4, showing calamistrum (overlying tarsus of right leg 4, on right) terminating in row of curved bristles to left, $\times 85$.
- Figs. 6, 9, 10. *Philoponella* sp., Lake Naivasha, Kenya; J. Murphy Coll. No. 1363, under ethanol. 6, Ventral view of posterior end of abdomen of immature male, showing spinnerets and cribellum in front, $\times 36$. 9, Left lateral view of immature male, $\times 13$. 10, Metatarsus of right leg 4 of mature female, showing curvature of superior surface with calamistrum, $\times 50$.



1



2



3



4



5



6



7



8



9



10

from a cribellate superfamily because mature males of many living cribellate genera commonly abandon web weaving with the concomitant degeneration of the cribellum and calamistrum, and the preserved specimens of both genera are mature males. However, evidence is presented below that *Cretaraneus* and *Macryphantes* show greater resemblance to araneoids than to any cribellate group. Tarsal adaptations (two claws, scopulae, tarsomeres, etc.) for cursorial, saltatorial, and other specialized locomotory habits, as found in the superfamilies Lycosoidea, Clubionoidea, Philodromoidea, Salticoidea, Thomisoidea, and Pholcoidea, are not found in *Cretaraneus* or *Macryphantes*, so referral of the fossil genera to any of these superfamilies is rejected. *Cretaraneus* and *Macryphantes* also lack the synapomorphies of Scytodoidea (Lehtinen 1986), Dysderoidea (Forster and Platnick 1985), Palpimanoidea (Forster and Platnick 1984; but see Archaeidae, below), and the superfamilies Hersilioidea, Dictynoidea, Hypochiloidea, and Agelenoidea.

Until recently, few strong synapomorphies could be mustered to support the monophyly of the superfamily Araneoidea (Coddington 1986). Those characters suggested by Coddington (1986) as araneoid synapomorphies (aggregate and flagelliform glands, paracymbium, serrate hairs, web construction technique) are not only difficult or impossible to see in fossils but also have yet to be thoroughly checked in many extant spiders both within and outside the superfamily. The problem of defining the Araneoidea was highlighted by Millidge (1988), in a discussion of the position of the Linyphiidae. He pointed out that the term 'paracymbium' covers a number of different morphological features on male palps in araneoid and some non-araneoid families, so this character should not be treated as a synapomorphy for the Araneoidea. He also argued that the sticky microdroplets present on the webs of some linyphiids are not produced by the same type of gland (aggregate glands) as in other araneoids, but may be more closely related to the sticky microdroplets found on agelenid webs. Millidge (1988) concluded (on the basis of other evidence as well as that reported here) that the Linyphiidae should be removed from the Araneoidea, and that the superfamily itself may be an unnatural grouping of families which merely share a lack of synapomorphies of other superfamilies. Millidge's arguments have not been accepted by Coddington (1990). Recent work by Coddington (1989a, b, 1990) has amassed a great deal more evidence supporting the monophyly of Araneoidea, including characters of the labium and the spinnerets.

Cretaraneus and *Macryphantes* are assigned to the superfamily Araneoidea. Cladistic analyses of the families within the Araneoidea were attempted by Heimer and Nentwig (1982) and Coddington (1986, 1989b, 1990). Shear (1986b) included the following major families in the Araneoidea: Theridiidae, Nesticidae, Linyphiidae, Araneidae (including Nephilinae, Metinae and Tetragnathinae), Theridiosomatidae, Symphytognathidae, Mysmenidae, and Anapidae. The latter four have synapomorphies (Forster and Platnick 1977; Platnick and Shadab 1978a, b; Coddington 1986) which are seen in neither *Cretaraneus* nor *Macryphantes*, so these families can be discounted. The familial status of Tetragnathidae is discussed below, under that family. The placement of *Cretaraneus* will be discussed first, followed by that of *Macryphantes*.

The following characters of *Cretaraneus* suggest the superfamily Araneoidea: broad, pyriform carapace lacking a distinct fovea, presence of a raised cephalic area, globose abdomen, three foot-claws with associated serrate bristles, serrate hairs, lack or paucity of trichobothria, paracymbium on the male palp, labium wider than long, and spinnerets in a compact group.

Members of the families Theridiidae and Nesticidae possess a comb of serrate setae on the inferior side of the fourth tarsus. Such a feature cannot be seen on *Cretaraneus*, but since the serrate setae are not always present, or not obviously serrate, in smaller species of living theridiids, the lack of this feature in the fossil genera does not necessarily exclude them from the Theridiidae. Levi and Levi (1962) gave as a diagnostic character for the Theridiidae, chelicerae with up to three teeth on the outer margin and rarely one to three teeth or denticles on the inner margin; *Cretaraneus* has more cheliceral teeth than this. One feature of *Cretaraneus* which suggests a link with the Theridiidae (but not the Nesticidae) is the labium which appears not to be rebordered. Palpal characters in *Cretaraneus* are not sufficiently distinct to suggest any particular araneoid family; although the simplest palps in the Araneoidea occur in the Theridiidae (Levi 1961), and the

Cretaraneus palp appears to be relatively simple for an araneoid, palps are variable within spider families. Therefore *Cretaraneus*, though apparently lacking a comb of serrate setae on the fourth tarsus, cannot be excluded with confidence from the Theridiidae.

Stridulatory ridges are commonly present on the chelicerae of male linyphiids, but may be obscure in some species, and the labium is usually rebordered. Neither stridulatory ridges nor a rebordered labium is seen in *Cretaraneus*. A link between *Cretaraneus* and linyphiids is provided by the raised cephalic area, a feature common in linyphiid males. However, a presumed lateral condyle on the chelicera and accessory tarsal claws (serrate bristles) are features not found in the Linyphiidae, but characteristic of the Araneidae.

The rotation of the male palpal sclerites in some Araneidae mentioned by Levi (1983) cannot be confirmed in *Cretaraneus* because of the rotation produced during fossilization, although the general appearance of the palp in the fossil genus is not reminiscent of the araneid palp. The apparent presence of a median apophysis in the palp of the fossil may provide information on its placement, but at present this character is unresolved (Coddington 1989*b*). The wide labium, presumed cheliceral condyle, and accessory tarsal claws of *Cretaraneus* are characteristic of most araneoids (Levi 1980). The rather large, forwardly directed chelicerae, and relatively simple palp of *Cretaraneus*, suggest the metine–tragnathine lineage, but the fossil lacks other characteristics of this group, and mature males of some linyphiids also possess enlarged chelicerae. Male palps with a superficially simple appearance are characteristic of the genus *Nephila* (Schult 1983), but *Cretaraneus* bears few other similarities to the genus.

The Jurassic spider *Juraraneus rasnitsyni* Eskov, 1984 was placed in a monospecific family, the Juraraneidae Eskov, 1984. Eskov (1984) defined the family on a unique combination of araneoid characters and could find no apomorphies for the family. *Cretaraneus* resembles *Juraraneus* in many ways, including: overall size and shape; leg (but not tarsal) lengths; approximate shapes of sternum, labium, and maxillae; general shape of chelicerae. *Cretaraneus* differs from *Juraraneus* in lacking the irregular group of denticles on the inner margin of the chelicera, and the palpal characters interpreted by Eskov (1984) as a large, hook-like paracymbium, a large, pointed median apophysis, and a long, straight conductor (= embolus?).

The family Archaeidae is included in the Araneoidea by many arachnologists but, in a radical revision of archaeids and some other small families (for example Mimetidae, previously always placed in Araneoidea), Forster and Platnick (1984) removed them to the Palpimanoidea. They also created the monogeneric families Pararchaeidae and Holarchaeidae for genera previously included in the Archaeidae. Forster and Platnick (1984, p. 99) proposed two synapomorphies for the superfamily Palpimanoidea: cheliceral peg-teeth (modified setae as opposed to cuticular teeth), and an elevated cheliceral gland mound. They also mentioned that peg-teeth are found in some unrelated thomisoid and scytodoid genera, as convergent phenomena, and have been secondarily lost in members of six families assigned by them to the palpimanoids. *Cretaraneus* possesses true teeth on the chelicerae, but is mentioned here because of some similarities with the Pararchaeidae. The Pararchaeidae differ from the other palpimanoids in having serrate, rather than plumose, hairs, and show similarity with *Cretaraneus* in the enlarged chelicerae with a prominent keel and large bristles, the pectinate paired foot-claws, uncinat median claw, serrate bristles and lack of an onychium on the tarsus. A cheliceral keel is also found in other groups, for example the Leptonetidae (Gertsch 1974). The male palp of pararchaeids has a strongly developed embolus and a large tegular plate (Forster and Platnick 1984, p. 70), features also apparent in the palp of *Cretaraneus*. It is possible, therefore, that some relationship exists between *Cretaraneus* and the Pararchaeidae, which may or may not be an araneoid family. An archaeid spider has been described from the Jurassic (Eskov 1987).

Since it seems impossible to refer *Cretaraneus* to an araneoid family, there are two available options. First, a new, monospecific family could be defined to accommodate *Cretaraneus*. This course of action would be difficult, given the lack of specialized features displayed by the fossil, and would not provide any additional phylogenetic information. The second option, and the one chosen here, is to leave the genus unplaced within the superfamily Araneoidea. It is possible that future

discoveries will reveal that *Juraraneus* and *Cretaraneus* belong to the same group of Mesozoic araneoids.

Genus *CRETARANEUS* gen. nov.

Derivation of name. Latin *creta*, chalk, and *araneus*, a spider.

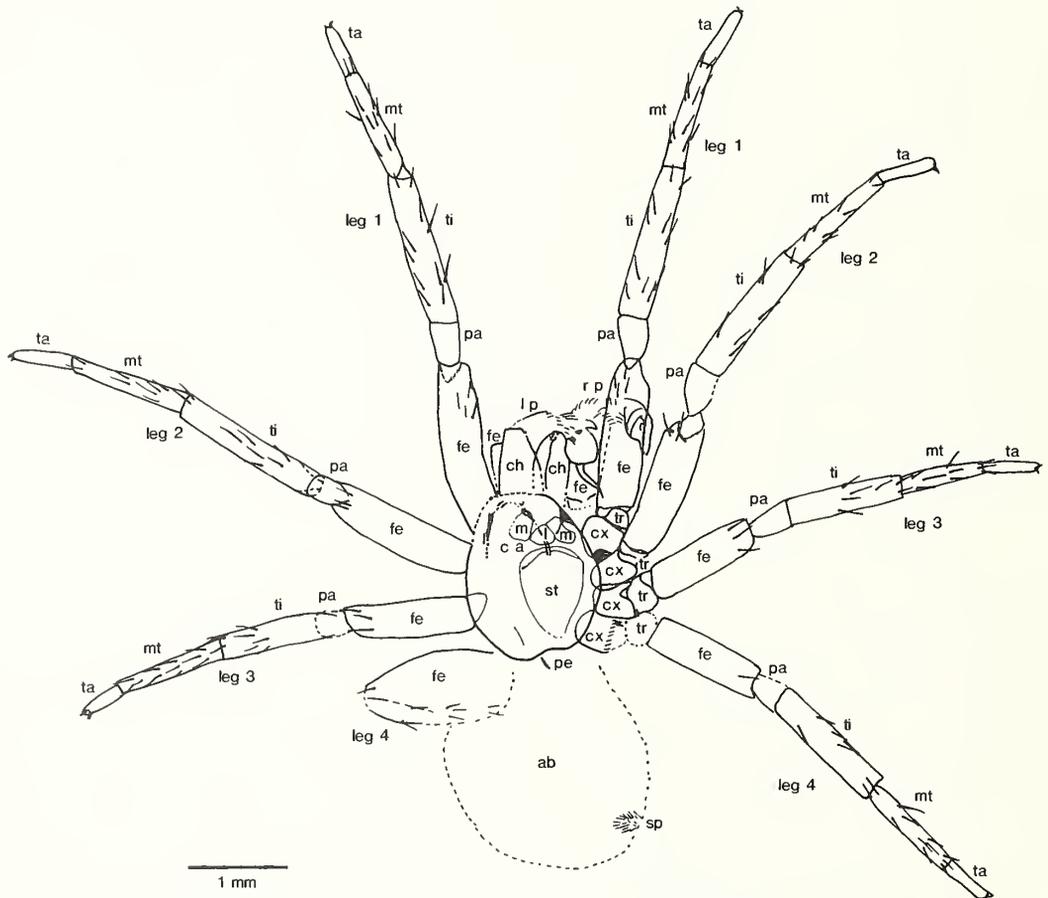
Type and only known species. *Cretaraneus vilaltae* sp. nov.

Diagnosis. Araneoid spider with subelliptical carapace bearing raised cephalic area and no fovea; subtriangular sternum; small, subtriangular labium; serrate setae covering all parts of body. Chelicerae relatively large (0.4 × length of carapace), forwardly directed (at least in adult male), with inner and outer row of denticles (not peg-teeth), and mesal ridge; male palp with long embolus, and small, proximal ?paracymbium; legs relatively equal in length, about three times the length of carapace; femora, tibiae and metatarsi with spines; tarsi with pectinate paired claws, small median claw, and associated serrate bristles; no true trichobothria; globose abdomen.

Cretaraneus vilaltae sp. nov.

Text-figs. 2-4

1986 Araneae: Lacasa and Martinez, p. 218; pl. 2, fig. 1.



TEXT-FIG. 2. *Cretaraneus vilaltae* gen. et sp. nov., holotype, LC 1150 IEI. Explanatory drawing for text-fig. 3. See *Terminology* for explanation of abbreviations.

Derivation of name. After Sr Ramón Vilalta-Oliva, President of the Institut d'Estudis Ilerdencs, Lérida.

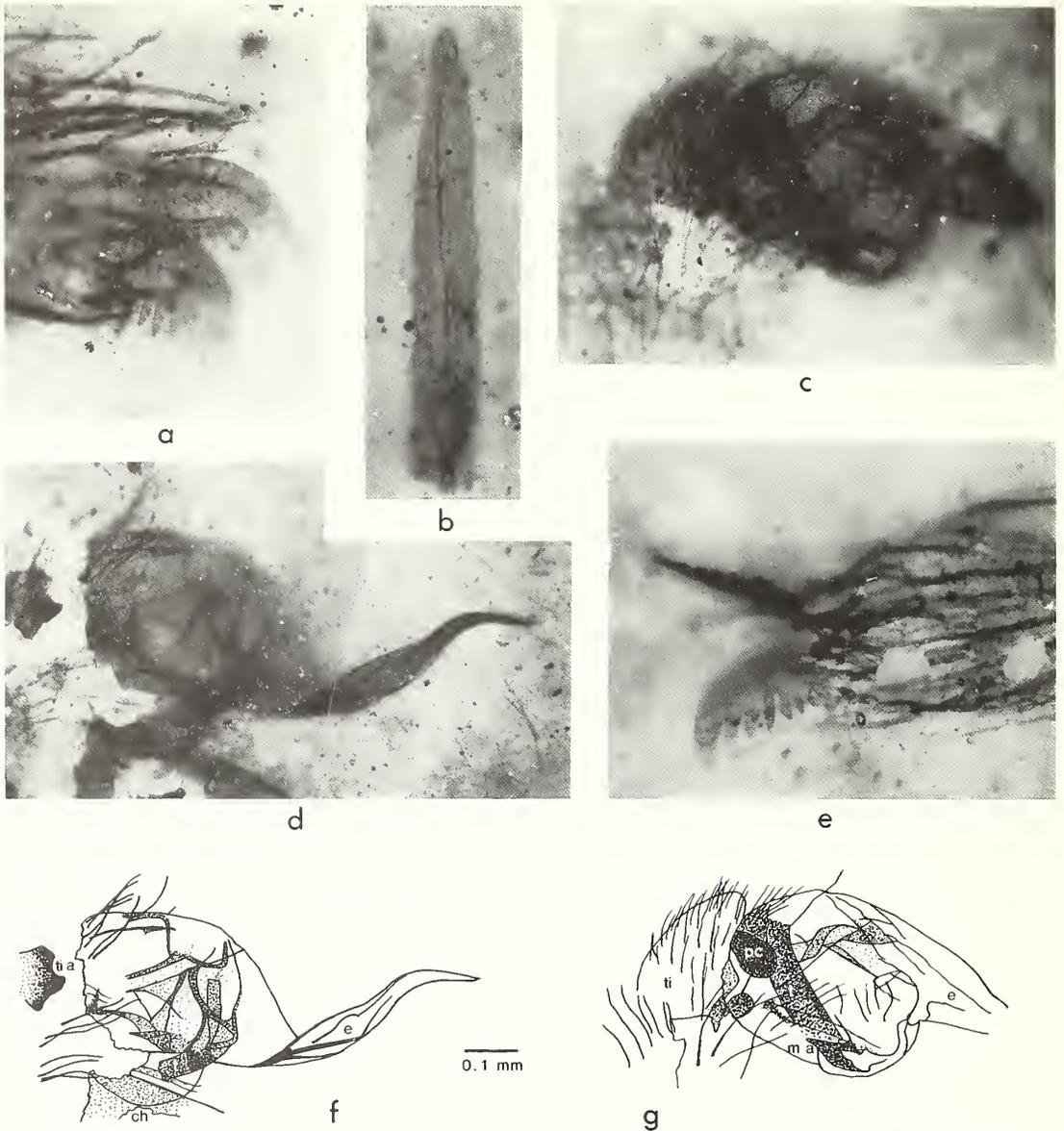
Type specimen. Holotype and only known specimen, LC 1150 IEI, complete specimen on single piece of limestone from quarry of La Cabrúa, Sierra de Montsech, north-east Spain; held in collections of Institut d'Estudis Ilerdencs, Lérida, Spain.

Diagnosis. As for the genus.

Description. A well-preserved spider, and the smallest of the specimens known from Montsech. The carapace cuticle is preserved and is golden brown in colour. The carapace is 1.73 mm long and 1.37 mm wide, and pyriform; its greatest width occurs at four-fifths of the length behind the anterior margin. From greatest width



TEXT-FIG. 3. *Cretaraneus vilaltae* gen. et sp. nov., holotype. Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain, LC 1150 IEI. See text-fig. 2 for explanation, $\times 13$.



TEXT-FIG. 4. *Cretaraneus vilaltae* gen. et sp. nov., holotype. Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain, LC 1150 IEI. *a*, tarsal claws on left leg 2; note large, pectinate, paired claws, small, uncinuate, median claw (bottom centre), and curved, serrate bristles, especially inferiorly. $\times 220$. *b*, typical spine, on tibia of left leg 1, showing striations $\times 400$. *c*, right palpal tibia and tarsus; see *g* for explanation, $\times 88$. *d*, left palpal tarsus; see *f* for explanation, $\times 88$. *e*, tarsal claws on right leg 4, $\times 220$. *f*, explanatory drawing of *d*. *g*, explanatory drawing of *e*. See *Terminology* for explanation of abbreviations.

the carapace edges converge in very gentle convex curves to the rounded anterior margin, and in similar shaped curves which converge more rapidly to the posterior margin. The posterior margin is broad and has a distinct median embayment. There is no prominent foveal depression, from which it can be concluded that a fovea was probably absent. About one-quarter of the way back from the anterior margin of the carapace, on each lateral margin, is a slight embayment and a dark patch of cuticle which forms a linear feature extending radially

inwards. This is interpreted as a shallow sulcus which reflects a condyle for articulation of the chelicera on the inner surface of the carapace. A radial crack in the posterior right-hand quadrant indicates some crushing of the carapace. Dark areas in the anterior half form a V-shape pointing forwards. The V-shape is asymmetrical with respect to the midline, the left limb being more parallel to the midline than the right, and the whole shape is left of the midline. Some folding is associated with the limbs of the V-shape. This shape is interpreted as a sulcus or break in slope separating the peripheral parts of the carapace from a raised cephalic area in the anterior half of the carapace. The asymmetry of the V-shape, in contrast to the symmetry of the rest of the carapace, indicates left-lateral compression of the cephalic area during compaction of the sediment. A small, semicircular, dark area of cuticle approximately centrally placed near the anterior border of the carapace is interpreted as the posterior border of a right eye, the anterior half of which is missing. Other eyes, if similar in size, are most likely to be obscured by the dark lines of crumpled cuticle around the anterior edge of the cephalic lobe. The whole carapace is separated from the ventral prosoma and moved slightly to the left, exposing the right coxae.

A pair of dark lines in the posterior half of the carapace, subparallel to the midline but diverging towards the anterior, are interpreted as left and right edges of the sternum. The anterior border of the sternum is seen as a transverse, recurved line just anterior to the midpoint of the carapace. Due to the left-lateral movement of the carapace, the sternum appears mainly to the right of the midline. The sternum is widest anteriorly, and narrows gradually to a blunt point situated between the coxae of the fourth pair of legs. In front of the anterior margin of the sternum are some rounded dark areas. The somewhat triangular dark area anterior to the midline of the sternum is interpreted as the labium. The labium is widest posteriorly, where it is distinctly separate from the sternum. The lateral edges converge to a rounded anterior margin. The two areas to the right of the sternum represent the right maxilla with the anterolateral carapace sulcus superimposed. The posterior part of the left maxilla can be seen to the left of the labium, but its anterior part is obscured by the right limb of the V-shape surrounding the carapace cephalic area. No serrulae can be seen on the maxillae; there are many setae visible in the intermaxillary area.

The chelicerae are about 0.69 mm long, and project forwards in front of the carapace. Their lateral sides are straight and parallel to each other, their inner sides are convex and partly overlap in the fossil. Their dorsal (superior) surfaces bear numerous short, stiff setae; laterally, curved bristles are present. Each chelicera bears two rows of denticles extending from the mesal side of the anterior border to about half-way down the inner edge, the outermost row bearing at least three and probably five denticles, the inner row with at least two denticles. The fangs are not preserved, and were presumably on the counterpart which was not collected. A prominent ridge, or keel, runs from the end of the tooth row (which is relatively short, about one quarter the length of the chelicera) along the mesal surface. No stridulatory ridges can be seen. The presence of a thickened sulcus on the anterolateral side of the carapace (see above), which probably reflects an internal apophysis for articulation of the chelicera, suggests the presence of a condyle on the chelicera; the condyle itself is not preserved on the specimen. From the morphology of the preserved cheliceral parts, it is apparent that the fangs worked transversely (labidognathous).

This specimen is a mature male because the palps are modified for the transmission of sperm (text-fig. 4c, d, f, g). Both palps are bent over to the right due to the left oblique compression of the specimen. The tarsus of the left palp now appears to the right of the right chelicera, and the right palpal tarsus lies beneath the femur of right leg I. The appearances of the sclerites on each palp differ because the palps are compressed in different ways. The left palp presents a mesal view, and the right an ectal view. The total length of the palp, from the maxilla to the tip of the bulb (i.e. excluding the embolus, see below) is approximately 2.20 mm. The palpal femur is about equal in length to the adjacent chelicera. The patella and tibia are covered with long setae. The tibia is a distally expanded, triangular podomere, bearing long bristles which radiate distally to partly cover the tarsus. Distal to the tibia is an ovoid body with numerous sclerites superimposed on it. The ovoid body is interpreted as the superimposed bulb and cymbium (modified tarsus). The cymbium is not separately recognizable from the bulb, and is therefore presumed to be no longer than the bulb and related parts. The right palp seems to present an approximately ectal view, and the left palp an approximately superomesal view. Immediately distal to the tibia, an elliptical dark area may represent a small, separate paracymbium. On the right bulb, a curved, lath-like sclerite extends from the suproproximal edge to the inferior side of the bulb. This may be the tegulum. On the left palp, the different direction of compression has caused this structure to appear curving from the apparent inferior edge towards the superodistal direction. On the right palp below the supposed tegulum is a rather complex, hooked structure, also visible on the left palp. This may represent a median apophysis. The interpretations of both tegulum and median apophysis are uncertain. The gently helical, acuminate structure, as long as the bulb itself, extending distally from the distal end of the bulb is interpreted as the embolus. It is easily seen on the left palp, but on the right palp only its basal part is visible, the remainder

disappearing into the matrix beneath. It is possible that this structure represents the conductor (see, for example, the helical conductors of some tetragnathines, Levi 1981) in which case the embolus cannot be seen.

The legs are short and nearly equal in length. The leg length formula is 1243. The coxae are visible on the right side. Each is about 0.39 mm long, and slightly longer than broad. The trochanters are very short (about half as long as broad), and each is about 0.19 mm in length. Approximate lengths of more distal podomeres and total leg lengths, in mm, are as follows. Leg 1: fe 1.73, pa 0.46, ti 1.64, mt 1.08, ta 0.58; total 6.07. Leg 2: fe 1.54, pa 0.46, ti 1.50, mt 1.17, ta 0.69; total 5.94. Leg 3: fe 1.25, pa 0.46, ti 1.04, mt 0.87, ta 0.52; total 4.72. Leg 4: fe 1.31, pa 0.46, ti 1.25, mt 0.92, ta 0.52; total 5.04.

All legs are thickly clothed in long, fine setae, and the femora, tibiae, and metatarsi bear spines. The setae are not plumose, under high magnification, but some appear to be sparsely serrate, and on the larger ones a rectilinear pattern, as observed on the spines, can be seen. Among the leg setae, especially on the distal podomeres, there are a few short and thin, gently S-shaped, rather crumpled, setae which extend outwards from the podomeres at high angles, and are set in follicles which appear rather too large for the thickness of the seta. Some of these hairs are interpreted as chemosensory setae, as described by Foelix (1970*b*). Others may have had a function akin to that of trichobothria; no undoubted trichobothria can be seen. The spines have a rectilinear sculpture (text-fig. 4*b*). The numbers of leg spines given here are the maximum number which can be seen on the specimen. This must be considered to be either the actual or the minimum number present in life, since in this specimen the counterpart was not collected, and some spines may be preserved on the counterpart only. However, since by far the greater part of both dorsal and ventral sides of the animal is preserved on the slab, it is considered likely that few spines are unaccounted for. The femora bear stout, curved spines and some curved bristles in the distal area. Four spines are present on fe1, all apparently on the superior side of the podomere, of which two are subdistal and two distal in position; there are three on fe2 and fe3, superior in position; there is at least one on the posterior side of fe4. No other spines are present on the femora. The patellae are spineless. The tibiae and metatarsi bear spines in three areas: proximal, median, and distal. The distal spines are stout, curved, and inferoanterior and inferoposterior in position; the others are longer, straighter, and occur on all sides of the podomeres. In addition, stiff bristles occur in the median and distal areas of these podomeres. Ti1 bears five spines in a whorl on the proximal area, four (supero- and inferoanterior and supero- and inferoposterior) in the median area, and two distally. Ti2 bears four spines (one superior and three inferior) in the proximal area, two superior median, and two in the distal area. Ti3 has no proximal spines, five in a whorl in the median area, and two distally. Ti4 bears at least five spines in various positions in the proximal and median areas, and two distal spines. Mt1 bears five proximal spines, two pairs in the median area, and two distally. Mt2 has four proximal spines, two in the median area, and two distally. Mt3 has three spines in each of the three areas. Mt4 bears three proximal spines, probably four in the median area, and at least three distal spines (one superior in addition to the usual anterior and posterior). All tarsi are spineless. Distally, pectinate paired claws are present, each with one row of nine teeth, and a small, unciform median claw, but no onychium (text-fig. 4*a, e*). Surrounding the claws are a number of serrate bristles; these are gently S-shaped at the end with the serrations on one side. There is no comb of serrate bristles along the shaft of this podomere.

The abdomen is 2.17 mm long and elliptical to subcircular in outline. Very little cuticle is preserved, so it is presumed to have been thin in life, but the abdomen outline is clearly seen due to its covering of setae. Cuticle between the setae can only be seen in ill-defined areas mainly in the left half of the abdomen; these are interpreted as ?dorsal pigmented areas in life. Generally darker coloration and greater density of setae indicate position of spinnerets which, however, are not separately discernible. The spinneret region can be seen on the right side of the abdomen (due to the left oblique compression) and appears to have been subterminal in position. A longitudinal dark streak left of the midline between the carapace and abdomen is presumed to represent the remains of the pedicel.

Family TETRAGNATHIDAE Menge, 1866

The familial status of Tetragnathidae has been supported by many authors (for example, Kaston 1948, 1978; Locket and Millidge 1953), but resisted by others (Levi 1980; Roberts 1985, p. 198) in the past. The situation is further complicated by the position of the Metinae, placed by some in Tetragnathidae and by others in Araneidae. The most recent opinions of Levi (1986), Coddington (1989*b*), and Platnick (1989) are that tetragnathines, metines, and nephilines should be placed together in the family Tetragnathidae, separate from the Araneidae. In the past, these subfamilies

have been placed in the family Araneidae, but Coddington (1989*b*, fig. 108) considered the clade Nephilinae + (Tetragnathinae + Metinae) as the sister group to Araneidae + Linyphiidae.

First impressions of *Macryphantes* suggested the 'crab-spiders' (superfamilies Thomisoidea and Philodromoidea), on account of the subcircular carapace, prominent eyes, subcircular palp, and long, spinose anterior legs. However, these features are not confined to crab-spiders, and the characteristic features of crab-spiders (two claws, tarsal scopulae, clavate setae, etc.) are lacking in *Macryphantes*. Furthermore, in thomisoids and philodromoids the legs are laterigrade, not densely setose, and the spines on the legs are concentrated on the mesal surfaces of the tibiae and metatarsi of the anterior prey-capturing legs. This is not the case in *Macryphantes*.

The presence of femoral trichobothria in *Macryphantes* points to the Deinopoidea or Araneoidea. As discussed above with regard to *Palaeouloborus*, only the Uloboridae (Deinopoidea) and the metines-tetragnathines in the Araneoidea bear femoral trichobothria. Since *Macryphantes* is an adult male, it could lack a calamistrum and cribellum, and correlated with the loss of cribellum and calamistrum in adult male uloborids appears to be the loss of the comb of macrosetae on the fourth tarsus (personal observation from *Uloborus walckenaerius*). Arguing against its inclusion in the Uloboridae are: the presence of serrate setae, the absence of plumose setae, and the absence of feathery setae. Serrate setae are characteristic of araneoids (Coddington 1986) and members of the superfamily lack plumose hairs which are found in deinopoids. Furthermore, the large, pectinate, paired tarsal claws of *Macryphantes* resemble those of araneoids more than the uloborid claw pattern of relatively small, sparsely toothed or non-pectinate paired claws.

The presence of femoral trichobothria in *Macryphantes* places it among the tetragnathines within the Araneoidea; this character has been used to distinguish tetragnathids in familial keys (Kaston 1948; 1972; Locket and Millidge 1953). As mentioned above, Coddington (1989*b*) has argued that the tetragnathines are closely related to the metines and nephilines. Whilst a number of other features, such as leg length and possible paracymbium, add weight to this assignation, some characters of *Macryphantes* are unusual for this group, including: subcircular or broadly pyriform carapace, planospiral embolus, and prominent, dorsally directed, posterior median eyes. Therefore, whilst the presence of femoral trichobothria appear to ally *Macryphantes* most closely with the tetragnathines, rather than the metines and nephilines which lack this feature, these other characters suggest that inclusion of the fossil in the Tetragnathinae is unwise.

Genus MACRYPHANTES gen. nov.

Derivation of name. Greek *makros*, long, large, and *yphantes*, a weaver.

Type and only known species. *Macryphantes cowdeni* sp. nov.

Diagnosis. Tetragnathid spider with subcircular, or broadly pyriform, foveate carapace; leg 1 six times the length of carapace and more than twice the length of leg 3; double row of prolateral trichobothria on femur of leg 3, single row of prolateral trichobothria on femur of leg 4; paired tarsal claws pectinate with six teeth, median claw long, curved, not pectinate, serrate bristles (accessory claws) present; male palp with planospirally coiled embolus; serrate, but not plumose, setae present.

Macryphantes cowdeni sp. nov.

Plates 3 and 4; text-figs. 5 and 6

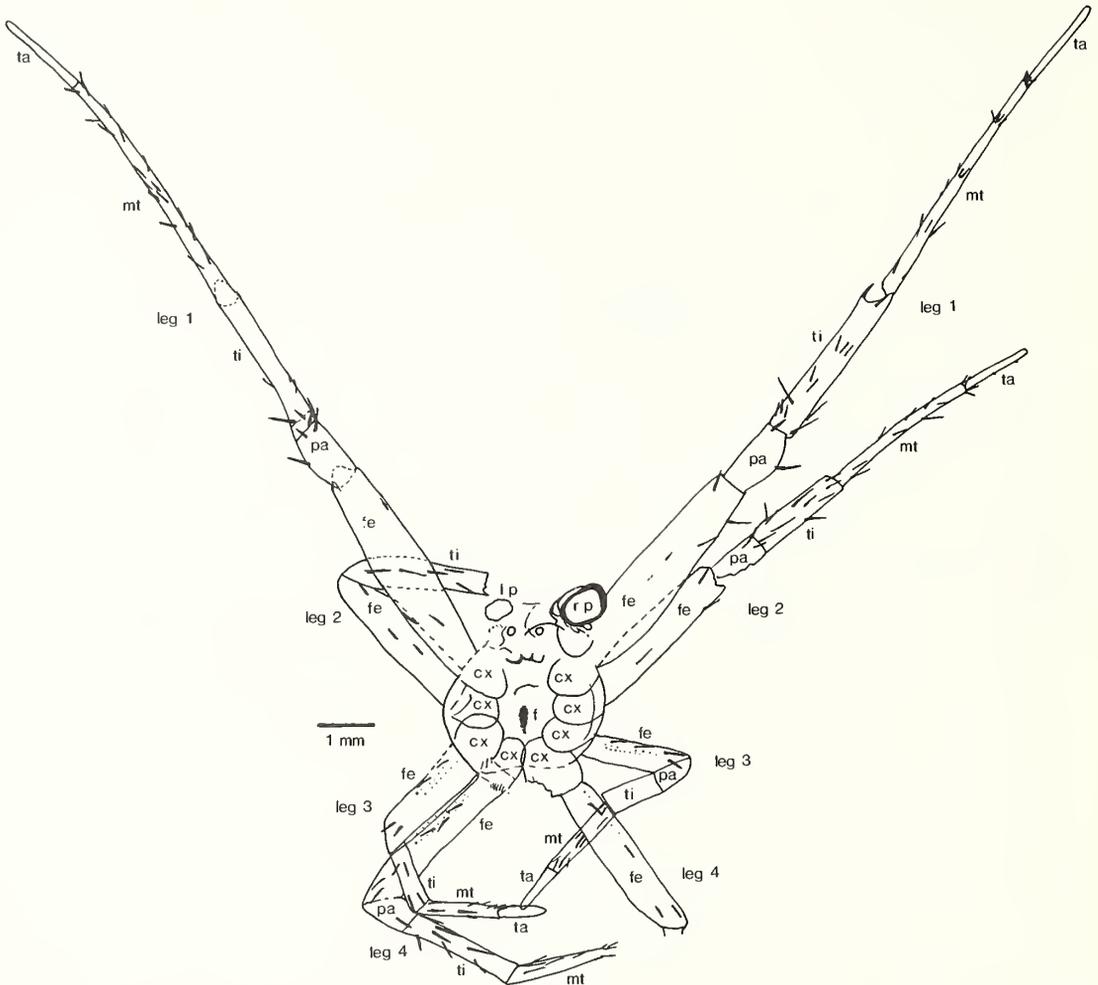
Derivation of name. In remembrance of a friend and a fellow arachnologist, Dr Douglas Cowden of Worcester.

Type specimens. Holotype, LC 1753 AP A (part) and LC 1753 AP B (counterpart). Paratype, LC 1754 AP A (part) and LC 1754 AP B (counterpart). Both are from the quarry of La Cabrúa, Sierra de Montsec, north-east Spain, and are held in the collections of the Institut d'Estudis Ilerdencs, Lérida, Spain.

Diagnosis. As for the genus.

Description. This is the largest and one of the best preserved of the spiders from Montsech, with long, outstretched legs 1. The description is based on specimen LC 1753 AP (Pl. 3; text-fig. 5), which is better preserved (though slightly smaller) than LC 1754 AP (Pl. 4, figs. 2 and 4; text-fig. 6); the latter is referred to for confirmation of details. Both specimens are mature males.

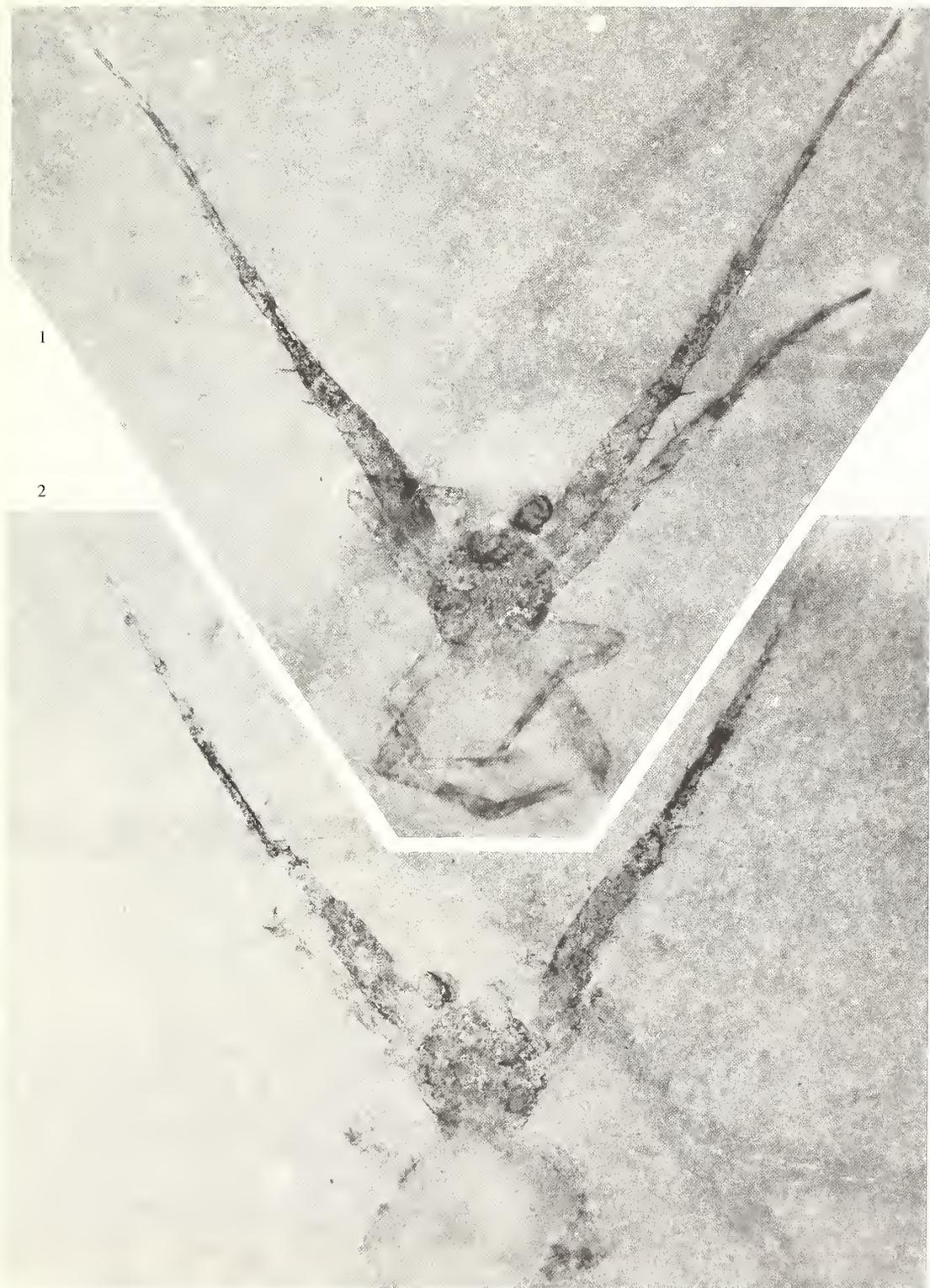
The carapace is slightly wider (2.83 mm) than long (2.65 mm), and is widest at about midlength. The carapace outline is subcircular, but may be somewhat produced anteriorly where the edge is not preserved. The



TEXT-FIG. 5. *Macryphantes cowdeni* gen. et sp. nov., holotype, LC 1753 AP B. Explanatory drawing for Pl. 3, fig. 1. See *Terminology* for explanation of abbreviations.

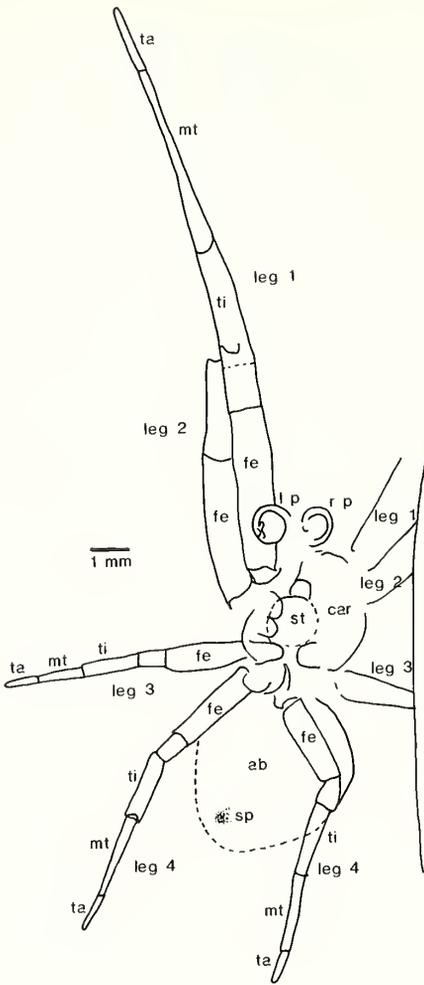
EXPLANATION OF PLATE 3

Figs. 1 and 2. *Macryphantes cowdeni* gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain; under ethanol. 1, LC 1753 AP B, lower slab, $\times 7$; see text-fig. 5 for explanation. 2, LC 1753 AP A, upper slab, $\times 7$.



SELDEN, *Macryphantes*

TEXT-FIG. 6. *Macryphantes cowdeni* gen. et sp. nov., paratype, LC 1754 AP A. Explanatory drawing for Pl. 4, fig. 4. See *Terminology* for explanation of abbreviations.



carapace is covered in setae. At the anterior side of the carapace, there are forwardly directed setae and long, curved bristles. At the anterior margin of the carapace two circular structures are interpreted as median eyes. Just posterior to the centre of the carapace, a deep, drop-shaped depression, with its blunt end anteriormost, marks the fovea. The carapace shape is confirmed by specimen LC 1754 AP, in which the carapace is 3.25 mm wide.

A pair of deep depressions just posterior to the anterior median eyes are surrounded posteriorly by dark

EXPLANATION OF PLATE 4

Figs. 1–7. *Macryphantes cowdeni* gen. et sp. nov., holotype and paratype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain. 1, 3, 5–7, LC 1753 AP B, holotype, oil immersion. 1, Trichobothria, setae, and spines on proteral surface of femur of right leg 3, $\times 85$. 3, Right palp, showing apophysis on right side, $\times 47$. 5, Distal end of tarsus of right leg 2, showing paired pectinate claws, long median claw, and curved, serrate bristles (accessory claws), $\times 320$. 6, Spines and setae on shaft of metatarsus of left leg 4, superior to top, $\times 85$. 7, Distal half of tarsus of right leg 2, showing terminal claws and short spine on inferior surface of podomere, $\times 130$. 2, LC 1754 AP B, paratype, upper slab, $\times 4.5$. 4, LC 1754 AP A, paratype, lower slab, $\times 3.6$; see text-fig. 6 for explanation. Both under ethanol.



1



2



3



4



5



6



7

cuticle. These structures are interpreted as the proximal ends of the chelicerae which are directed ventrally; the chelicerae presumably disappear into the matrix beneath the specimen. The sternum appears to be circular; its shape is suggested by the arrangement of the coxae, as seen on both LC 1753 AP and LC 1754 AP. The coxae of legs 4 meet in the midline, and on both the holotype and paratype some remnants of the anterior edge of the sternum can be discerned.

The palp on the right side of LC 1753 AP B (the left side of LC 1753 AP A) is preserved (Pl. 4, fig. 3), and confirms that the specimen is an adult male. The palpal tarsus is subcircular in outline with a mesal bulge. This bulge represents either the mesal part of a circular cymbium or a mesally situated crescentic cymbium. The bulge extends beyond the oval dark band which is interpreted as the embolus (this structure could be the conductor or some other sclerite functioning as a guide for the embolus). The embolus is coiled in a horizontal planospiral, which in LC 1754 AP A can be seen to be sinistral on the left palp, and dextral on the right, as viewed from above. On the proximolateral side, a thick, reniform lobe is interpreted as a median apophysis. A dark area can be seen on the proximal edge of the cymbium within the coiled embolus; this is inferior in position; this dark area belongs to a sclerite of the palp. A smaller dark patch occurs just anterior to the midpoint of the palp, on the inferior surface; this represents part of another sclerite. Numerous long bristles run right laterally from the base of the tarsus, and some curved bristles are present on its superior surface. Larger, curved spines are present around the base of the tarsus; these appear to originate proximal to the tarsus, that is, on the tibia, which is otherwise poorly preserved.

The leg length formula is 1243. The legs are very unequal in length, leg 1 being more than twice the length of leg 3. The coxae are approximately equidimensional, each about 0.58 mm long and wide. The trochanters are not easily visible, but each measures about 0.25 mm in length. Lengths of the more distal podomeres and total leg lengths, in mm, are as follows: leg 1: fe 4.33, pa 1.35, ti 3.00, mt 4.55, ta 1.70, total 15.76; leg 2: fe 3.17, pa 1.00, ti 1.64, mt 3.00, ta 1.15, total 10.79; leg 3: fe 2.01, pa 0.39, ti 1.15, mt 1.64, ta 0.85, total 6.87; leg 4: fe 3.00, pa 0.81, ti 2.04, mt 1.98, ta not preserved (presumed to be *c.* 0.95 by comparison with ratio of mt4 to ta4 seen in LC 1754 AP, see below), total *c.* 9.61. LC 1754 AP is poorly preserved, and slightly larger than LC 1753 AP, and its leg measurements are as follows (in mm but with a lesser degree of certainty than in LC 1753 AP): coxae 0.9, trochanters 0.3; leg 1: fe 4.7, pa 1.4, ti 3.1, mt 5.0, ta 1.8, total 17.2; leg 2: fe 3.8; leg 3: fe 2.3, pa 0.6, ti 1.4, mt 1.3, ta 0.9, total 7.7; leg 4: fe 2.8, pa 0.9, ti 1.9, mt 2.1, ta 1.0, total 9.9.

All legs are thickly clothed with long setae. These setae appear smooth, but high magnification reveals minute accessory spines, especially distally; thus they are the serrate type. No plumose or feathery hairs can be seen. Spines are mostly large and numerous, occurring on all podomeres except the coxae and trochanters. Some spines show a helical pattern of longitudinal lines. Most spine are quite large (mean length 0.48 mm) and straight (Pl. 4, fig. 6), but spines at the distal end of podomeres are commonly curved and/or short. Fe1 bears five pairs of spines along the superior surface and an inferoanterior distal spine (this may be one of a pair). Fe1 also has many very short, fine hairs on the inferior surface of the distal half of the podomere. Pa1 bears a prominent posterior spine, and antero- and posteroinferior distal spines. Ti1 bears a whorl of about five spines proximally, two pairs of spines inferiorly and two single spines superiorly along the podomere, and postero- and anteroinferior distal spines. Mt1 bears eight pairs of spines along the inferior surface, including and distal pair. Fe2 bears four pairs of superior spines along the shaft, and postero- and anteroinferior distal spines. Pa2 bears one lateral and antero- and posteroinferior distal spines. Ti2 bears ten long spines along the shaft of the podomere, and two short distal spines. Mt2 bears a pair of spines proximally, a whorl of four spines and then five more along the shaft, with a whorl of five spines distally. Ta2 on the right side of LC 1753 AP B is particularly well preserved (Pl. 4, figs. 5 and 7), and shows curved paired claws each with six teeth, an equally long curved median claw, and numerous serrate accessory claws (i.e. hypertrophied bristles, as seen in living Araneidae, see Foelix 1970a). Ta2 bears two small spines on its inferior surface. Along the superior prolateral side of the proximal three-quarters of fe3 are about 24 trichobothria arranged mainly in two rows (Pl. 4, fig. 1). The trichobothrial hairs are not feathered. This podomere bears many fine, curved hairs inferiorly, two median superior spines, and two posterior distal spines. Pa3 appears to be spineless. Ti3 bears long, stiff setae, and one median and two subdistal spines. Mt3 has three inferior and one superior proximal spines, one superior, antero- and posterolateral, and two short inferior median spines, followed by one lateral and three curved inferior spines and a whorl of five distal spines. Ta3 bears two small spines on its inferior surface, like those which occur on Ta2. Fe4 bears at least one superior prolateral row of about sixteen trichobothria, fine, curved hairs inferiorly, three superior median spines, and three superior subdistal spines. Pa4 bears one lateral spine. Ti4 has three superior, two inferior, and two lateral spines along the shaft, and apparently no distal spines. Mt4 bears antero- and posteroinferior and posterolateral spines proximally, two inferior median spines, one small curved superior median spine, two small curved distal spines, and two small and one large inferior distal spines. The numerous setae on the superior surface of mt4 are gently curved, giving

the appearance of a weak calamistrum (Pl. 4, fig. 6). However, the high density of setae may be an artefact of compression, since a similar density of curved setae is observed on the opposite side of the podomere, and high magnification reveals that the setae are no different in structure from any others. Thus mt4 does not bear a calamistrum.

No trace of the abdomen is preserved on LC 1753 AP, but it is preserved on LC 1754 AP; it is oval, and measures 4.80 mm long and 4.20 mm wide. The greatest width is in the anterior half. The abdomen is compressed to the right in LC 1754 AP A, and was probably quite bulbous in life. The spinnerets are not elongated, and form a compact group in a subterminal position on the abdomen.

MODES OF LIFE

Palaeouloborus can be compared most closely with the Uloboridae. Uloborids are orb-web weavers which use a characteristic 'wrap attack' to subdue prey (Robinson 1975). In *Uloborus* and *Hyptiotes* (Nielsen 1932) the median tarsal claw is relatively large, the paired claws are fine and bear few (*Hyptiotes*) or no teeth (*Uloborus*), and in both genera there are large, serrate accessory claws. A similar pattern of tarsal claws occurs in *Palaeouloborus*, and it is unlike that found in araneoids, in which the paired claws are large and pectinate (see, for example, Levi 1978). Nielsen (1932, pp. 26–28) described the method of silk handling by *Hyptiotes* using this claw pattern. Whilst accessory claws are widespread among web-spinning spiders, and are used for silk handling, they are particularly well developed in orb-web weavers; the pattern in the living uloborids studied seems distinctive, and these genera are orb-web weavers.

Trichobothria occur on the femora of *Palaeouloborus* and uloborids. The function of these is not known, but it is interesting that among living araneomorph spiders they are found only in tetragnathines and uloborids, both of which are orb-web weavers. Femoral trichobothria are absent from some adult *Pachygnatha*, tetragnathines which make no web when adult (Levi 1980). Many orb-web weavers have no femoral trichobothria, but their presence in tetragnathines and uloborids appears to be linked with the habit. Another behavioural similarity between tetragnathines and uloborids is in resting postures (Levi 1980). Tetragnathines and many metines rest with their long legs 1 and 2 stretched out forwards, the fourth legs outstretched behind, and the short third legs pointing backwards and where necessary gripping the twig on which the spider is resting. Opell and Eberhard (1983) distinguished four types of resting posture in uloborids; in three, legs 1 and 2 are stretched forwards in some manner, whereas in the fourth, legs 1 and 2 are held folded with the femora projecting at right angles to the long axis of the body. Opell and Eberhard (1983) remarked on the close similarities of resting postures between uloborids and araneids. The femoral trichobothria are generally on the superior or retrolateral sides of femora 1 and 2, and on the prolateral sides of femora 3 and 4 (Opell 1979). Thus they point laterally when the animal is in the normal resting posture. It is likely that the presence of femoral trichobothria is linked with the uloborid and tetragnathine–metine resting postures. These behavioural characters may be due to convergence, but could conceivably be synapomorphies for all orb-web weavers (Shear 1986a). The great similarity in leg lengths, femoral trichobothrial pattern, and tarsal claws between *Palaeouloborus* and the Uloboridae suggests that the web-building and resting behaviour of the fossil genus resembled that of typical members of the living family.

The wrap-attack prey capture in uloborids was described by Opell (1979) and Lubin (1986). In it, the spider hangs by the first and second pairs of legs whilst throwing silk over the prey using the fourth leg-pair. After further entanglement of the prey in these threads, the spider approaches closer to the prey and, holding it now with the second and third leg-pairs, wraps it more tightly with silk combed by the row of macrosetae on the fourth legs. A wrap attack is found in a number of spider groups, such as the Theridiidae and Nesticidae (both of which have a comb of setae on the fourth legs), Metinae, Tetragnathinae, Araneidae, Oecobiidae, Hersiliidae, and Pholcidae (Coddington 1986). The wrap attack of uloborids differs from that of other spider families because uloborids lack poison glands and the prey is killed by digestive enzymes during feeding (Opell 1979). Since a wrap attack is found in families which do not have a comb of setae on the fourth legs, such a comb is

not essential for this method of prey capture. Wrap attack is therefore a possible method of prey capture in *Palaeouloborus*.

Macryphantes compares most closely in general appearance with large, long-legged araneoids such as the argiopine araneids, tetragnathines, and nephilines. Argiopines are similar in general appearance and habits to uloborids (both are orb-web weaving wrap-attack predators) but they lack femoral trichobothria. *Macryphantes* has an araneoid pattern of tarsal claws, and bears femoral trichobothria. Therefore, it is suggested that *Macryphantes* wove an orb web, rested in a posture like that of uloborids or metines-tetragnathines, and may have used a wrap-attack method of prey capture.

Cretaraneus has few positive features which would indicate its possible mode of life. The fossil genus is small, short-legged, and bears pectinate, paired claws and serrate accessory claws, which indicate that it is a web-weaving spider. Small, short-legged araneoids, such as *Cretaraneus* and most theridiids and linyphiids, are weavers of sheet webs in litter, undergrowth, or bushes; such webs catch pedestrian or small flying prey. It is likely that *Cretaraneus* occupied a similar ecological niche.

A great variety of orb webs are woven by uloborid and araneoid spiders, each designed to capture a specific type of prey. They are put up for short periods or longer, day or night, and in open or secluded situations (Riechert and Gillespie 1986; Stowe 1986; Lubin 1986). They vary from massive, collective structures to minimalist devices hardly recognizable as orb web derivatives. It is impossible to suggest what type of prey *Macryphantes* and *Palaeouloborus* captured with their orb webs. There was a wide diversity of insect life in the Montsech area during the early Cretaceous, which suggests that prey specialization may have been practised by orb-web weavers at that time.

CONCLUSIONS

Described here are the oldest known representatives of the spider superfamily Deinopoidea, the family Tetragnathidae, and the second oldest record of the superfamily Araneoidea in the fossil record. The Deinopoidea and the Araneoidea both contain weavers of orb webs of remarkable similarity. Indeed, there is continuing debate about whether the orb web evolved only once, in the common ancestor of the Deinopoidea and Araneoidea, or is a convergent phenomenon in these two groups. Shear (1986a) comprehensively reviewed the evidence for and against these conflicting hypotheses, and further discussion is not attempted here. However, the presence of well-defined deinopoids and araneoids in the Lower Cretaceous indicates that, whichever hypothesis is favoured, both groups of orb-web weavers were in existence at that time, and suggests that the orb web originated earlier in the Mesozoic, if not before.

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GIANT ACANTHOMORPH ACRITARCHS FROM THE UPPER PROTEROZOIC IN SOUTHERN NORWAY

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ABSTRACT. Large microfossils from a single phosphatic pebble in the late Riphean–early Vendian ($> 612 \pm 18 - 665 \pm 10$ Ma) Biskopås Conglomerate in the Hedmark Group in southern Norway were described by Spjeldnæs (1963) under the name *Papillomembrana compta* and interpreted as a possible dasycladaccan alga. The microfossils are evidently organic-walled and here regarded as giant acanthomorph acritarchs. The diagnosis of *Papillomembrana compta* is emended. Possibly related Proterozoic taxa are discussed. A new acanthomorph acritarch, *Ericiasphaera spjeldnaesii* gen. et sp. nov., found with *P. compta* within the same petrographic thin-section is described. Contrary to former conceptions, recent data seem to indicate that large complex acritarchs were common in late Proterozoic times.

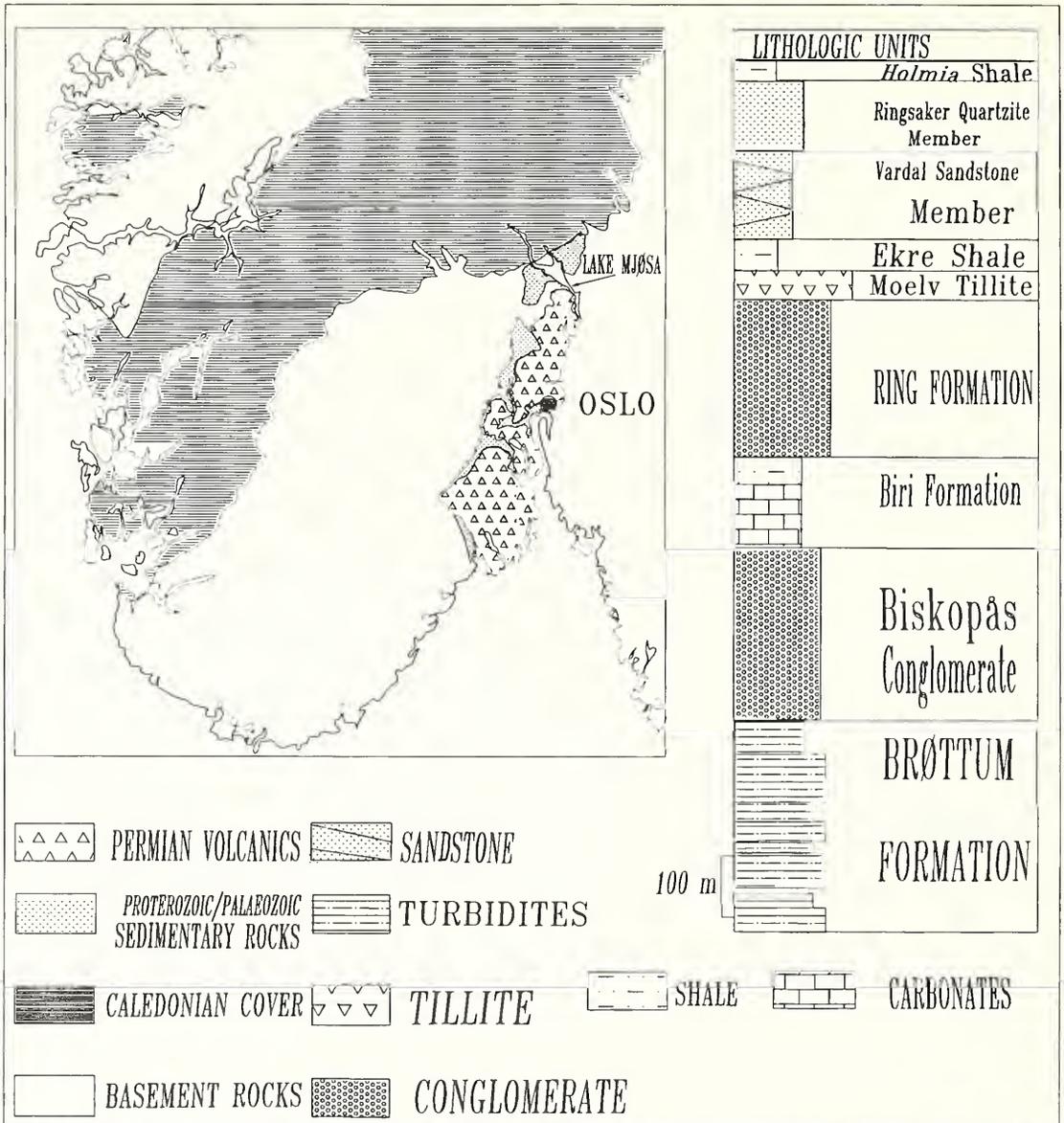
RECENT studies of Precambrian fossils reveal a formerly unsuspected degree of complexity in the late Proterozoic biota (Knoll and Calder 1983; Vidal and Knoll 1983; Knoll 1985; Butterfield *et al.* 1988; Zhang, 1989; Zang and Walter 1989). At the same time, the emerging picture sheds additional light on the importance of microfossils of planktonic primary producers for the understanding of the metazoan radiation at, or near the Proterozoic–Cambrian boundary (Germs *et al.* 1986; Moczyłowska and Vidal 1986; Knoll and Swett 1987). In this light a proper understanding of the taxonomic affinity of Proterozoic fossils seems of prime importance as it aids the acquisition of a more precise picture of the complexity of existing food webs (Knoll and Calder 1983).

In this paper, as a result of an ongoing study of the micropalaeontology of Proterozoic–Cambrian sections in southern Norway (Vidal and Nystuen, unpublished data), previously reported microfossils from the Upper Proterozoic Hedmark Group (Spjeldnæs 1963, 1967) are reinterpreted as acritarchs and a new acritarch taxon is described.

GEOLOGICAL SETTING AND AGE

The Hedmark Basin is located within the southern limit of the Scandinavian Caledonides. The basin contains the Upper Proterozoic Hedmark Group (text-fig. 1), a sequence that has been comprehensively studied, particularly with respect to its general lithostratigraphy, structural geology, sedimentology and depositional history (Bjørlykke *et al.* 1967; Nystuen 1981; Kumpulainen and Nystuen 1985; Nystuen 1987). The Hedmark Group (Bjørlykke *et al.* 1967) is a wedge of predominantly detrital rocks with subordinate carbonate and igneous rocks which until recently were widely referred to as ‘sparagmites’. The group has a variable thickness of 1500–4000 m (Bjørlykke *et al.* 1976) and consists of eight formal rock units in part overlain by epicontinental Cambrian–Silurian deposits which attain a thickness of approximately 1000 m. Both the Hedmark Group and the overlying Cambrian–Silurian strata underwent folding and thrusting during the Caledonian Orogeny. The Hedmark Group is considered to have been deposited in connection with fault-bounded basins (Kumpulainen and Nystuen 1985; Nystuen 1987); either within intra-cratonic rift-valleys (Bjørlykke *et al.* 1976; Bjørlykke 1978) or an aulacogen (Roberts and Gale 1978; Kumpulainen and Nystuen 1985; Nystuen 1987). The deposition history and facies associations were related to a model of development of the Hedmark Basin which involves succeeding episodes of crustal stretching, deep crustal fracture and ensuing block faulting and a final phase of thermal cooling and slow subsidence (Kumpulainen and Nystuen 1985; Nystuen 1987).

The Biskopås Conglomerate (Bjørlykke *et al.* 1967) is a clastic wedge within the Biri Formation (Bjørlykke *et al.* 1976). It occurs in several distinctive fan-shaped bodies in the southern and western part of the Sparagmite Basin (Bjørlykke *et al.* 1976), and the conglomerates interfinger basinward into the Brottum turbidite sandstones or shales of the Biri Formation (Nystuen 1982). Its thickness varies between 200 and 15 m.



TEXT-FIG. 1. Sketch map showing location of Sparagmite Basins in southern Norway. Composite section of the Hedmark Group in the Lake Mjøsa region (after Nystuen 1987). The fossiliferous sample with *Papillomembrana* derives from the basal sedimentary breccia in the Biskopås Conglomerate (Spjeldnæs 1963).

The formation consists of well-rounded pebbles and cobbles and occasional boulders in a coarse-grained, slightly clayey arkosic matrix (Bjørlykke *et al.* 1976) interbedded with massive sandstone layers.

The conglomerate contains carbonate and phosphate clasts in its lower part which are believed to have been eroded from the early transgressive part of carbonate deposits in the Biri Formation which accumulated in shelf area adjacent to the basin (Bjørlykke 1966; Spjeldnæs 1967). Absence of sedimentary structures appears to indicate deposition in a submarine environment. The conglomerate beds contain clasts, matrix-supported textures and massive and inversely graded bedding. Accordingly, the conglomerates were interpreted as

subaqueous fans laid down in front deltas by gravity sediment flow processes (R. Otter, pers. comm. in Nystuen 1982). Bjorlykke *et al.* (1976) favoured deposition in connection with floods as coarse sheet flows being deposited directly into the basin, or as a fluvial delta becoming reworked into a submarine environment. They also considered it unlikely that the depositional depth could have been greater than 200–300 m. Bjorlykke *et al.* (1976) pointed out that the conglomerate resembles Quaternary glaciofluvial conglomerates, and that pebbles are often faceted and similar to Quaternary glaciofluvial pebbles. However, they clarified that there is no evidence of ice-contact and that sorting is generally better than in glacial outwash deposits. Roundness and pebble contents suggest long transport (Bjorlykke *et al.* 1976).

The Biri Formation containing the fossiliferous Biskopås Conglomerate is 50–100 m thick and comprises a variety of lithofacies, including subtidal micritic limestone, intertidal to supratidal carbonates and shales with some dolomite displaying mud cracks and intraformational conglomerates, carbonate platform margin oolithic limestones, platform-slope calcareous shales and sandstones and intra-basin dark shale (Bjorlykke *et al.* 1976). Rocks of the lower member of the Biri Formation are locally missing, probably as a result of erosion preceding the deposition of the Biskopås Conglomerate. Both the upper and lower junctions of the formation are evidently diachronous. Where the Ring Formation is missing, rocks of the Biri Formation are overlain by the Moelv Tillite, while in areas where the Biskopås Conglomerate is absent the Biri Formation is in contact with the Brottum Formation (Bjorlykke *et al.* 1976). Normal salinity and open marine deposition conditions were suggested by Bjorlykke *et al.* (1976).

Phosphate pebbles in the Biskopås Conglomerate yielded scattered microfossils (Manum 1967) and specimens of the problematic fossil *Papillomembrana compta* (Spjeldnæs 1963, 1967) and *Ericiasphaera spjeldhaesii* sp. nov., and a number of quartz replaced, circular structures in the fossiliferous thin-section may represent sections of microfossils as indicated by Spjeldnæs (1967). In fact, some resemble transverse sections of siliceous casts of vase-shaped microfossils (perhaps similar to *Melanocyrrillum* Bloeser, in Bloeser 1985) as recorded in siliceous phosphates from the late Riphean Visingsö Group in Sweden (Knoll and Vidal 1980).

Acritarchs and cyanobacterial microfossils (Vidal and Sicdlecka 1983; Vidal and Nystuen unpublished data) occur in detrital rocks of several units of the Hedmark Group and in the overlying Lower Cambrian units (Downie 1982; Moczydlowska and Vidal 1986).

Age data from rocks of the Hedmark Group are restricted to one single, Rb/Sr whole rock age (Welin unpublished; Rankama 1973) of 612 ± 18 Ma on the Ekre Shale. An indirect estimation of the age of the Hedmark Group is offered by Rb/Sr whole rock dates of the Ottfjället dolerite dike swarm (Claesson 1976, 1977; Claesson and Roddick 1983) which yielded ages of 720 ± 260 and 665 ± 10 Ma. Acritarchs from the Biskopås Conglomerate and the Biri Formation indicate a late Riphean to early Vendian (*sensu* Vidal and Sicdlecka 1983) age for units underlying the Moelv Tillite.

DISCUSSION

Microfossils of organic-walled microorganisms are generally abundant in Proterozoic rocks. Their proper taxonomic affiliation is poorly understood and they are therefore treated among the acritarchs (Downie *et al.* 1963; Evitt 1963; Downie 1973), although morphologically simple forms are occasionally considered among the cryptarchs (Diver and Peat 1979). The probable algal affinity of Proterozoic and early Palaeozoic acritarchs is generally accepted, as it is the idea that they may represent the abandoned organic envelopes of encysted and/or motile stages of prasinophycean green algae, dinoflagellates, or similar groups now extinct (Dale 1977; Tappan 1980).

The diagnostic features of acritarchs are the general shape of the vesicle, its surface ornamentation and (if present) the shape and ornamentation of processes and excystment mechanism (Tappan 1980). Being restricted to these few taxonomically diagnostic attributes, descriptions are often imprecise and accompanied by poor illustrations. These are features which have probably contributed to the erroneous generic attribution of some Proterozoic acritarchs to early Palaeozoic genera. Irrespective of this, the taxonomy of acritarchs is meaningful only at the species level, because acritarch genera are simple groupings of form-species sharing superficially similar morphological features which do not necessarily imply close biological affinity.

Wide-ranging dimensional variability is a feature observed among modern eukaryotic plant protists. This same feature appears to apply to Phanerozoic acritarchs, which generally display a broad size range (5–500 μm ; Tappan 1980). Despite this, the significance of large acritarchs in the total picture of the late Proterozoic biota has been strongly overemphasized in the past. Certain

Proterozoic acritarchs have been compared to the phycoma stages of prasinophycean green algae (Knoll and Calder 1983; Vidal and Knoll 1983), which may be the living counterparts of several acritarch form-genera such as *Leiosphaeridia*, *Tasmanites* and *Cymatiosphaera*. Prasinophycean phycomata are initially about 10 μm in diameter, but the mature cyst may be as much as 100–175 μm in diameter (Tappan 1980). This attribute may be particularly significant to the interpretation of the taxonomic affinity of certain Proterozoic acritarchs which display polymodal, often megascopic or nearly megascopic dimensions (Vidal 1974, 1976; Vidal and Ford 1985).

Until quite recently the generally accepted view was that Precambrian acritarchs are mainly spheroidal, morphologically simple forms lacking diagnostic features (Downie 1973). Timofeev *et al.* (1976) and Vidal (1976) first reported Proterozoic acanthomorphs ornamented with simple, conical and complex membrane-bounded processes, and polygonomorphic acritarchs, a degree of morphological complexity once thought to be restricted to Phanerozoic fossils (Brasier 1977). However, recent data (Vidal 1981; Knoll and Calder 1983; Knoll 1984; Awramik *et al.* 1985; Pjatiletov and Rudavskaya 1985; Vidal and Ford 1985; Yin 1985; Butterfield *et al.* 1988; Knoll and Ohta 1988; Zang 1988; Zang and Walter 1989) seem to demonstrate that complex acritarchs were relatively common in the late Proterozoic. It now appears that *Papillomembrana compta* Spjeldnæs (1963) (and an additional acanthomorph acritarch; see below) from the late Proterozoic Biskopås Conglomerate in the southern Norway Sparagmite Basins (Spjeldnæs 1963) may in fact be the earliest report of giant Proterozoic acanthomorph acritarchs (Zhang 1989).

Most occurrences of late Proterozoic acanthomorph acritarchs are in probably early diagenetic cherts within subtidal shallow shelf carbonates (Knoll and Calder 1983; Knoll 1984; Awramik *et al.* 1985; Yin 1985, 1987; Knoll and Ohta 1988), and subtidal shallow marine shales and carbonates (Timofeev *et al.* 1976; Vidal 1976, 1981; Vidal and Ford 1985; Pjatiletov and Rudavskaya 1985; Butterfield *et al.* 1988). Zang and Walter (1989) suggested that a rather diverse acritarch assemblage from the late Proterozoic Pertatataka Formation accumulated in distal turbidites and explained the apparent rarity of late Proterozoic 'giant' acanthomorphs as perhaps depending on insufficient sampling of deep-marine settings. Lack of convincing sedimentological evidence to support hypothetical turbidite deposition in the Pertatataka shales leaves the occurrence of Proterozoic 'giant' acanthomorphs open to alternative explanations (Knoll and Butterfield 1989).

Late Proterozoic (Riphean and Vendian) turbidites have been extensively studied, with results differing much from those reported by Zang (1988) and by Zang and Walter (1989). Thus, laminated hemipelagic mud deposits are usually rich in detrital organic matter (Palacios-Medrano 1986) and yielded chiefly planktonic microfossils interpreted as chroococcalean cyanobacteria (Mansuy and Vidal 1983; Vidal and Siedlecka 1983; Palacios-Medrano 1986). The scarcity or absence of identifiable non-cyanobacterial acritarchs in turbidite sequences does not imply total absence of eukaryotic plankton in the overlying water column. In fact, cysts may simply have not been produced or alternatively, if produced, had low fossilization potential or accumulated in insignificant numbers (Vidal and Siedlecka 1983). As for any other microfossil group, the concentration of acritarchs in submarine fan deposits would be expected to be small compared with that of adjacent shallow shelves. Thus, while early Cambrian-age platform siliciclastic and carbonate rocks yield rich acritarch assemblages, time-equivalent turbidites in southeastern Poland yield extremely rare acritarchs (Pozaryski *et al.* 1981).

Little is known about the preservation potential of motile stages of microscopic algae or of reproductive structures of thallophytes (e.g. cysts, aplanospores or zygotes), although some inferences are perhaps possible from dinoflagellate data (Evitt 1985). However, routine microscopic examination of thin-sections of numerous rock samples failed to reveal the existence of such hypothetical stages. In fact, it is possible that, like the geologically more recent dinoflagellates, Proterozoic acritarchs may have alternately produced preservable and non-preserved cysts (Evitt 1985).

In the above context environmental information concerning the *Papillomembrana*-bearing Biskopås Conglomerate is of some interest. Available models favour deposition either as subaqueous fans laid down in front deltas (R. Otter, pers. comm. in Nysteun 1982), coarse sheet

flows being deposited directly into the basin, or a fluvial delta becoming reworked into a submarine environment Bjørlykke *et al.* (1976). In any event it appears that numerous features apparently indicate deposition in a submarine environment. Carbonate and phosphate clasts in the lower part of the formation are believed to have been eroded from early transgressive shallow shelf carbonate deposits in the Biri Formation (Bjørlykke 1966; Spjeldnæs 1967). Complex acritarchs occur sporadically in the Biskopås Conglomerate and in the Biri Formation (Vidal and Nystuen, unpublished data). On the other hand, as in many previous reported occurrences (see above), greywackes and hemipelagic mudstones from the turbidite-dominated Brøttum Formation yield a monotonous assemblage consisting of benthic (possibly reworked) and planktonic cyanobacterial microfossils.

SYSTEMATIC PALAEOONTOLOGY

The symbol v* means that the type specimen of the species has been examined.

All specimens come from a single petrographic thin-section of a phosphorite pebble from the basal part of the Biskopås Conglomerate (for details see Spjeldnæs 1963, 1967) with specimen number PMO 73173. The number refers to the collections of the Palaeontological Museum, Oslo. England Finder coordinates are herein provided for figured microfossil specimens (thin-section label orientated to left side of the microscope stage).

Group ACRITARCHA Evitt, 1963

Genus ERICIASPHAERA gen. nov.

Type species. Ericiasphaera spjeldnaesii gen. et sp. nov.

Diagnosis. As for the type and only species of the genus, *Ericiasphaera spjeldnaesii*.

Derivation. From the Latin *ericus*, meaning hedgehog, referring to the spiny appearance, and *sphaera* meaning 'sphere', a spiny, hedgehog-like sphere.

Ericiasphaera spjeldnaesii sp. nov.

Plate 1, fig. 1

v* 1985 *Comasphaeridium?* sp. Yin, p. 239, pl. 2, figs. 1 and 2; text-fig. 12.

v* 1985 *Baltisphaeridium* sp. Yin, p. 239, pl. 4, figs. 5–8.

v* 1987 *Baltisphaeridium maximum* sp. nov., Yin, p. 439, pl. 14, figs. 14 and 15.

Diagnosis. Large, spherical or spheroidal vesicle which bears numerous evenly scattered, simple, conical processes. Processes are solid and lack communication with the vesicle cavity. Processes are closely arranged, with conical-shaped bases which taper into cilia-shaped distal portions. Diameter of the vesicle cavity is about 280 μm . Diameter of the periphery including the processes is about 300 μm . Space between conical shaped bases is 2–4 μm . Length of processes is 6–10 μm .

Holotype. Specimen PMO 73173, England Finder coordinate H/35. Pl. 1, fig. 1.

Derivation. Named in honour of Professor Nils Spjeldnæs.

Type locality. Lower part of Biskopås Conglomerate (Spjeldnæs 1963, p. 65) at locality Hjellund. Topographic Map Sheet Gjøvik, UTM coordinates 585400/676900.

Description. The holotype and only specimen in the present material is strongly deformed, thus providing an irregular section of the vesicle. The digitalized periphery was converted into a circular projection, which indicates that the minimum diameter of the vesicle cavity could have been at least 277 μm . The restored circular

periphery of the distal end of processes indicates a diameter of about 292 μm . The space between the conical-shaped bases is 2–4 μm . Digitalized measurements of the processes indicate lengths of 6–10 μm (\bar{x} = 7.6 μm , σ = 1.68 μm , nine measurable processes). A reconstruction of *E. spjeldnaesii* is shown in text-fig. 2.

Discussion. *B. maximum* Yin (1987) and other microfossils from the late Proterozoic, Doushantuo Formation in western Hubei, China (Yin 1985, 1987) were examined during 1983 and colour micrographs were produced. The microfossils are rare, and occur in black early diagenetic chert within dolomitic limestones of the Doushantuo Formation (Yin 1985). The diagnosis given by Yin (1987) indicates with some uncertainty a diameter of 215–345 μm for the apparently only section of the single-walled vesicle. Digitalized images of colour micrographs suggest a minimum diameter comparable to that calculated for *E. spjeldnaesii*. The major difference is in the closely spaced conical-shaped processes of *B. maximum*, but this feature appears to vary considerably on parts of the section of the apparently only available specimen. From the examination of the holotype it is evident that the processes are simple and solid, having conical bases. No connection could be observed between the vesicle cavity and the thin processes. This excludes the specimen from the most diagnostic feature of the Lower Palaeozoic acritarch genus *Baltisphaeridium*. Furthermore, *B. maximum* displays dimensions and a vesicle diameter/process length relationship different from Palaeozoic forms. The estimated minimum diameter for the preserved section of this specimen is c. 300 μm (length = 197–232.5 μm , width = 99–112.5 μm ; Yin 1985). It thus appears likely that *B. maximum* is most likely conspecific with *E. spjeldnaesii*.

Some doubts remain on the taxonomic attribution of the specimen described by Yin (1985) as *Comasphaeridium* sp. This has to do with the more widely spaced and longer processes. However, this kind of discrepancy might be within the acceptable limits of the same acritarch taxon. In any event the specimen has overall dimensions and vesicle diameter/process length relationship not seen among species of *Comasphaeridium* Staplin *et al.* (1965). Yin (1985) also expressed strong uncertainty as for the taxonomic attribution.

The late Proterozoic, Upper Riphean *Nucellohystrichosphaera megalea* Timofeev, in Timofeev *et al.* (1976) and *Trachyhystrichosphaera aimika* German, in Timofeev *et al.* (1976) (undoubtedly conspecific with the former) bear a superficial resemblance to *E. spjeldnaesii*. The type material of *N. megalea* and *T. aimika*, and another similar species, *T. vidalii* Knoll (1984) has been examined. *T. vidalii* has membrane-bounded tubular processes and is very different from any of the forms under discussion. *N. megalea* and *T. aimika* possess cylindrical processes and differ substantially from the taxa discussed in this paper. However, it deserves mentioning that the diagnoses of both taxa are extremely generalized and that they take into account non-diagnostic features such as compactional folds, colour and presence of condensed intra-vesicular organic matter.

Genus PAPILOMEMBRANA Spjeldnæs emend.

Type species. *Papillomembrana compta* Spjeldnæs emend.

Diagnosis (emended). As for *Papillomembrana compta*. Type and only known species of the genus.

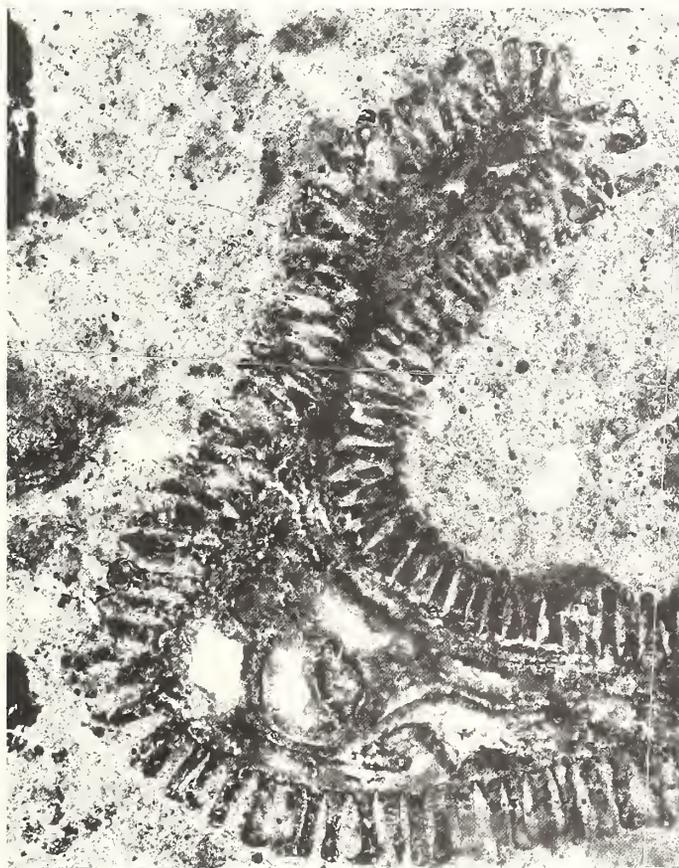
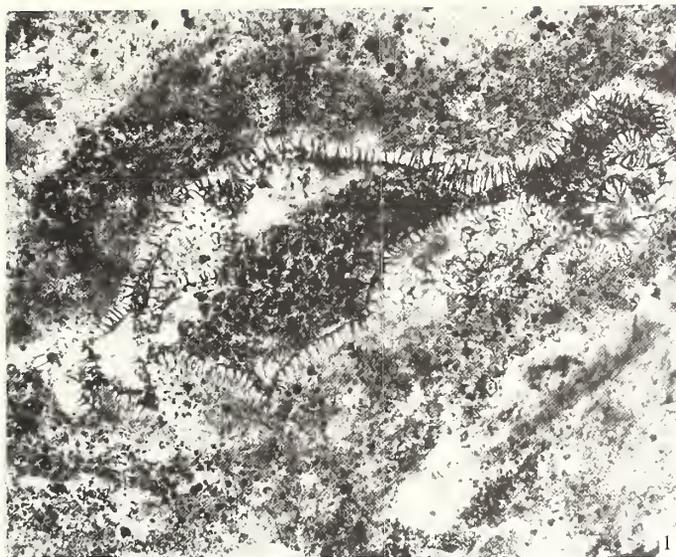
EXPLANATION OF PLATE I

Specimen number refers to the collections of the Palaeontological Museum, Oslo. England Finder coordinates are given for each microfossil specimen (label orientated on left side of microscope stage).

Fig. 1. *Ericiasphaera spjeldnaesii* gen. et sp. nov. (holotype). Specimen PMO 73173, England Finder coordinates H/35. Transmitted light micrograph, $\times 240$.

Fig. 2. *Papillomembrana compta* emend. Vidal. Specimen PMO 73173, England Finder coordinates V/33. Transmitted light micrograph, $\times 190$.

Fig. 3. *Papillomembrana compta* emend. Vidal (holotype). Specimen PMO 73173. England Finder coordinates R/31. Transmitted light micrograph, oil immersion, $\times 240$.



VIDAL, *Ericiasphaera*, *Papillomembrana*

Papillomembrana compta Spjeldnæs emend.

Plate 1, figs. 2 and 3; Plate 2, figs. 1–3

v* 1963 *Papillomembrana compta* gen. et sp. nov. Spjeldnæs, p. 63, figs. 1–3.v* 1967 *Papillomembrana compta* Spjeldnæs; Spjeldnæs pp. 78, 79, pl. 1, figs. 1–3; pl. 2, fig. 1.

Diagnosis (emended). Large, spherical or spheroidal vesicles which bear numerous (> 131 on the holotype) evenly spaced, tightly arranged processes. The processes are hollow, cylindrical, with angular proximal contacts and bulbous or bifurcated distal ends. Connection between vesicle and process cavity is not evident. Diameter of the inner cavity is c. $518 \mu\text{m}$, while the diameter of the total periphery including processes is c. $768 \mu\text{m}$. Length of processes is $30\text{--}42 \mu\text{m}$ ($\bar{x} = 36.5 \mu\text{m}$, $\sigma = 3.1 \mu\text{m}$, $n = 30$), with bases $9\text{--}13 \mu\text{m}$ in width ($\bar{x} = 11.6 \mu\text{m}$, $\sigma = 1.6 \mu\text{m}$, $n = 9$), while the width of the top of the processes is $7\text{--}15 \mu\text{m}$ ($\bar{x} = 9.6 \mu\text{m}$, $\sigma = 1.8 \mu\text{m}$, $n = 20$). Wall thickness not measurable.

Holotype. PMO 73173, England Finder coordinates R/31. Pl. 1. fig. 3.

Type locality. Lower part of Biskopås Conglomerate (Spjeldnæs 1963, p. 65) at locality Hjellund. Coordinates on the Topographic Map Sheet Gjøvik, UTM coordinates 585400/676900.

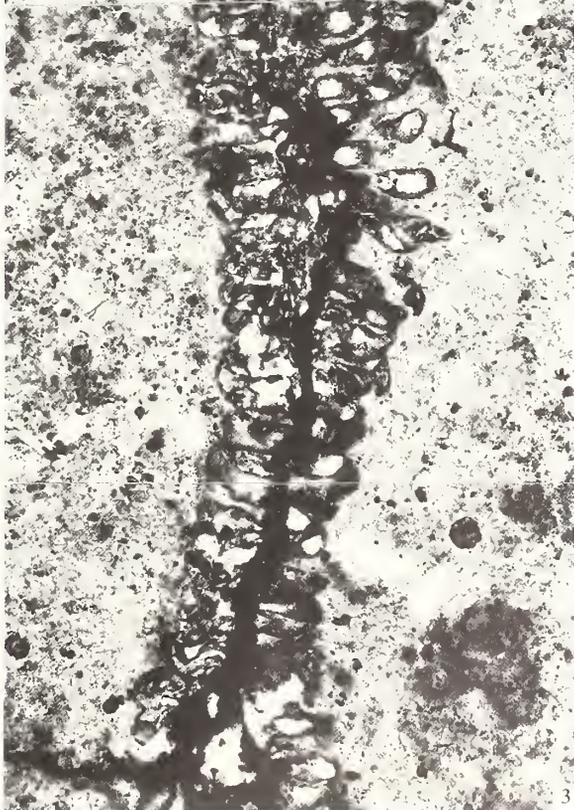
Description. The holotype of *P. compta* is deformed, a feature which results in an irregular section of the vesicle. The compressed vesicle has vertically standing processes, a feature which can be observed at the right corner of the micrograph on Pl. 1, fig. 3 (holotype). This indicates that the whole surface of the vesicle was probably covered with cylindrical, bulbous processes (text-fig. 3). Digitalized added images produced from optical sections of the rather thick petrographic thin-section appear to support this conclusion. The digitalized peripheries of the three best-preserved specimens (Pl. 1, figs. 2 and 3, Pl. 2, figs. 1 and 2) were converted into circular projections which indicate the minimum diameters of the sectioned specimens. In the case of the holotype (Pl. 1, fig. 3), the measured inner diameter is $517.8 \mu\text{m}$, while the diameter of the outer periphery including the processes is $767.7 \mu\text{m}$. The inner diameter of the specimen in Pl. 2, fig. 2 is $331.5 \mu\text{m}$. The outer diameter is c. $381 \mu\text{m}$. These dimensions are probably not more than rough estimates since the specimen is completely compressed and the inner cavity is not evident. The same appears true of the specimen in Pl. 1, fig. 2. The holotype (Pl. 1, fig. 3) displays irregular convolute organic strands, most likely irregularly folded, condensed cellular remains. However, it cannot be excluded that they may constitute a deformed inner layer of the vesicle wall.

Discussion. Spjeldnæs (1963, p. 63) pointed out some superficial resemblance to dasycladacean green algae. He also indicated that the fossil is not carbonate encrusted, a feature which, although common, is not general among dasycladaceans. The general features of the dasycladacean thallus, which has an undivided erect axis bearing whorls of simple or bifurcated lateral branches, are in any event missing in *Papillomembrana*. The taxonomic affiliation of the fossil remains unknown and is here treated among the acritarchs. Nevertheless, this does not exclude the possibility that the fossil(s) could be reproductive structures of thallophytes (e.g. cysts, aplanospores or zygotes). There is compelling evidence indicating that metaphytic green and red algae were extant in late Proterozoic times (Hofmann 1985; Butterfield *et al.* 1988; Zhang 1989; Vidal 1989). It is evident

EXPLANATION OF PLATE 2

Specimen number refers to the collections of the Palaeontological Museum, Oslo. England Finder coordinates are given for each specimen (label orientated on left side of microscope stage).

Figs. 1–3. *Papillomembrana compta* emend. Vidal. 1, low magnification view showing surrounding phosphate matrix, specimen PMO 73173, England Finder Coordinate V/29, $\times 67$. 2, poorly preserved specimen, specimen PMO 73173, England Finder coordinates K/41, $\times 200$. 3, detail view of specimen in 1, note the hollow processes, England Finder coordinate as for specimen in fig. 1. Transmitted light micrograph, $\times 200$.



that *P. compta* resembles a number of comparatively large pre-Phanerozoic acritarchs, and another 'acritarch-like' form (*E. spjeldnæsii*) was found in the same sample.

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A DISCOGLOSSID FROG FROM THE MIDDLE JURASSIC OF ENGLAND

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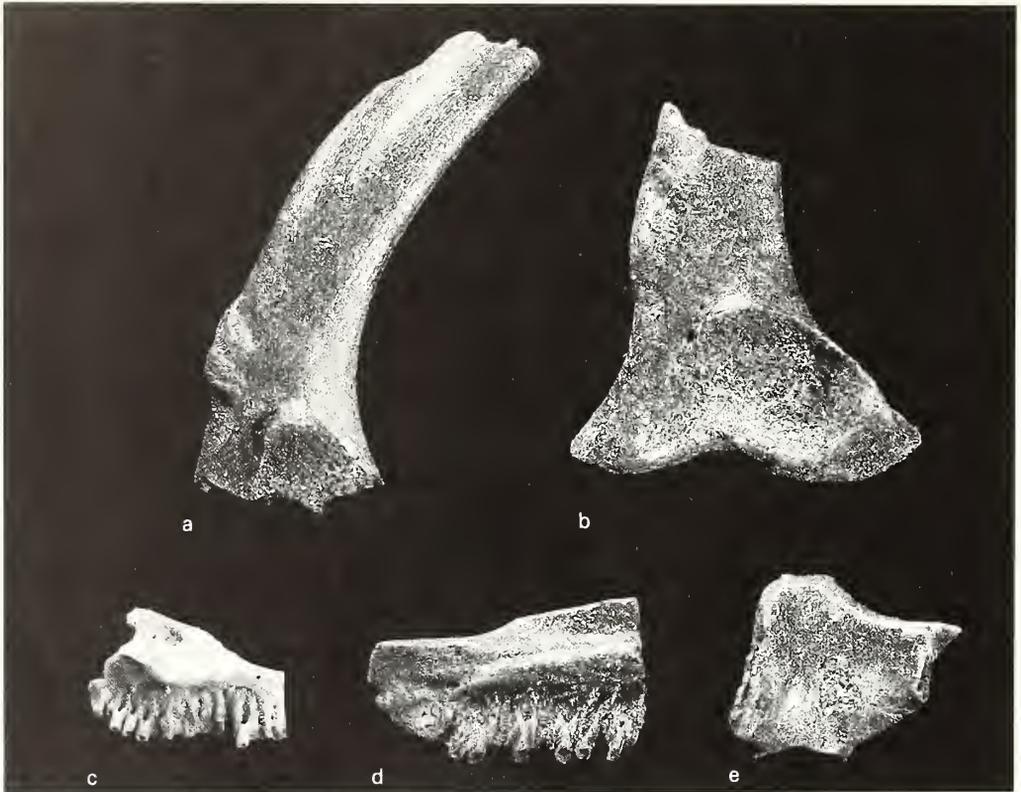
ABSTRACT. A discoglossid frog, *Eodiscoglossus oxoniensis* sp. nov. is described from the Upper Bathonian Forest Marble of Oxfordshire. It closely resembles *Eodiscoglossus santonjae* from the Jurassic-Cretaceous boundary of Spain but can be distinguished by characteristics of the ilium and premaxillary. The *E. oxoniensis* specimens represent the earliest European material critically identifiable as a frog and the earliest discoglossid yet recognised. An association of *Eodiscoglossus* with *Albanerpeton* and a *Marmorerpeton*-like salamander may have characterized certain freshwater ecosystems in Europe for about 50 million years from the Bathonian to the Barremian-Aptian.

THE fossil record of frogs prior to the Cretaceous is poor. The single specimen of *Triadobatrachus* from the Lower Triassic of Madagascar demonstrates that stem-anurans with just a few anuran skeletal characteristics had evolved by the beginning of the Mesozoic (Rage and Roček 1986, 1989; Milner 1988). However, no other Triassic anurans are known and few frogs have been described from Jurassic rocks, although these are all crown-group representatives with the full suite of anuran skeletal characteristics. They are known from eight localities and are reviewed in the discussion (below).

The Middle Jurassic frog material described here was obtained from the microvertebrate assemblage in the Kirtlington Mammal Bed at Kirtlington in Oxfordshire from which Freeman (1979) first recorded frog material. It represents the first discoglossid frog to be reported from pre-Upper Jurassic rocks and also the earliest known critically determinable frog material from Europe. The specimens described and figured here were collected either by Professor K. A. Kermack and colleagues or by Mr E. F. Freeman and have been donated to the Department of Palaeontology, British Museum (Natural History) (BMNH). Mr Freeman is undertaking palaeoecological work with his collections and the specimens collected by him retain his catalogue number (prefixed by EF). Comparative study was also made of *Eodiscoglossus* material at the Museum National d'Histoire Naturelle, Paris (MNHN).

LOCALITY AND HORIZON

The new material was collected from various parts of the Old Cement Works Quarry, near Kirtlington in Oxfordshire, (Ordnance Survey Grid Reference SP 495200; Freeman 1976, 1979; Kermack *et al.* 1987). The techniques of collection and preparation of microvertebrates from this locality were described by Kermack *et al.* (1987). The productive horizon is the Kirtlington Mammal Bed, near the base of the Forest Marble, which is of Upper Bathonian age (approximately 170 Ma; Harland *et al.* 1982). A full account of the local stratigraphy is given by Freeman (1979). The palaeoenvironment appears to have been a shallow non-stagnant water body, with occasional influxes of poorly sorted sediment (Freeman 1979). The Mammal Bed has produced a rich microvertebrate fauna of which only some of the mammals (Freeman 1976, 1979; Kermack *et al.* 1987) and salamanders (Evans, Milner and Mussett 1988) have been described so far.



TEXT-FIG 1. *Eodiscoglossus oxoniensis* n. sp. a, BMNH R. 11700, holotype right ilium in lateral aspect; b, BMNH R. 11720, right ilium in lateral aspect; c, BMNH R. 11703, right premaxillary in lingual aspect; d, BMNH R. 11704, right maxillary in lingual aspect; e, BMNH R. 11707, atlas centrum in dorsal aspect.

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA

Order ANURA

Suborder DISCOGLOSSOIDEI Sokol, 1977

Family DISCOGLOSSIDAE Guenther, 1859

Genus EODISCOGLOSSUS Villalta, 1957

Type species. *Eodiscoglossus santonjae* Villalta, 1957.

Range. Bathonian to Barremian/Aptian; Spain and Great Britain.

Diagnosis. Discoglossid frog resembling *Discoglossus* in one derived character: ilium with dorsal crest and dorsal tubercle; and several primitive characters: 15–18 premaxillary teeth, about 50 maxillary teeth, coronoid process smooth and convex with no notches, anterior vertebrae bearing free ribs and posterior vertebrae bearing no ribs, iliac synchondrosis absent.

Discussion. *Eodiscoglossus* has no apomorphic characters, but is more plesiomorphic than *Discoglossus* in at least three features: pterygoid process of maxillary poorly developed, elongate flattened atlantal cotyles, neural arches lacking upturned flared posterior margins. It is more

plesiomorphic than the similar *Wealdenbatrachus* from the Barremian/Aptian of Uña, in that the ilium bears a single dorsal tubercle whereas *Wealdenbatrachus* has a pair of tubercles in this position.

The diagnosis is based on characters, most of which can be seen in both the Montsech and the British material. It is not entirely satisfactory in that there are no apomorphic characters for the genus, and it is probable that *Eodiscoglossus*, as defined here, is a primitive grade of *Discoglossus*-group discoglossid. However, as *E. oxoniensis* lacks obvious autapomorphic characters and clearly has a close phenetic resemblance to *E. santonjae*, a new genus cannot be justified and it is most practical to place both species in one genus.

Eodiscoglossus oxoniensis sp. nov.

Text-figures 1-4d, 5, 6a-c.

Derivation of name. From the county of Oxfordshire.

Holotype. British Museum (Natural History) Department of Palaeontology R. 11700, a right ilium lacking the end of the iliac blade and part of the acetabulum (text-figs. 1a, 6a, 6b).

Paratypes. BMNH R. 11701 (EF 75:10:1:6), R. 11720, 2 right ilia with fully preserved acetabular regions (text-figs. 1b and 6c); R. 11702, 11703, 2 right premaxillaries (text-figs. 1c, 2a-c); R. 11704, 11705, 2 right maxillaries (text-figs. 1d, 2e, f); R. 11707, R. 11708, 2 broken atlas centra (text-figs. 1e and a-e).

Referred material. 5 premaxillaries, 33 maxillaries, 9 angulosplenials (including R. 11706), a broken atlas (R. 11721), 30 isolated neural arches (including R. 11709-R. 11712), 7 broken scapulae (including R. 11722, R. 11723), 2 right humerus distal heads (R. 11713, R. 11714), a radioulna (R. 11715), 51 ilia, 2 ischia (including R. 11716 (EF 76:13/14:36:4)) and 10 tibiofibulae (including R. 11718 (EF 75:3:1:10) and R. 11719 (EF 76:4:1:2)).

Locality. Old Cement Works Quarry, Kirtlington, Oxfordshire, England, Ordnance Survey Grid Reference SP 495200.

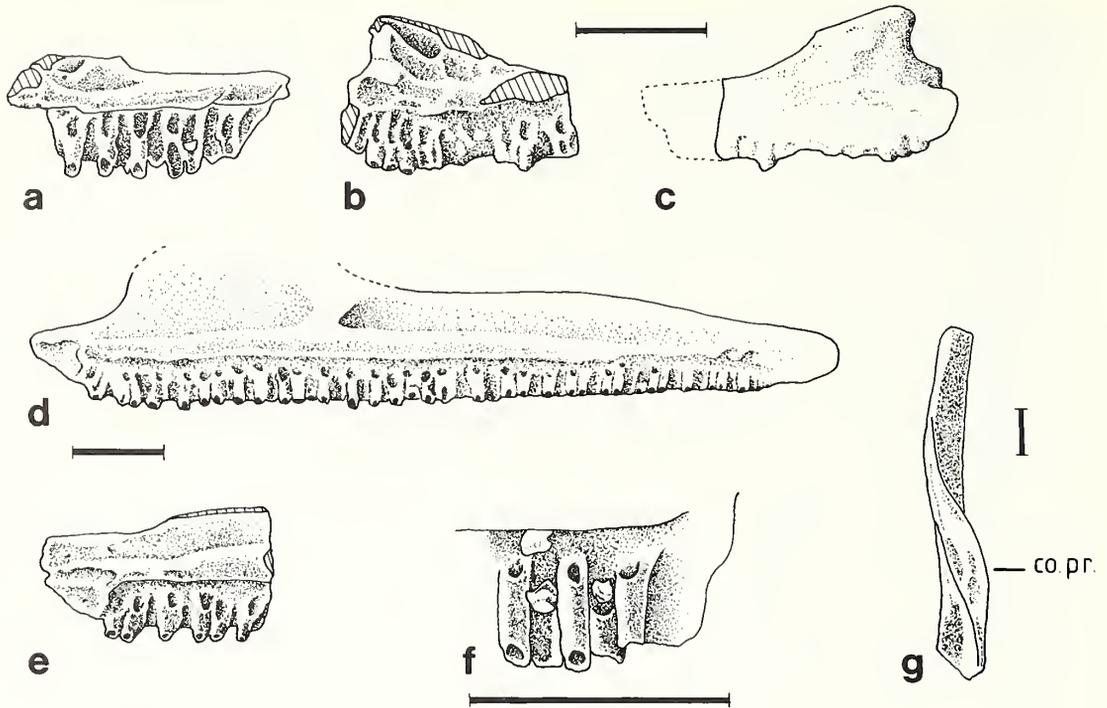
Horizon. Kirtlington Mammal Bed, near base of the Forest Marble, *aspidioides* Zone, Upper Bathonian, Middle Jurassic.

Diagnosis. Species of *Eodiscoglossus* in which the ilium shows the following features in contrast to that of *E. santonjae*: iliac shaft flattened and broad but narrow in cross-section with lateral ridge; little waisting at the junction of the shaft and the acetabular region; dorsal tubercle poorly developed, shallow and flush with the surface of the iliac shaft; supraacetabular fossa deep. The premaxillary of *E. oxoniensis* apparently has a low alary process in contrast to the elongate process of *E. santonjae*. Other bones appear to be indistinguishable in the two species.

DESCRIPTION

General features

The present material comprises about 160 elements as listed above. Scaled against skeletons of *Rana temporaria*, the larger elements belong to medium-sized frogs of 80 mm snout-vent length, although many of the bones derive from smaller animals. There is no more than one morphological type of any given bone and this, coupled with the numbers of ilia (53) and maxillaries (35), strongly suggests that only a single form is present. The bones are either diagnostically discoglossid or consistent with attribution to the Discoglossidae and so unity of the material is assumed.



TEXT-FIG. 2. *Eodiscoglossus oxoniensis* n. sp. *a*, BMNH R. 11702, right premaxillary in lingual view; *b*, *c*, BMNH R. 11703, right premaxillary in *b*, lingual and *c*, labial views; *d*, reconstruction of right maxillary in lingual view; *e*, BMNH R. 11704, anterior region of right maxillary in lingual view; *f*, BMNH R. 11705, detail of partial right maxillary showing pedicels and developing crowns of teeth; *g*, BMNH R. 11706, left angulosplenial in dorsal view. Scale bars = 1 mm. Abbreviation: co. pr. coronoid process.

Skull

Premaxillary (text-figs 1*c* and 2*a-c*). Seven specimens were collected, none of which is complete. The premaxillary has a broad pars dentalis with at least 15 tooth positions (about 18 in *E. santonjae*, Vergnaud-Grazzini and Wenz, 1975, p. 22). The lateral region of the pars dentalis is long and the medial region is short, as in other discoglossids including *E. santonjae*. The alary process is low and of moderate width, quite unlike that of other discoglossids including *E. santonjae* in which this process is as tall as the bone is wide (e.g. Vergnaud-Grazzini and Wenz 1975, fig. 1). It is convex anteriorly and concave posteriorly, with a deep medial excavation which probably received a peg of cartilage from the nasal capsule (text-figs. 1*c* and 2*b*). At the anteromedial junction of the alary process and the pars dentalis, there is an excavation showing that the alary processes were separated in the midline. The pars palatina (palatal shelf) is narrow laterally and wider medially. At the medial end, it curves sharply backwards into a medial expansion. The end of this expansion is incomplete, so it is not possible to determine whether it was pointed or blunt posteriorly.

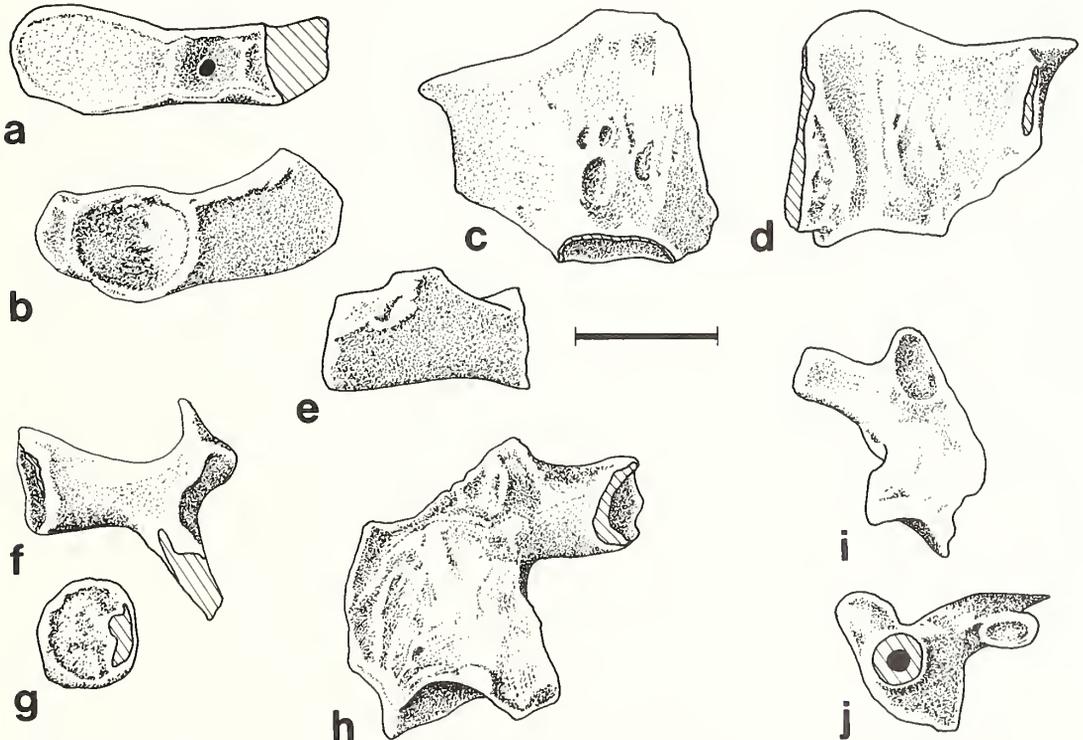
Maxillary (text-figs. 11*d* and 2*d-f*). About 35 maxillaries were recovered, none of which is complete. The pars dentalis is long and bears approximately 50 tooth positions, a similar number to that in *E. santonjae*. The pars facialis is long and divided into three regions:

- (i) a straight, narrow anterior process with a medial, slightly concave overlap surface for the premaxillary, anterior to the tooth-row (text-fig. 2*e*);
- (ii) behind the anterior process, the bone expands dorsally for a short distance back to the leading edge of the orbit;
- (iii) further back, the bone levels off and runs back as a low wall below the orbit.

Medially, at the level of the anterior orbital border, the maxillary bears a depression which opens into a foramen for the superior alveolar nerve. Laterally, the maxillary bears a shallow longitudinal groove at the level of the base of the tooth row. Otherwise the lateral face of the bone is featureless except for several small sensory nerve foramina. The pars palatina, or palatal shelf, begins just behind the anterior process of the bone as a low rounded ridge. Posteriorly, however, this expands into a small narrow shelf – the pterygoid process – where the lateral part of the pterygoid abuts against the maxillary. This process ends at the same level as the tooth row, but the bone continues for a short distance behind the tooth row although the posterior tip is not preserved in our material. The shape of the maxillary bears a close resemblance to that of *Wealdenbatrachus* (Fey 1988, fig. 22).

Dentition (text-fig. 2f). The premaxillary and maxillary teeth are slender and pedicellate. The crowns are always lost on fully erupted teeth but several specimens show isolated crowns either at the tooth bases or moving into position on broken teeth. The crowns are small and bicuspid, and show no other obvious specialization. Hecht (1970) regarded the maxillary of *Eodiscoglossus* as toothless, but the material described by Vergnaud-Grazzini and Wenz (1975, fig. 1) shows that *E. santoniae* has toothed premaxillaries and maxillaries.

Angulosplenial (text-fig. 2g). The angulosplenial is represented by nine specimens. It bears a coronoid process which is a long low convex bulge with no anterior or posterior notches.

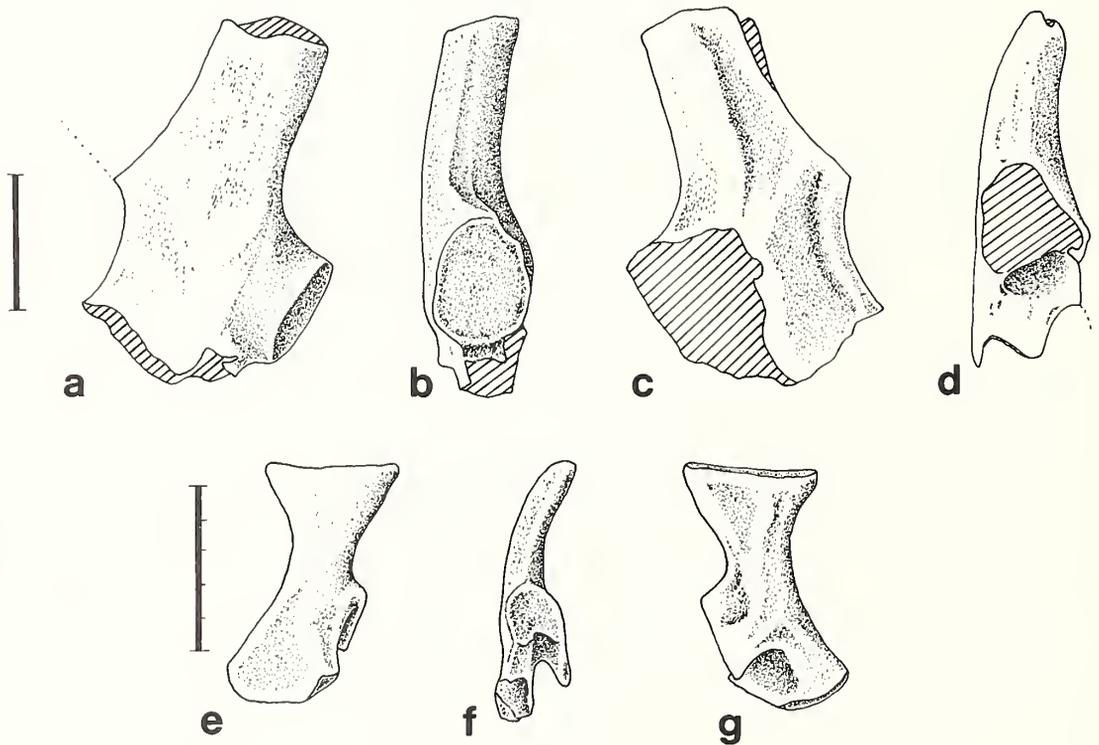


TEXT-FIGURE 3. *Eodiscoglossus oxoniensis* n. sp. *a-d*, BMNH R. 11707, atlas vertebra in *a*, anterior, *b*, posterior, *c*, ventral and *d*, dorsal views; *e*, BMNH R. 11708, atlas vertebra in left lateral view; *f*, *g*, BMNH R. 11709, anterior trunk vertebral arch in *f*, anterior view and *g*, lateral view of rib facet; *h*, BMNH R. 11711, posterior trunk vertebral arch in dorsal view; *i*, *j*, BMNH R. 11712, posterior trunk vertebral arch in *i*, dorsal and *j*, lateral views. Scale bar = 1 mm.

Axial skeleton

Atlas vertebra (text-figs. 1e and 3a-e). Three incomplete atlantal centra were recovered. The atlantal centrum is dorsoventrally flattened. The anterior cotyles are of depressed oval shape. Medially, they are moderately separated by an intercotylar region bearing a small notochordal pit (text-fig. 3a), but with no medial notch as seen from above or below. The long axes of the anterior cotyles are not horizontal but are orientated at a shallow obtuse angle. Posteriorly, there is a small circular cotyle which may be imperforate (R. 11707, 11708) or perforate (R. 11721). The presence of this cotyle implies that the following trunk vertebra is opisthocelous with an anterior condyle. The atlantal centrum is anteroposteriorly short but broad. The ventral surface is smooth except for a few small pits on either side of the midline. The dorsal surface is concave, with weak grooves on either side of a small rounded central ridge. The neural arch pedicel is broad-based but narrows dorsally, leaving an anterolateral notch for the exit of the first spinal nerve, and a long sloping posterolateral border. This atlas with such flattened, slightly separated anterior cotyles corresponds to the type II atlas of Lynch (1971). The distinction between this and the Lynch type III atlas in which the cotyles are confluent, is not always clear. Trueb (1973) identified the atlas of the extant leiopelmatids as type III but now considers them to be type II (pers. comm. in Clarke, 1988). Estes and Sanchíz (1982*b*) identified the atlas of the Galve material of *E. santonjae* as type III, but it appears to be very similar to the atlantal centrum described here. The degree of separation of the cotyles is apparently variable and not always clear in imperfect material. The apparent difference between the type II atlas of *E. oxoniensis* and the type III atlas of *E. santonjae* described by Estes and Sanchíz may not be of great significance.

Trunk vertebrae (text-fig. 3f-j). No complete trunk vertebrae were collected, although over 30 broken neural arches were recovered. The vertebrae have very narrow pedicels and lightly built arches which are apparently

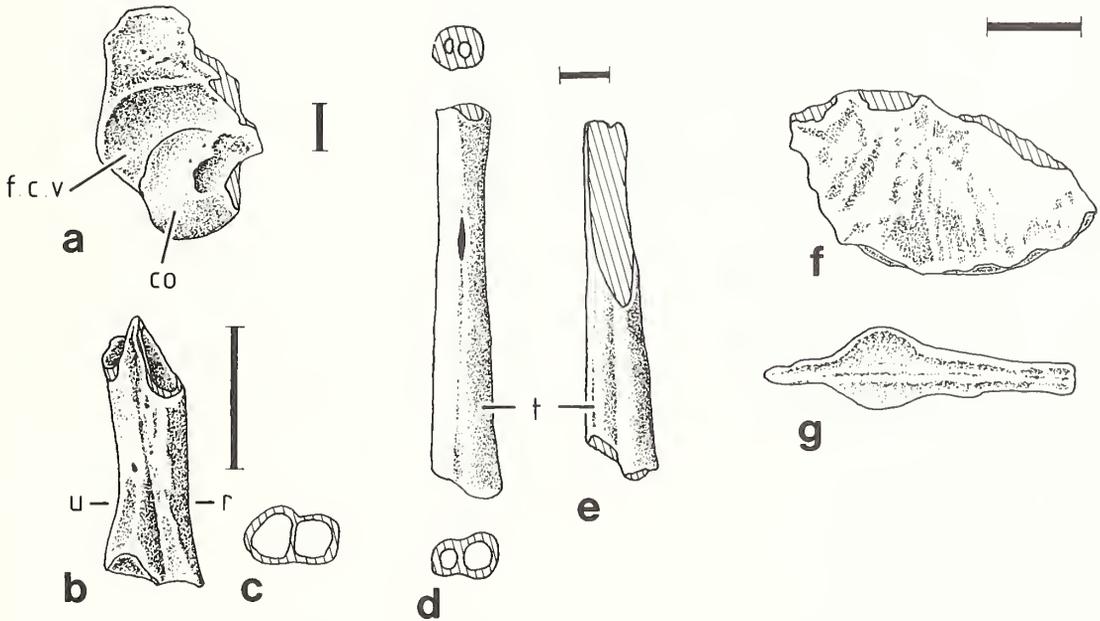


TEXT-FIG. 4. *Eodiscoglossus oxoniensis* n. sp. a-c, BMNH R. 11722, broken left scapula in a, lateral, b, posterior and c, medial views; d, BMNH R. 11723, broken left scapula in posterior view; e-g, *Rana temporaria*, left scapula in e, lateral, f, posterior and g, medial views. Scale bars = 1 mm (a-d), 5 mm (e-g).

easily broken. The neural arches are flattened, with almost horizontal pre- and postzygapophyses. The pedicel is narrow and there is a small horizontal backwardly-directed neural spine between the postzygapophyses (e.g. text-fig. 3*h*, *i*). Between the neural spine and the postzygapophyses, the posterior surface of the arch is excavated into deep pockets for intervertebral ligaments. The neural arches were probably imbricate but there is no suggestion of flaring of the posterior margin as in some discoglossids. Each pedicel bears a slender transverse process, usually broken at the tip. In a few isolated arches, however, the lateral process is expanded distally and bears a pitted terminal surface for the attachment of a free rib (text-fig. 3*f*, *g*). Other lateral processes were not terminally expanded and presumably bore no rib, not even a rudiment (text-fig. 3*i*). In *E. santonjae* and *Wealdenbatrachus*, free ribs are present on the anterior presacrals only and this appears to have been the condition in *E. oxoniensis*. Although no trunk centra are known, the presence of a posterior cotyle on the atlantal centrum means that the first trunk vertebra must have had an anterior condyle and have been opisthocoelous. In the absence of other evidence, all the presacral trunk vertebrae are assumed to have been opisthocoelous. Only three frog families have such presacral vertebrae, namely the Discoglossidae and the pipoid families Rhinophrynidae and Pipidae.

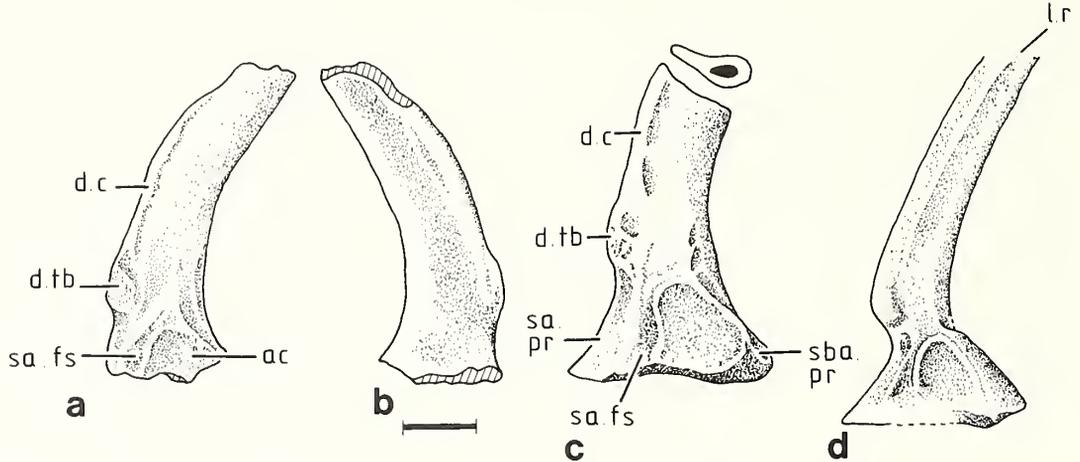
Appendicular skeleton

Scapula (text-fig. 4*a-d*). Of the pectoral girdle elements only 7 broken scapulae have been recovered. They are all too incomplete for the general shape to be determined and a scapula of *Rana temporaria* is figured comparatively (text-fig. 4*e-g*) to clarify the orientation of the fragment figured in text-fig. 4*a-c*. The scapulae appear to have been bicapitate, i.e. with separate articulations for the clavicle (pars acromialis) and coracoid (pars glenoidalis). Although the pars acromialis is not visible on any specimen, it is clear that there is a distinct pars glenoidalis demarcated ventrally by a deep pocket (text-fig. 4*d*) which must have separated the ventral region of the scapula into two heads.



TEXT-FIG. 5. *Eodiscoglossus oxoniensis* n. sp. *a*, BMNH R. 11713, distal head of right humerus in ventral view; *b*, *c*, BMNH R. 11715, left radioulna in *b*, ventral and *c*, cross-sectional views; *d*, BMNH R. 11718, incomplete tibiofibula, midshaft region together with proximal and midshaft cross-sections; *e*, BMNH R. 11719, incomplete tibiofibula, distal shaft region; *f*, *g*, BMNH R. 11716, ischial plate in *f*, right lateral and *g*, ventral views. Scale bars = 1 mm. Abbreviations: co, articular condyle; f.c.v. fossa cubitus ventralis; r, radius; t, tibia; u, ulna.

Fore-limb (text-fig. 5a-c). Of the fore-limb bones, only the distal heads of two humeri (R. 11713 and R. 11714) and a left radioulna (R. 11715) have been recovered. The shape of the humeral heads suggests that both derive from right humeri, but there is little preserved except the hemispherical articular condyle and a deep fossa cubitus ventralis (Estes and Sanchiz 1982b). The radioulna is distinguished from the tibiofibulae by its shorter broader shape (text-fig. 5b, c). There is a prominent radioulnar groove along the visible length of the specimen, a very primitive feature, but as the specimen derives from a very small individual, this may simply reflect immaturity.



TEXT-FIG. 6. *Eodiscoglossus oxoniensis* n. sp. a, b, BMNH R. 11700, holotype right ilium in a, lateral and b, medial views; c, BMNH R. 11701, right ilium in lateral and cross-sectional views; d, *Eodiscoglossus santonjae* MNHN MSE.5, right ilium. Scale bar = 1 mm. Abbreviations: ac. acetabulum; d.c. dorsal crest; d.tb. dorsal tubercle; l.r. lateral ridge; sa.fs. supraacetabular fossa; sa.pr. supraacetabular process; sba. pr. subacetabular process.

Ilium (text-figs. 1a, b and 6a-c). More than 50 ilia were collected, most showing only the thickened acetabular region. Three specimens, R. 11700 (the holotype), R. 11701 and R. 11720 show the important features. The following description uses the terminology of Vergnaud-Grazzini (1966). The iliac shaft is broad, anteriorly recurved and mediolaterally flattened (text-fig. 6c). The dorsal crest is moderately developed and separated from the smooth convex lateral surface by a narrow groove. Posteriorly, at the base of the shaft, the ilium bears an elongate but shallow tubercle (for the *musculus iliofemoralis*), separated from the remainder of the bone by dorsal and ventral pits. The acetabular region is thickened, but its ventral articular surfaces are completely preserved only in two specimens, R. 11701 and R. 11720. The acetabulum is prominent and roughly oval, lying towards the anterior edge of the bone (text-figs. 1b and c). Anterodorsally, a small pit (for the *musculus iliacus internus* Estes and Sanchiz 1982a) separates the acetabular surface from the shaft. Anteroventrally, the bone is drawn out into a small triangular subacetabular process. Posteroventrally, there is a larger supraacetabular process, separated from the acetabulum by a long supraacetabular fossa (text-fig. 1b). The ventral border of the bone is lightly forked, with pitted surfaces for the pubis and the ischium. Medially, the acetabular region shows little detail. There is no evidence of an iliac synchondrosis, although the medial edge of the pubic facet is roughened, suggesting a ligamentous attachment.

In comparison with the ilium of *Eodiscoglossus santonjae* (MNHN MSE. 5) (text-fig. 6d), that of *E. oxoniensis* is similar in general structure but several consistent differences can be itemized.

(i) In cross-section, the iliac shaft of *E. santonjae* is triangular, one corner of the triangle being formed by the prominent lateral ridge which extends up the lateral face of the shaft (text-fig. 6d). In *E. oxoniensis*, there is no lateral ridge and the shaft is narrow in cross-section (text-fig. 6c).

(ii) The shaft of *E. santonjae* is narrow in lateral view whereas that of *E. oxoniensis* is flattened and broad.

(iii) At the junction of the shaft and the acetabular region, the ilium of *E. santonjae* is sharply waisted; this is less marked in *E. oxoniensis*.

(iv) The dorsal tubercle of *E. santonjae* is more prominent than that of *E. oxoniensis*. That of *E. santonjae*

extends well above the surface of the iliac shaft, while the dorsal tubercle of *E. oxoniensis* is shallow and flush with the surface.

(v) The supraacetabular fossa is deeper and more marked in *E. oxoniensis* than in *E. santonjae*.

These features are constant on all the ilia of *E. oxoniensis* recovered and the differentiating characters were constant on those ilia of *E. santonjae* which were examined and serve to distinguish the species.

The ilium of the recently described Cretaceous discoglossid *Wealdenbatrachus jucarensis* (Fey 1988, figs 32–35) is similar in general shape to those of both *Eodiscoglossus* species. In the holotype specimen (Fey 1988, figs. 34 and 35), there is a dorsal tubercle which is prominent like that of *E. santonjae* but there is also an accessory tubercle. This tubercle is not found in either *Eodiscoglossus* species and appears to be the most diagnostic character of *Wealdenbatrachus*. The ilia of the paratype specimens of *Wealdenbatrachus* (Fey 1988, figs. 32 and 33) differ from that of *E. oxoniensis* in that they show greater development of the supra- and subacetabular processes and greater differentiation of the shaft and crest.

Ischium (text-fig. 5f, g). Two specimens of fused ischia were recovered (R. 11716, R. 11717). The compound bone is semicircular with a pitted margin and a pronounced posteroventral ridge radiating out from the acetabular region as in modern *Rana*. The posterior region is not preserved and it is not clear whether there was a posterodorsal expansion or not.

Tibiofibula (text-fig. 5d, e). Ten tibiofibular shafts were recovered (e.g. R. 11718, R. 11719). The larger tibia and smaller fibula are firmly fused, being barely distinct in the central shaft but partly separated by deep grooves towards the proximal and distal ends. The tibiofibulae were long and gracile resembling those of jumping anurans such as *Rana* rather than walking anurans such as *Bufo*.

DISCUSSION

Interrelationships of primitive frogs and the systematic position of E. oxoniensis

The Leiopelmatidae (*Leiopelma*, *Ascaphus*) and Discoglossidae (*Discoglossus*, *Alytes*, *Barbourula*, *Bombina*) are widely perceived as the most primitive families of living frogs. Clarke (1988) has recently completed a 95-character analysis of the osteology of all but one of the living species in these two families (*Bombina fortinuptialis* was not available for study), and has concluded that each family is monophyletic but that their interrelationships are uncertain. The Leiopelmatidae and Discoglossidae are frequently grouped together as the Discoglossoidae or Discoglossoidae, but it is not clear whether this group is a monophyletic sister-clade to the remaining frogs or a primitive grade of frog with the Discoglossidae closer to the higher frogs. Sokol (1975, 1977) has argued that the Discoglossoidae are a clade and that the Discoglossidae and Leiopelmatidae share derived characters of the tadpole branchial system, namely (i) absence of the interbranchialis III muscle and (ii) extensive fusions between the copula II and the hypobranchials. No characters to support this relationship have been found in the adults however and in Lynch's cladogram (1973, fig. 3.6), the Discoglossidae share two characters with the higher frogs, namely: (i) presacral column reduced to eight vertebrae or fewer and (ii) *musculus caudaliopuboischiotibialis* lost. Both sets of characters are small and the interrelationship of leiopelmatids, discoglossids, and higher frogs is effectively an unresolved trichotomy.

Clarke (1988) has used his osteological data to analyse the internal relationships of the extant genera and species of the Discoglossidae. He concluded that *Alytes* is the sister-taxon to the other genera and that, within the remaining forms, *Discoglossus* is the sister-taxon to *Barbourula* and *Bombina*. The following discussion of the characters of *E. oxoniensis* is based, where possible, on the derived characters supporting this hypothesis of relationships.

Eodiscoglossus oxoniensis can be placed within the family Discoglossidae on the basis of two derived characters. Neither is unique to the Discoglossidae, but the combination characterizes only this family and one pipid genus, namely *Hymenochirus*.

(i) Opisthocoealous vertebrae. These only occur in three anuran families, the Discoglossidae, Pipidae and Rhinophrynidae (Trueb 1973). This Kirtlington material shows no other general features of pipids or rhinophrynids.

(ii) Ilium bearing a dorsal crest. Such ilia are found in the Discoglossidae, Leptodactylidae, Ranidae, and the pipid genus *Hymenochirus*, but the Kirtlington material shows no other characteristics of the latter three taxa.

In Clarke's (1988) hypothesis of relationships based on osteology, the subfamily Discoglossinae (*Discoglossus*, *Bombina* and *Barbourula*) is defined by six osteological characters. One is found in *E. oxoniensis*:

(iii) Occipital condyles with major axes at shallow or steep angle. The occiput of *E. oxoniensis* is unknown but the atlantal cotyles slope upwards at a shallow angle and so presumably the occipital condyles must have as well.

Clarke also defines the Discoglossinae by the presence of neural arches with flared posterior margins but these are not present in *E. oxoniensis*.

Other derived features, which occur in some but not all discoglossines, are also found in *E. oxoniensis*. These characters are not distributed congruently with each other, or with other characters within the Discoglossidae (Clarke 1988), but broadly support a relationship between *E. oxoniensis* and the Discoglossinae:

(iv) Imbricated vertebrae. These are found in most but not all discoglossine species.

(v) Groove at the base of the tooth row on the lateral face of the maxillary. This occurs in *Discoglossus* and one species each of *Bombina* and *Barbourula*.

(vi) Neural spines moderately developed. This occurs in *Bombina* and some *Discoglossus* species.

The Kirtlington material can be associated with the genera *Discoglossus*, *Wealdenbatrachus*, and *Eodiscoglossus* on the basis of one derived character:

(vii) The ilium has a distinct dorsal tubercle, not as well-developed as in *E. santonjae* or the other two genera but more so than in other discoglossids (Estes and Sanchíz 1982a; Fey 1988; Clarke 1988). There are no derived characters which suggest immediate relationship to *Alytes*, *Barbourula* or *Bombina*.

The Kirtlington material can be associated with *Eodiscoglossus* on the basis of one character of uncertain polarity:

(viii) The atlas has extremely flattened anterior cotyles (Estes and Sanchíz 1982b).

As noted under the generic diagnosis, there is no certain derived character shared by *E. santonjae* and *E. oxoniensis*, but the phenetic resemblance is sufficiently great that a new genus cannot be justified. Finally, the Kirtlington material merits a separate species because of the differences in ilium and premaxillary construction listed under the species diagnosis and the descriptions of those elements.

Eodiscoglossus oxoniensis does not provide major new insights into the anatomy of early discoglossid frogs. However, it does combine a derived character of *Discoglossus* (ilium with dorsal tubercle) with a primitive feature that places it outside the *Discoglossus-Barbourula-Bombina* group (neural arches lack flared posterior margin). This suggests that the characters used to define the taxa, based on modern material, have either been subject to convergence or reversal, or their polarity is not fully understood. The new material extends the stratigraphical range of the genus *Eodiscoglossus* and the family Discoglossidae down to the Bathonian, and the geographical range of both taxa to include the British Isles. Finally, although the evidence is not strong, such osteological characters as are present suggest that the *Alytes*-group and *Discoglossus-Barbourula-Bombina* group had already differentiated by 170 Ma.

The fossil record of Jurassic frogs

Jurassic frogs have now been described from six localities and reported from a further two. The sole described Lower Jurassic frog is the type and only specimen of *Vieraella herbstii* from the Roca Blanca Formation of Argentina (Reig 1961; Casamiquela 1965; Estes and Reig 1973). Estes and Reig assigned this genus to the Leiopelmatidae (referred to as the Ascaphidae in that work). However, they noted that the leiopelmatid characters of the specimen were all primitive anuran characters and *Vieraella* could equally be a stem-frog with no immediate relationship to any modern

family. It does not prove the existence of a cladistically defined Leiopelmatidae in the Lower Jurassic.

The only Middle Jurassic specimens described in the literature are a possible anuran omosternum from the Bajocian of Aveyron (Seiffert 1969; but see Estes and Reig 1973 for a critical reappraisal) and the Kirtlington material first reported by Freeman (1979) and described in this paper.

Upper Jurassic frogs have been described or reported from five areas as follows.

(i) In the nineteenth century, the Morrison Formation of Como Bluff, Wyoming, U.S.A. produced a few fragments of frog skeleton including two humeri which have been named: *Eobatrachus agilis* Marsh and *Comobatrachus aenigmatis* Hecht and Estes (reviewed by Hecht and Estes 1960; Estes and Reig 1973). The latter authors concluded that the *Eobatrachus* humerus might belong to a pipoid but could not be determined further, while *Comobatrachus* was indeterminate. Estes and Sanchíz (1982*a*) noted that the *Comobatrachus* humerus had some resemblances to those of discoglossids. Further frog material was collected from the Morrison Formation between 1968 and 1970 but has not yet been described (Prothero and Estes 1980, p. 484).

(ii) The Matildense Formation of Argentina has produced several specimens of a frog named *Notobatrachus degiustoi*. Principal descriptions are by Reig (1957), Casamiquela (1961) and Estes and Reig (1973). Estes and Reig assigned *Notobatrachus* to the Leiopelmatidae (as the Ascaphidae).

(iii) The lithographic limestones of the Sierra del Montsech, Lérida, Spain, dated as uppermost Jurassic or basal Cretaceous, have produced several specimens of at least two types of frog. Most are of the discoglossid frog, *Eodiscoglossus santonjae*, which has most recently been described or discussed by Hecht (1963, 1970), Estes and Reig (1973), and Vergnaud-Grazzini and Wenz (1975). A single specimen of a second frog, *Neusibatrachus wilferti*, was described by Seiffert (1972) and it can be assigned to the Palaeobatrachidae (Estes and Reig 1973; Vergnaud-Grazzini and Wenz 1975). A third named form, also based on a single specimen, is *Montsechobatrachus gaudryi* (Vidal 1902). This poor specimen is generally agreed to be indeterminate, although some features suggest that it may be a palaeobatrachid (Estes and Reig 1973; Vergnaud-Grazzini and Wenz 1975).

(iv) Anuran material has been reported, but not described, from the Lower Kimmeridgian lignites of Guimarota, Portugal (Seiffert 1973).

(v) New localities in the Purbeck Formation of Dorset, England have recently produced fragments of an anuran which have not yet been determined (Ensom 1988). This material is currently being studied by two of the authors (S.E.E. and A.R.M.).

The fossil record as yet permits us to make very few testable statements about the evolution and diversification of frogs in the Jurassic. It is clear that true frogs were present in the Lower Jurassic, but there is no evidence for differentiation into recognizable modern families at that time. By the Bathonian, discoglossids were not only present but may have begun to differentiate as discussed above. However, because of the uncertainty of the interrelationships of primitive frog families to higher frogs and to each other, we cannot yet say which other frog families might be expected also to be present. By the Jurassic-Cretaceous boundary, differentiation at least into leiopelmatids, discoglossids, and palaeobatrachids had taken place.

Ecology and chronology

The Kirtlington assemblage is incompletely described at present, but preliminary quantification of the amphibian material suggests that it may in future be possible to recognize the associations or communities which included *Eodiscoglossus*. In the samples studied, the *Eodiscoglossus* material could not have come from fewer than 28 specimens (right ilia). The five other amphibians recognized, together with the minimum numbers of individuals represented, are: *Marmorerpeton kermacki* (19 atlantes), *Marmorerpeton freemani* (1 atlas), a third small salamander (4 atlantes) a primitive salamander (340 atlantes) and an albanerpetontid (1 atlas). It appears that the assemblage incorporated a major association of *Eodiscoglossus*, *Marmorerpeton kermacki* and the primitive salamander, with the other forms as exotic elements in the fauna.

This association may have been long-lived, at least at the family level. Estes and Sanchíz (1982*b*)

described similar material from Galve in Spain, including several specimens each of *Eodiscoglossus*, *Albanerpeton*, and an unnamed *Marmorerpeton*-like salamander. The small salamander *Galverpeton* was represented by only a single specimen. The Galve assemblage is Barremian-Aptian and hence 125–113 Ma in age (Harland *et al.* 1982), so it is possible that an amphibian faunal association of *Eodiscoglossus*, albanerpetontid, and *Marmorerpeton* (or similar forms) may have characterized certain freshwater ecosystems in Europe for over 50 million years from the Middle Jurassic to the late Lower Cretaceous. Testing this association against other faunas might eventually be possible but at present most of the assemblages of Mesozoic lissamphibians from Spain and Portugal (e.g. Guimarota, Uña) are still undescribed.

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Since completion of the manuscript, vertebral material, including a sacrum and urostyle, has been recovered. The trunk centra and sacrum are identical to those figured for *E. santonjae* (Estes & Sanjiz 1982*b*). The urostyle has small anterior transverse processes, as in many recent frogs, and is consistent with attribution to the Discoglossidae.

LATE CAINOZOIC BRACHIOPODS FROM THE COAST OF NAMAQUALAND, SOUTH AFRICA

by C. H. C. BRUNTON *and* N. HILLER

ABSTRACT. An unusual late Tertiary – early Quaternary brachiopod assemblage from shallow water shoreline deposits on the Namaqualand coastal plain of South Africa is described. New species described are *Kraussina rotundata*, *K. laevicostata*, *K. cuneata* and *Cancellothyris platys*, with subspecies *C. platys platys* and *C. platys petalos*. *In situ* specimens, shell growth, abrasion and epizoans all indicate crowded living conditions, commonly on bedrock. Diversity, shell size and shell thickness are consistent with waters having been warmer than in the region today; Atlantic cooling took place from the late Tertiary.

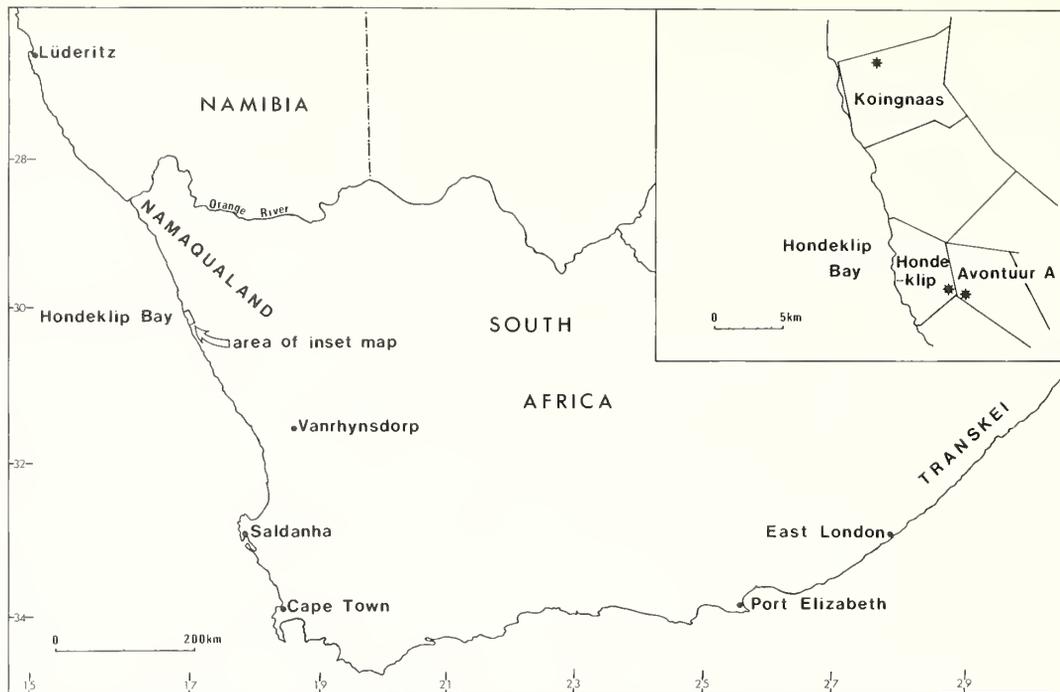
TERTIARY and Quaternary brachiopod faunas are poorly known throughout the world, with a few notable exceptions, such as those from New Zealand or the Mediterranean. Their presence, commonly in shallow marine sediments, can provide important evidence about the marine conditions of their locations during this period of major temperature and sea-level fluctuations. We were delighted, therefore, to be presented with a well-preserved late Cainozoic brachiopod fauna from Namaqualand, South Africa, particularly as it contains representatives of genera much larger than any seen hitherto, and the *in situ* relationship with the bedrock of some species allows the formulation of well-founded palaeoecological conclusions. Faunas such as this help our understanding of the origins of Recent brachiopods and we are able to suggest possible connections between this fauna and the Recent brachiopods of southern Africa.

Since the discovery of diamonds on the west coast of southern Africa (Wagner and Merensky 1928), considerable attention has been given to the nearshore marine sediments of late Tertiary to early Quaternary age, including papers on their contained fossils. Houghton (1932) presented an overview of the west-coast deposits, and described a number of mollusc species and the brachiopod *Kraussina lata*. Since then, papers by Carrington and Kensley (1969), Kilburn and Tankard (1975), Kensley (1972, 1977) and Kensley and Pether (1986) have added to the knowledge of the molluscan fauna.

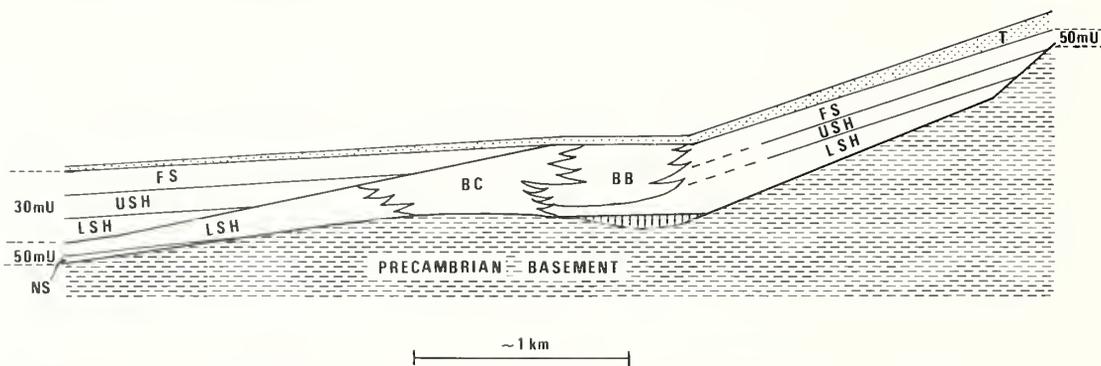
This project started in the mid 1970s when Dr A. J. Carrington presented one of us (C.H.C.B.) with a small collection of brachiopods, thought to be of Pliocene to Pleistocene age, collected during diamond exploration on the Namaqualand coast. Because data on their provenance were not available, work on the specimens ceased until Dr B. Kensley and Mr J. Pether presented us with well-documented comparable material from the same region.

This paper describes seven brachiopod species belonging to three genera which were recovered during diamond-mining activities on the three properties Koingnaas, Hondeklip and Avontuur A in the Hondeklip Bay area of Namaqualand coast (text-fig. 1).

Geological Setting. Over the years a number of authors have described and interpreted the Cainozoic coastal stratigraphy of the South African west coast. In particular, papers by Carrington and Kensley (1969), Tankard (1975) and Hendey (1981*a, b*) have helped to elucidate the succession and determine the depositional environments. In this paper we follow the scheme of Pether (1986*a*), who has summarized and revised the previous work. Pether's brachiopods were recovered from two regressive sedimentary units that are at present included in the Alexander Bay Formation (South African Committee for Stratigraphy 1980; Pether 1986*a*). Within each unit, named after the immediately preceding transgressive altimetric maximum, Pether (1986*a*) has recognized lower



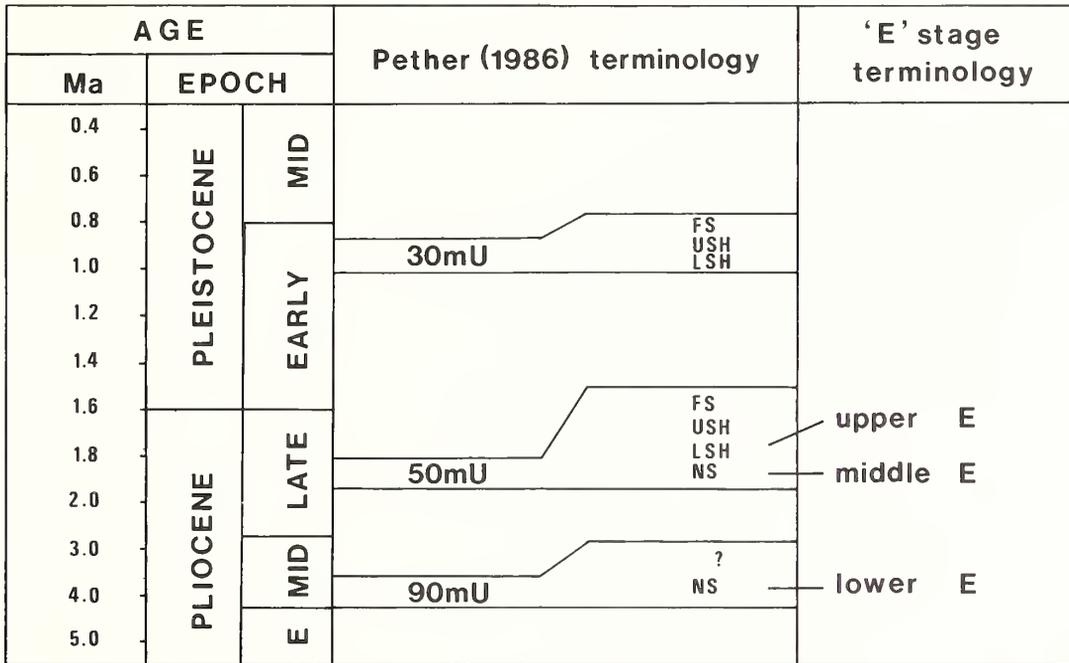
TEXT-FIG. 1. Locality map with inset showing the positions of the main collecting localities (stars).



TEXT-FIG. 2. Schematic cross-section showing the stratigraphic relationships of the two regressive sedimentary units (after Pether 1986a). T = younger terrestrial deposits; FS = foreshore facies; USH = upper shoreface; LSH = lower shoreface; NS = nearshore shelf; BC = barrier complex; BB = back-barrier. Vertical lines indicate an erosional remnant of a nearshore shelf deposit belonging to an earlier (mid-Pliocene) 90 m Unit.

shoreface, upper shoreface and foreshore facies (text-fig. 2). The older 50 m Unit, which rests on an eroded Precambrian gneissic basement, also contains sediments interpreted as belonging to a barrier complex, including tidal inlet deposits, and back-barrier environments. Pether (pers. comm. 1986) has reported that brachiopods are found scattered throughout the sands belonging to both units, but those in the 50 m Unit are better preserved than those in the 30 m Unit, having suffered less breakage and abrasion before burial. This may reflect the higher energy open coast conditions prevailing during deposition of the younger unit compared to the more sheltered, quieter conditions of the partially barred coast during deposition of the 50 m Unit (see Pether 1986a and text-fig. 2).

The only information with the Carrington specimens are markings indicating the mid or upper E stage and the Koingnaas locality, where mining exploration was proceeding at that time. The E Stage terminology was introduced by mining geologists and has been variously correlated during subsequent years, but here we follow Pether (1986*a*; see our text-fig. 3). The Carrington collection is less well preserved than the more recently collected material from Pether, and some was probably reworked in the Upper E Stage. Unless specifically mentioned, the descriptions of species are based upon the Pether collections.



TEXT-FIG. 3. Correlations of terminology and ages of the sedimentary units recognised in Namaqualand, based on Pether 1986*a*.

Age of the fauna. The precise age of the Cainozoic deposits of Namaqualand has been the subject of debate for some time. In the earlier literature a broad late Tertiary – Recent age was considered good enough, but Carrington and Kensley (1969) concluded, on the basis of their mollusc studies, that both of the regressive units described above were of Pleistocene age. Later work by Tankard (1975) and Hendey (1981*a, b*) suggested that these deposits were of Pliocene age. Kensley and Pether (1986) and Pether (1986*a*) have re-examined the evidence and on the basis of the percentage of extant species in the molluscan fauna, along with comparisons with the Neogene and Quaternary sea-level curves of Vail and Hardenbol (1979) and Beard *et al.* (1982), they concluded that the 50 m Unit is of late Pliocene age and the 30 m Unit can be dated as early Pleistocene (text-fig. 3). More recently, the recovery of a vertebrate fossil renders this interpretation problematic and Pliocene ages for both units must be considered (Pether 1986*b*).

THE BRACHIOPODS

The late Pliocene – early Pleistocene brachiopod fauna of the Namaqualand coastal plain is a very conservative one, but even so the diversity appears to be a little greater than that of the brachiopod fauna occupying a similar position offshore at the present time. The late Tertiary – early

Quaternary fauna comprises seven species compared to only four found in water less than 20 m deep around the southern African coast today, namely *Terebratulina abyssicola* (Adams and Reeve, 1850), *Megerlina pisum* (Lamarck, 1819), *Discimisca tenuis* (Sowerby, 1847) and *Kraussina rubra* (Pallas, 1766). Of these four, the first two are apparently confined to the warmer waters of the east coast, *D. tenuis* is found only in the cold waters along the Namibian Coast, and *K. rubra* ranges from west to east coasts (Penrith and Kensley 1970). This last-named species seems to be the only element of the fossil fauna to have survived to the present, perhaps as a result of its greater range of temperature tolerance.

Phyletic relationships of the various members of the fauna are difficult to establish. The Kraussinidae are regarded as rapidly evolved neotonous forms that appeared with apparent suddenness in the Upper Tertiary (Asgaard 1986). Recently Collins *et al.* (1988) have used immunological techniques on skeletal macromolecules from Recent brachiopods to suggest affinities within the terebratulids. Their study indicated a close relationship between *Kraussina* and *Megerlia*, followed by a relationship with *Argyrotheca*, as might be expected from current classification, all three being terebratellaceans. The earliest *Megerlia* specimens are Miocene with *Kraussina*, here described, already established by late Pliocene. Elliott (1949) for Recent *Megerlia*, and Ruggiero (1985) for Pleistocene *Megerlia* from southern Italy, have shown that the earliest brachidium in brachial valves up to about 5 mm wide is a simple V-shaped structure similar to that of adult *Kraussina*, hence the suggestion of neotonous development.

Collins *et al.* (1988) further suggested that the next level of relationship for these terebratellaceans is with terebratulaceans, such as the living *Gryplus* and *Liothyrella*. This break from the usual classification is challenging. However, the immunological work is in its infancy and this result may prove false; certainly their study, if accepting the above derivation of *Kraussina* from a *Megerlia*-like species, has to explain the derivation of a terebratellacean loop in *Megerlia* from the short-looped terebratulaceans, within which are few known wide hinged, strongly costate Mesozoic shells looking at all as if they could have given rise to the kraussinids. Possibilities would seem to be limited to *Meonia* and similar cancellothyrids. The alternative opinion of derivation from the long-looped terebratellaceans might lead to investigation of species like the late Cretaceous (?dallinid) *Gemmarcula*. The South African Cretaceous and Palaeogene brachiopod faunas, best known from the eastern coastal regions, are not known to contain any terebratellaceans.

K. lata Haughton, 1932 and *K. laevicostata* sp. nov. are recorded from only the 50 m Unit, so they do not seem to extend into the Pleistocene. *K. rotundata* sp. nov. is tentatively recorded from the 30 m Unit, as well as the 50 m Unit and thus ranges from the Pliocene into the Pleistocene. *K. rubra* can be taken as extending from the Pliocene to the Recent; it occurs in Cape waters along with *K. crassicostata* Jackson, 1952 and the poorly known *K. cognata* (Sowerby, 1847), a species almost devoid of ribs. Thus there is, at present, a gap in the geological record of *Kraussina* in South Africa equivalent to the middle and late Pleistocene, and it is during this period that any possible connections between the fossil and extant forms must exist. On the basis of its fairly coast ribbing and quite convex shape, one might suggest that *K. crassicostata* is derived from *K. lata*, but evidence for this connection is lacking.

Palaeoecology

Most of the specimens were recovered from sands deposited in an upper-lower shoreface setting which Pether (1986a) interprets as representing water depths of 1.5 m to 10 m. The associated biota includes crustaceans (crabs and barnacles), gastropods, bivalves, scaphopods, polyplacophorans, an oculinid coral, bryozoans, foraminifera, and possible sedentary polychaetes.

Rare occurrences of specimens in life position are known (text-fig. 4). *Kraussina rotundata* sp. nov. and *Cancellothyris platys platys* subsp. nov. have been found *in situ* in crevices in the Precambrian bedrock where they tend to form species clusters, although the two occur in close association. Evidence from the collected and studied specimens indicates that *K. rotundata* lived more commonly within these crevices than *C. platys*, especially at the Koingnaas locality. In this area almost all specimens of *K. rotundata* have abraded posterior regions; in some it is so severe as

TEXT-FIG. 4. Photograph showing specimens of *Kraussina rotundata* sp. nov. in life position in crevices in Precambrian bedrock exhumed as a result of diamond mining activity. The locality, on Avontuur A, represents a palaeodepth of 4–5 m near the upper shoreface/lower shoreface boundary. The pen is approximately 150 mm long.



to have removed part of the cardinal process and part of the sockets and teeth. This has led to the enlargement of the pedicle aperture, but in life much of this opening would have been closed by a tough 'skin' surrounding the actual pad-like pedicle. This 'skin' incorporated muscles which attached to the pedicle collar and these, along with the extensive adjustor muscles (see *K. rotundata* description) moved the shell around the pedicle and, by contraction, held the shell tightly to the substrate in a closed condition. Many of the shells display abraded areas on their flanks where the valves moved against rock, while opening and closing. Others display growth distortion as a result of growth around either neighbouring shells or protruding rocks (text-fig. 6A–C; Pl. 3, figs. 12–16). The intense nature and local distributions of these abrasions and distortions shows that they occurred during the life of the brachiopod, rather than after death, and this is further supported by the good preservation of other areas of valve surface. Similar, closely clumped associations of living *K. rubra* are to be found (text-fig. 5G, H) in which younger shells are attached to older individuals which attached to rocks or pebbles. In these situations the individual shells display a little distortion and abrasion of the ventral umbo, but in comparison to the crevice dwelling *K. rotundata*, they are free to move in open water.

Cancellothyris specimens display less abrasion and distortion. This may be because of their different pedicles. Unlike *Kraussina*, the pedicle of living *Cancellothyris* is long and narrow, furnished with contractile muscles and the ability of adjusting the growing shell to constraints in its immediate environment. The shell of *Kraussina* could not lift much above its original attachment point, whereas *Cancellothyris* could, thus enabling its valves greater freedom of growth and movement. Presumably the slight abrasion of the pedicle aperture seen on some *Cancellothyris* occurred while the shells were held down onto the substrate when closed and 'avoiding danger'. On other specimens there are patches of abrasion on the flanks posteriorly, commonly affecting both valves, indicating that the umbos were probably attached within a rock crevice. More rarely, in some specimens short lengths of their lateral commissures have growth distortions which have produced cavities (Pl. 4, fig. 11). Within these the growth lines developed normally, although somewhat accentuated, but the normal geometry of shell secretion was interrupted by some hard object impinging on the edges of the shell. The internal surfaces of the valves in these areas, apart from being internally convex, appear normal. From the dispositions of the growth lines in these cavities it would seem that biological interference with the valve margins did not take place, but that

as the shell grew, a short length of its margins was increasingly prevented from normal growth. A protrusion from the edge of the rock crevice in which the specimen grew seems the most likely cause.

Another feature, seemingly related to the close hold-fast nature of the *Kraussina* pedicle and the abrasion of shell affecting the articulation, is the anterior zig-zag commissure. A commissure of this sort provides great stability to the positioning of the valves when closed and resists torsion between the valves. Normally, terebratulid articulation is sufficiently strong to resist any torsion between the valves, but in those specimens that have weakened articulation, through shell abrasion, the zig-zag commissure must have been helpful in aiding stability. In two examples, severe posterior abrasion has led to a slight dislocation of one valve relative to the other so that the anterior commissure apparently no longer fitted exactly, although the ribs of one valve still partially interlock with the interrib spaces of the other valve.

Some species range down into the distal lower shoreface and nearshore shelf environment, and *Kraussina laevicostata* sp. nov. and *Cancellothyris platys petalos* sp. et subsp. nov. appear to be confined to this deeper water niche. Table 1 shows the distribution of the fossil brachiopods between the two sedimentary units. This indicates that all seven species are found in the older 50 m Unit, whereas only three are known from the 30 m Unit. Commenting on the diversity contrast between the two units, Kensley and Pether (1986) state that the higher diversity of the 50 m Unit, also

TABLE 1. Species of brachiopods from three localities in the Hondeklip Bay area of the Namaqualand coast, showing the regressive unit and depositional facies from which they were obtained. USH = upper shoreface; LSH = lower shoreface; NS = nearshore shelf.

Species	50 m Unit			30 m Unit	
	USH	LSH	NS	USH	LSH
<i>Cancellothyris platys platys</i> sp. et subsp. nov.	X	X	X	X	X
<i>Cancellothyris platys petalos</i> sp. et subsp. nov.	.	.	X	.	.
<i>Kraussina rubra</i>	X	X	X	X	X
<i>Kraussina laevicostata</i> sp. nov.	.	.	X	.	.
<i>Kraussina lata</i>	.	X	X	.	.
<i>Kraussina rotundata</i> sp. nov.	X	X	.	.	X(?)
<i>Kraussina cuneata</i> sp. nov.	.	X(?)	.	.	.
<i>Pelagodiscus</i> (?) sp.	X	X	.	.	.

EXPLANATION OF PLATE I

Scanning electron micrographs of borings and encrusters.

Figs. 1 and 2. *Cancellothyris platys platys* sp. nov. brachial valve interior. BD6757. 1, part of the posteromedian region, with part of the cardinal process on the right and one crus extending to the bottom edge, showing the blistered appearance of the valve floor resulting from intense boring from the outer surface. $\times 12$. 2, an enlargement of the valve floor showing shell mosaic, endopuncta and the irregular, blistered shell growth. $\times 80$.

Figs. 3-8 are all examples of *Kraussina rotundata* sp. nov. with various encrusters and borers. 3, an example of the foraminifera *Cibicides lobatulus* (Walker and Jacob) adhering immediately anterior to a growth line. BD6719. $\times 64$. 4, a cluster of the bryozoan *Hippothoa* in an interrib space. BD6720. $\times 55$. 5, part of a colony of the sheet-like bryozoan *Celleporella* growing away from the valve margin (bottom left). BD6716. $\times 24$. 6, part of the bryozoan *Tubulipora*, associated with *Hippothoa*, on the mid region of a brachial valve. BD6715. $\times 24$. 7, the mid-lateral region of a brachial valve from which much of the primary shell layer has been removed by 'grazing', perhaps with the destruction of the edge of the *Celleporella* colony. *Hippothoa* has grown onto the 'grazed' area. BD6716. $\times 23$. 8, the thick-shelled umbonal area of the brachial valve with excavated pits showing some signs of marginal chipping or scratching. The abraded umbo is to the top right. BD6716. $\times 22$.



1



2



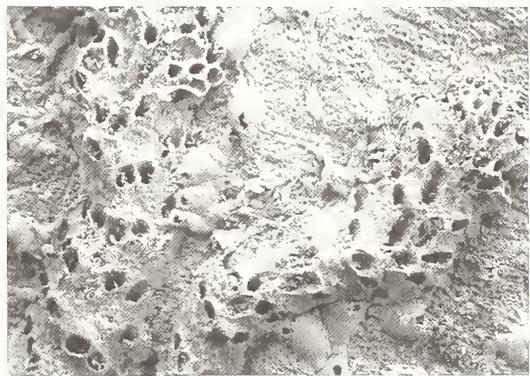
3



4



5



6



7



8

reflected in the molluscan fauna, is either real or is possibly an unavoidable bias due to the nature of the available exposures.

The reduction in diversity from the 50 m Unit to the 30 m Unit through to the present time possibly reflects a gradual reduction in water temperatures. Kensley and Pether (1986) document the presence of warmer water West African and east coast forms among the fossil molluscs from Hondeklip Bay. On this basis they concluded that the two sedimentary units were deposited in waters significantly warmer than at present and, although the evidence is not clear-cut, they inferred a cooling trend over the period of deposition of the two units. Dingle *et al.* (1983) have summarized the available data on South African Neogene and Pleistocene palaeoclimates. These point to a general cooling from the time the upwelling of cold central Atlantic water in the Benguela Current system was established in Upper Miocene times (Siesser 1978). The most intense upwelling occurred during the Pleistocene and surface water temperatures reached a minimum during the last glacial maximum (Embley and Morley 1980). Detailed localized palaeotemperature data from oxygen isotope analysis of fossil oyster shells from the Hondeklip Bay area are still awaited.

All the species in this fauna attached themselves to the substrate by means of a strong functional pedicle and were thus well adapted for living in high energy shallow water conditions. All the species other than *K. cuneata* are larger than other known representatives of these genera, and the shell material in *K. lata*, *K. laevicostata* and to a lesser extent in *K. rotundata* is much thicker than met with elsewhere. The secretion of abundant calcium carbonate in shell material is associated with waters warmer than now found off Namaqualand.

External encrusters, grazers and borers

Many of the well preserved specimens, especially *K. rotundata* from Avontuur, have bryozoans, foraminifera and rare arenaceous tubiculous polychaetes encrusting their surfaces. Less commonly, specimens have been abraded or bored by organisms.

The commonest encrusting bryozoan is the ascophoran cheilostome, *Hippothoa*, a chain-like and branching form having a distal orifice with a sinus (Pl. 1, figs. 4, 7). Less commonly the ascophoran sheet-like genus *Celleporella* (Pl. 1, fig. 5) and stem-like hexagonally patterned *Tubulipora* (Pl. 1, fig. 6) are preserved, but abraded. Living species of these genera are characteristically epiphytes, living on algae, but they also encrust stones and shells.

Hippothoa commonly can be seen to have originated posteriorly, on either valve, and grew essentially anteriorly, as the brachiopod grew. In strongly ribbed areas the bryozoan grew mostly in the interrib spaces (Pl. 1, fig. 4) and, less commonly, transversely within the 'step' of major growth lines. Overgrowth is quite common and where a valve is shared also by *Tubulipora* they overgrew each other, although anteriorly the latter overgrew *Hippothoa* more frequently, as well as individual *Cibicides* foraminifera. Only one shell has an extensive colony of *Celleporella* (Pl. 1, fig. 5).

There is no bryozoan encrustation on any of the areas of physical abrasion on *K. rotundata*, indicating that the bryozoans grew on the brachiopods while living in their rock crevices. There is, however, some sign (Pl. 1, fig. 7) of *Hippothoa* growing on areas which appear to have been abraded by grazing benthos (see below). The flattened, normally attached foraminifera *Cibicides lobatulus* (Walker and Jacob 1789) is found both adherent to outer surfaces of these brachiopods (Pl. 1, fig. 3) as well as loose within the sands filling some shells. This species is known on Recent algae, but on *Kraussina* lived between ribs or below the 'steps' of major growth lines near the margins of shells.

Kraussina and *Cancellothyris* specimens display scratch marks resembling those made by the radula of chitons or by echinoids while grazing. The normal valve exterior probably was not attractive to grazers, but if acting as the substrate for algae, sponges, or bryozoa, these surfaces may have provided valuable nutrient (Pl. 1, fig. 7). None of the above encrusters, nor signs of grazing abrasion, have been found on inner valve surfaces, so most, if not all, the associations occurred during the life of the brachiopods.

Most species, but especially *Cancellothyris*, display borings from the valve exteriors which, in

some specimens (text-fig. 10E), has resulted in the removal of the complete external surface over considerable areas. These areas start as a series of minute holes dispersed over a circular area (text-fig. 10D, E) about 1.5–2 mm in diameter. Progressive removal of shell led to the pitted, corroded surface of extreme examples. Many of these borings appear to have gone sufficiently deeply into the shell material to have affected the mantle epithelia, which reacted by secreting extra shell material over the areas involved. The resultant inner surface is clearly thickened, somewhat irregular and tending towards a blistered appearance (Pl. 1, figs. 1 and 2). Such a sequence of events shows that the borings occurred during the life of the brachiopod.

Other elongate trough-like borings, at the ends of which are small (*c.* 0.5 mm) circular holes penetrating the valve thickness, occur rarely (Pl. 2, figs. 9 and 10). Several *K. rotundata* specimens are excavated posteriorly, where the shell is thick, leaving pits up to 5 mm in diameter penetrating up to 2 mm into the shell substance. The edges and bottoms of these may display marks which appear to be scratches left by a predator (Pl. 1, fig. 8). Their disposition makes it unlikely that they were produced by echinoids.

Apparently confined to *Cancellothyris* specimens are microscopic boring ramifications attributed to microscopic marine algae or fungi. The extent of infestation varies from a few patches posteriorly to most of the shell substance. These borings would seem to have invaded the thick shell at the umbos and sockets and to have spread anteriorly from there. Although they extend through the shell thickness they are best seen just below the relatively smooth internal surfaces, and we feel that the endolithic microorganism is more likely to have invaded after the brachiopod's death.

The grazings and some borings removed shell material during the brachiopod's life. The endolithic ramifications, where intense, weakened the general shell fabric, so that in concert with the loss of organic material (fibre sheaths etc.) from the secondary layer, the shell material was weakened and made vulnerable to physical degradation. Collins's (1986) study of taphonomy in a moderately-deep brachiopod community showed how the shell of Recent *Terebratulina* weakened over a period of about 200 days, becoming increasingly liable to physical breakage. This was attributed to the loss of organic material, perhaps resulting from the action of moulds or bacteria. Thus the occurrence of many of these brachiopods, from a shallow-water environment yet in a good state of preservation, is surprising, and we suggest results only from rapid burial by the regressive sands in which they occur.

Biogeography

The dominant genus is *Kraussina*, endemic to African, especially southern African, waters at the present time. The only previous fossil records of the genus are also from South Africa. A rather unexpected connection with the Australian region comes in the form of *Cancellothyris* which is not known from off South Africa at the present, but occurs in Australian waters. A Miocene species is recorded from New Zealand. *Pelagodiscus* is a very widespread genus in the modern oceans, although it usually occurs in deep waters. However, possible shallow water fossil species are described from Belgium and England.

At the species level, four members of the fauna described herein are named as new species, one cannot be named because of insufficient material, and two previously described species, *K. lata* and *K. rubra*, are known only from South Africa. Thus it may be concluded that the Namaqualand brachiopod fauna is endemic, although there is a possible connection with the Australasian region. One of the extinct gastropods from the 50 m Unit, *Argobuccinum casus*, is also linked to that region (Pether pers. comm. 1986).

SYSTEMATIC PALAEOLOGY

Specimens are housed in the British Museum of Natural History, London (BD and ZB registration numbers), or the South African Museum, Cape Town (SAM numbers).

Class INARTICULATA Huxley, 1869
 Superfamily DISCINACEA Gray, 1840
 Family DISCINIDAE Gray, 1840
 Subfamily DISCINISCINAE Schuchert and LeVene, 1929
 Genus PELAGODISCUS Dall, 1908

Pelagodiscus(?) sp.

Text-fig. 5A-F

Material and horizon. A total of thirty-one brachial valves plus some fragmentary material that may include parts of pedical valves, from the 50 m Unit on the farm Hondekliip.

Description. Small subcircular brown phosphatic shells; brachial valves are conical with the apex more or less centrally situated, or slightly posterior of centre. The outline is almost circular, although many specimens display an almost straight posterior margin. Height of the cone is equal to about one-half of the shell diameter. In profile, the posterior slope is slightly shorter and steeper than the anterior slope. Ornament of irregular concentric growth lines, but one specimen displays faint radial ornament developed after the shell attained a diameter of 4.3 mm. The pedicle valve is unknown.

Dimensions. Typical dimensions (in mm) of specimens are as follows, where a = anterior to posterior diameter, b = left to right diameter, c = height of cone.

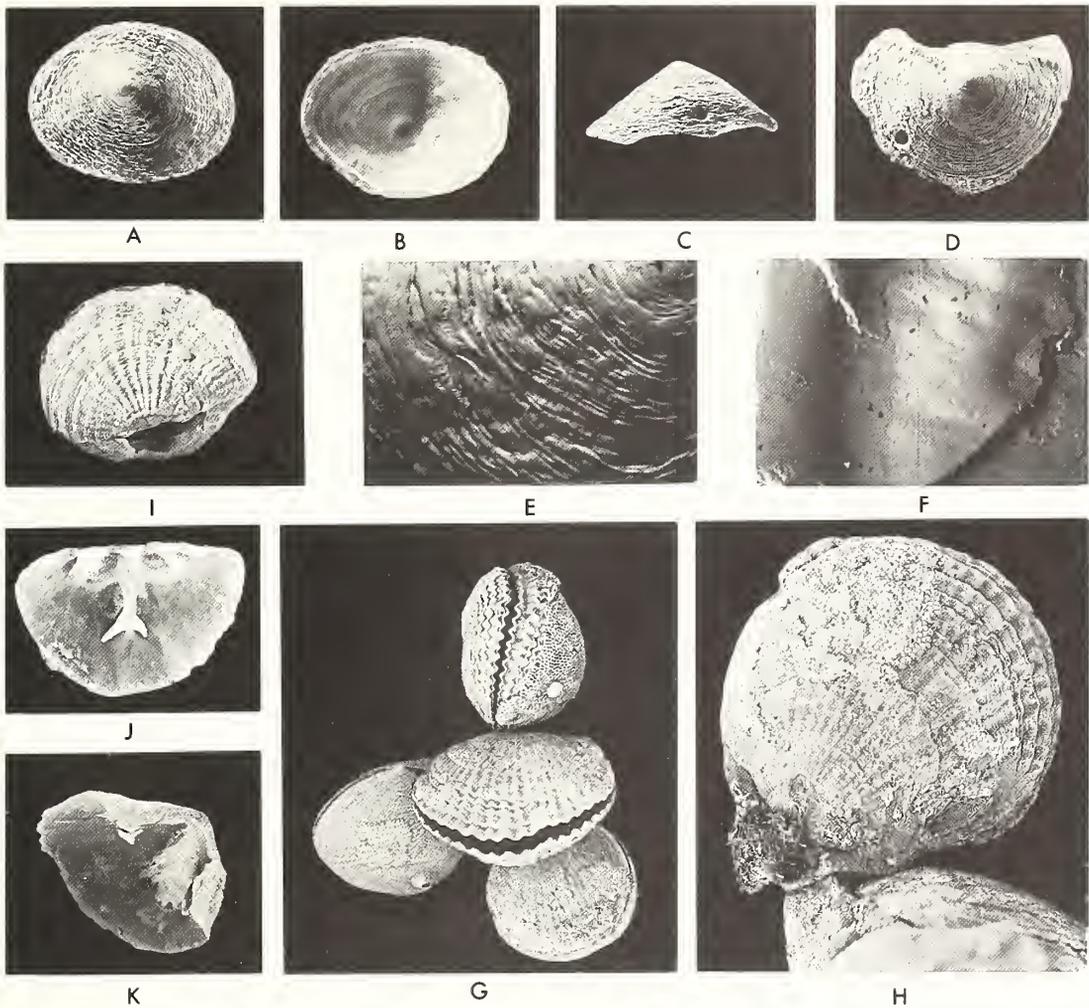
	a	b	c
SAM PQ HB 913	10.6	10.4	5.8
	12.3	11.9	6.0
	14.8	12.4	6.8
	11.3	10.9	5.3
SAM PQ HB 662	8.5	8.6	4.5
	6.0	6.9	3.2

Discussion. The specimens described here are tentatively assigned to *Pelagodiscus* on the grounds that the overall morphology of the brachial valve is virtually identical to that of the type species, the living *P. atlanticus* (King 1868). The various extant species of the closely related genus *Discinisca*, all tend to have the apex of the cone more posteriorly situated or they have a marked radial ornament. However, the main difference between these genera is in the form of the lophophore, with *Pelagodiscus* possessing a schizolophe while that of *Discinisca* is spirolophous. Thus, without the soft parts it is impossible to be unequivocal about the current assignment.

The earliest-formed shell of some limpets living off South Africa resemble these shells, but we reject them for two reasons. There is no sign of twist to their umbos, as seen in the molluscs, and secondly, the shell material is a mineral virtually unknown amongst molluscs. Infra-red spectrum and X-ray analysis indicates that the shell material is a carbonate-fluorine-hydroxy substitute apatite, similar to Dahllite. The presence of chitin was not clearly demonstrated by the analysis, but may have been screened.

Fossil *Pelagodiscus* are poorly known. Thomson (1927) included in the genus two Tertiary species; *Discina suessi* Bosquet 1858 from the Lower Miocene of Belgium, which he included tentatively, and *Discina fallens* Wood 1874 from the Crag deposits of East Anglia, England which are of late Pliocene-early Pleistocene age. If the latter is indeed a *Pelagodiscus* then it represents another shallow water species.

P. atlanticus is perhaps the most widespread of all living brachiopod species, living mostly in the depths of the abyssal and lower bathyal regions. Its overall depth range is given as 366-5530 m, although empty shells have been found as deep as 7600 m in the Romanche Trough in the Central Atlantic (Zezina 1980). The recovery of the specimens described here from shallow water sediments would indicate that they occupied quite a different habitat one to two million years ago than the living species. Another difference between the two is in their size; most known specimens of *P.*



TEXT-FIG. 5. A-F, *Pelagodiscus* sp. from Hondeklip. A-B, a brachial valve exterior and interior, BD6670. $\times 3$. C-D, a brachial valve viewed laterally and dorsally, BD6671. $\times 3$. E, detail of the external ornamentation, near the brachial valve apex, scanning electron micrograph (uncoated), $\times 23$. F, detail of the brachial valve interior, close to the margin, showing the smooth but slightly grooved surface. SEM (uncoated), $\times 37$. G and H, *Kraussina rubra* (Pallas), from the Agulhas Bank, South Africa, at 22 fathoms. J. W. Jackson collection, ZB2240-43. G, clump of four specimens. The specimen at the top appears to have been attached to sponge, the central specimen is attached to the first and the remaining two are attached to the central one. $\times 1$. H, detail of the central specimen's attachment to the first specimen; note the tight fit of the pedicle aperture onto the substrate, here the umbo of another specimen. $\times 2$. I-K, *Kraussina rubra* (Pallas), from Koingnaas, BD6677, $\times 2$; posterodorsal view of the complete shell, the brachial valve interior, and the pedicle valve viewed posterodorsally.

atlanticus have a diameter in the range 3-5 mm, whereas these fossil specimens are larger with some exceeding 13 mm in diameter. Thus it seems that relatively large Cainozoic shallow-water species migrated to deeper water, and became smaller, during the last two million years.

Class ARTICULATA Huxley, 1869
 Superfamily TEREBRATELLACEA King, 1850
 Family KRAUSSINIDAE Dall, 1870
 Genus KRAUSSINA Davidson, 1859

Type species. *Anomia rubra* Pallas 1776, designated by Davidson 1853, for *Kraussia* Davidson 1852, but renamed in 1859 (see text-fig. 5G, H).

Diagnosis. Ventribiconvex, rounded to transverse, broad hinged, multicostate to (rarely) smooth shells. Cardinal process low, broad. Dorsal median septum supporting pair of stout ventrolaterally projecting arms of brachidium.

Discussion. Until now, with few exceptions, *Kraussia* species have only been found from present seas around southern Africa. In that region there are four named species in addition to the type: *K. cognata* (Sowerby 1847), *K. gardineri* Dall 1910, *K. mercatori* Helmcke 1939, and *K. crassicostata* Jackson 1952. The only named fossil species, *K. lata* Haughton 1932, also came from South Africa, somewhat south of, but of about the same age as, the present fauna. Thus *Kraussia*, as presently known, is strongly endemic to seas around southern Africa.

It is noteworthy that we propose five species of *Kraussia* for the Pliocene/Pleistocene seas off south-west Africa (*K. rubra*, *K. lata*, *K. rotundata* sp. nov., *K. laevicostata* sp. nov., and *K. cuneata* sp. nov.), the same number as named in today's waters. Although the time span of the older 50 m Unit, from which all five species were collected, may be about half a million years, the number of species apparently living in the same region is surprising. We suggest, however, that the late Tertiary was a period of evolutionary radiation for *Kraussia*, with only *K. rubra* continuing to the present. *K. lata* could well have evolved into *K. crassicostata*, while *K. rotundata*, with further loss of ribbing, may have become *K. cognata*.

Kraussia rubra (Pallas, 1766)

Text-fig. 5I-K

- 1766 *Anomia rubra* Pallas, p. 182, pl. 14, figs. 2-11.
 1952 *Kraussia rubra* (Pallas); Jackson, p. 22, pl. 3, figs 1 and 2.
 1986 *Kraussia rubra* (Pallas); Hiller, p. 129, fig. 16.

Material and horizon. Five conjoined valves, two pedicle valves and three brachial valves from the 50 m Unit on Hondeklip, Avontuur A and Koingnaas plus six pedicle valves and one brachial valve, as well as fragmentary material, from the 30 m Unit on Hondeklip.

Description. Biconvex shells with variable transversely oval outlines. The hinge line is nearly straight, almost nine-tenths as wide as the valve. The anterior commissure is rectimarginate to broadly and very gently sulcate. The beak is suberect and irregularly truncated by a large incomplete submesothryridid foramen. The palintropes are triangular, bounded by the foramen and beak ridges. Ornament consists of concentric growth lines and strong rounded ribs which may increase by branching or intercalation; ribbing density is of 2-6 ribs, most commonly 3, in a 5 mm sector at the 10 mm growth stage.

The pedicle valve is gently convex in lateral profile but strongly convex, especially medianly, in anterior profile. Brachial valves are gently convex in lateral profile; in anterior profile they are flat or gently sulcate medianly, with gently convex flanks.

Pedicle valve interiors have small teeth, without dental plates; a pedicle collar, where preserved, is very short and sessile. Other details are obscure. Brachial valve interiors have widely divergent socket ridges bounding narrow sockets. A small cardinal process is situated between the posterior ends of socket ridges in small specimens but is reduced by abrasion in large specimens. The notothyrial platform consists of a pair of suboval thickenings between the socket ridges and the posterior end of the median septum; rounded depressions on the platform mark the sites of attachment of pedicle muscles. A low median septum extends anteriorly from the

notothyrial platform and supports, at its distal end, a pair of ventrally divergent lamellae. The rest of the brachidium is unknown. Small submarginal tubercles are present in some specimens.

Dimensions. Dimensions of conjoined valves are (in mm):

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM PQ AV 610	14.9	16.9	9.1
	19.6	19.8	10.5
SAM PQ HB 217	14.9	17.8	9.6
	17.0	17.3	10.8
	18.1	20.4	12.6

Discussion. A small proportion of the kraussinids recovered from the 50 m Unit can probably be assigned to *Kraussina rubra* (Pallas 1766), and it seems that most of those from the 30 m Unit can be similarly assigned. We describe our material since it differs slightly from the living specimens upon which all previous descriptions have been based. The most tangible difference is that the fossil shells tend to be slightly more coarsely ribbed. A small sample of *K. rubra* recovered live from off the southern Cape coast gave figures of 3–6 ribs per 5 mm sector at the 10 mm growth stage on one, thirteen, twenty-two and four shells. Comparable figures for the fossil material described here are 2–6 ribs on two, eight, seven, six and one shells. This difference is thought not to be significant.

Fossil *K. rubra* has been found in shallow marine deposits of late Tertiary to early Quaternary age in other places around the South African coast. Haughton (1932) listed the species from limestone quarries at Hoedjies Bay, near Saldanha, about 300 km south of Hondeklip Bay. In the same area Kensley (1972) recorded it from the 'E' quarry at Langebaanweg and it is known from the Alexandria Formation, a late Pliocene – Pleistocene shoreline deposit cropping out in the coastal areas in the vicinity of Port Elizabeth. These occurrences suggest that the distribution of *K. rubra* in late Pliocene – early Pleistocene times is very similar to its present distribution, i.e. in intertidal and shallow subtidal settings from Transkei, in the east, to Lüderitz on the Namibian coast, in the west. Fossil shells from these other areas show a similar ribbing density to the specimens described here.

Kraussina lata Haughton, 1932

Plate 2, figs. 1–13

1932 *Kraussina lata* Haughton, p. 34.

Diagnosis. Somewhat transverse, ventribiconvex *Kraussina* with strong coarse ribbing.

Type. Haughton's (1932) original material from the 'basal grit' at 'The Point', on the north side of the Olifants River, cannot be traced. We select, therefore, a brachial valve from Koingnaas, which appears to conform to Haughton's brief description, as Neotype (Pl. 2, figs. 1 and 2), BD6681.

Material. In addition to the neotype, in the Carrington collection are six pedicle valves and fourteen brachial valves. From the Pether collection there are one extra pedicle valve and four brachial valves from Koingnaas.

Description. The outline is very broadly obovate and the lateral profile strongly ventribiconvex, the brachial valve convexity largely resulting from a weak median sulcation. Pedicle valves are not folded, but the anterior commissure is weakly sulcate. The hinge line is just posterior to the widest part of the shell, but may form the widest part of the brachial valve. The pedicle aperture and interareas are characteristically wide and subject to abrasion. External ornamentation is of growth lines and strong, coarse costae, costellae being added rarely by branching. The total number of ribs varies from 8 to 16 on brachial valves, with 10 or 11 being the commonest number of costae.

Pedicle valve interiors are scarce. Teeth appear to have been short and stubby. There is a sessile pedicle collar and the muscle scars are essentially as in *K. rotundata*, but the pedicle adjustor muscle scars tend to be shorter

and wider, and only narrowly separated medianly. On one specimen secondary shell growth has allowed the merger of these sears (Pl. 2, fig. 6). Submarginal tubercules are preserved on some brachial and pedicle valves.

<i>Dimensions</i> (in mm)	<i>Length</i>	<i>Width</i>	
Neotype b.v.	24.6	30.7	BD6681
b.v.	25.8	c.30.0	BD6682
b.v.	27.8	35.8	BD6683
p.v.	24.8	29.8	BD6684
p.v.	32.6	33.7	BD6685
p.v.	25.7	32.6	BD6686

Discussion. The species is the commonest representative in the collections originally presented by Carrington. Unfortunately details of locality are unknown, but some specimens are noted as from the mid or upper E Stage and marked 'A 32' (Pl. 2, figs. 3–6). No complete shell is preserved and all show signs of erosion, in some specimens this is severe and has removed structures. Also in the Carrington collection are several incomplete valves of *Kraussina* we consider as a variety of *K. lata*. These are unusually wide shells with strongly thickened brachial valves (Pl. 2, figs. 14–21) in which the pedicle adjustor muscle scars extend anterolaterally well beyond the anterior ends of the sockets. Unfortunately all these valves are badly eroded so rib counts cannot be made. However, the few remaining ribs indicate that they were more frequent than on *K. lata*; we term these specimens *K. cf. lata*.

As Haughton's description (1932) was so brief we have provided a full description and comparison with other species. In general outline and profile *K. lata* resembles *K. laevicostata*, and both tend to be sulcate anteriorly. They differ markedly in the strong ribbing on *K. lata*, which manifests itself also on the insides of valves. This costation, with rare added costellae, covers the valves, although their prominence decreases towards the posterior margins. This is in contrast to *K. rotundata* in which the costae are non-existent on the flanks and posterolateral areas. *K. rubra* specimens are smaller than *K. lata* and have much finer ribbing (see Table 2).

EXPLANATION OF PLATE 2

Figs. 1–13. *Kraussina lata* Haughton. 1 and 2, neotype, a brachial valve viewed externally and internally. BD6681. $\times 1$. 3 and 4, external and internal views of a brachial valve with a series of growth distortions affecting the left posterior hinge line, the valve medianly and in its mid-length right side sector; the shell is bored posteromedianly leading to extra thickening on the right side of the median septum. Carrington collection, A32, mid to upper E stage. BD6682. 5 and 6, external and internal views of a large brachial valve with borings from the external surface producing 'blistering' of the internal surface; there is a small open canal from the pedicle adjustor muscle field to the posteroventral surface of the median septum (arrowed). Carrington collection, A32. BD6683. 7 and 8, external and internal views of a well preserved pedicle valve showing external ornamentation and the pedicle collar. Koingnaas. BD6684. 9 and 10, external and internal views of a somewhat abraded adult pedicle valve with borings, some of which broke through to the inner surface. The pedicle aperture is abraded ventrally and the muscle scars can be distinguished. Carrington collection, A32. BD6685. 11–13, external, internal and posterior views of a pedicle valve with a strongly abraded umbo and consequently reduced pedicle collar. Carrington collection, A32. BD6686. All $\times 1$.

Figs. 14–21, *Kraussina* cf. *lata* Haughton, Carrington collection. 14 and 15, external and internal views of a large and badly eroded brachial valve displaying posterior abrasion and external pitting, the possible result of borings; the 'ME' is for mid E stage. BD6691. 16 and 17, external and internal views of a partially eroded brachial valve with the median part of its hinge line removed by abrasion; note the anterolaterally extended pedicle adjustor scars. Upper E. BD6692. 18 and 19, external and internal views of a partially eroded brachial valve. Anteromedial ribbing is well preserved; the pedicle adjustor scars compare with those of fig. 15, but contrast with those of figs. 17 and 21. Mid E. BD6693. 20 and 21, external and internal views of a badly worn brachial valve, having lost all its ribbing; the anterior extension of the pedicle adjustor sears seems characteristic of the Upper E specimens. BD6694. All $\times 1$.

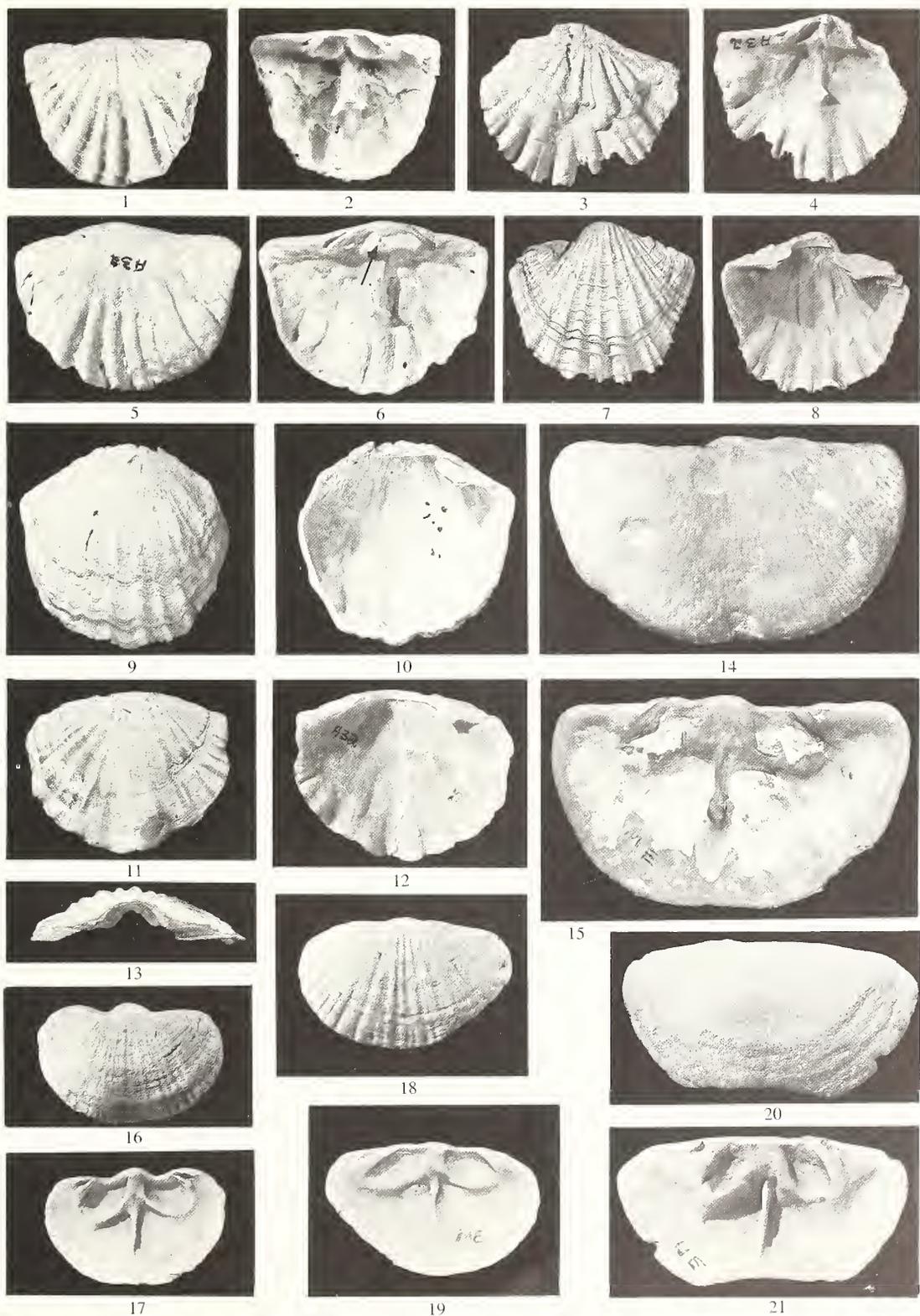


TABLE 2. Summary of ribbing densities on species from Hondeklip Bay plus *K. rubra* and *K. crassicosata* (Recent) from off the southern Cape coast.

Species	Number of ribs in 5 mm sector at 10 mm growth stage			
	Range	Mode	Sample Size	Age
<i>K. rubra</i>	3-6	5	40	Recent
<i>K. crassicosata</i>	3-4	3	5	Recent
<i>K. rubra</i>	2-6	3	24	Pliocene-Pleistocene
<i>K. lata</i>	2-3	3	8	Pliocene
<i>K. rotundata</i>	1-4	2	18	Pliocene
<i>K. cuneata</i>	12-16	15	12	Pliocene
<i>K. laevicosata</i>	'Ribs' develop only after 30 mm growth			
	at 20 mm growth stage			
<i>Cancellothyris platys</i>	12-17	13	26	Pliocene

Growth distortion is uncommon in *K. lata*, and although their pedicle apertures are abraded to some extent, it is never as severe as in *K. rotundata*. This indicates that *K. lata* lived attached to hard substrate but not in crowded conditions or in rock crevices.

Until now *K. lata* was the only described kraussinid from the late Tertiary to early Quaternary deposits of South Africa. Amongst living *Kraussina* in South African waters *K. crassicosata* Jackson has a similar number of costae, but it does not grow to the dimensions of *K. lata* and tends to be as wide as long. It is, however, possible that a reduction in size and relative width in *K. lata* could have resulted in the living *K. crassicosata*.

EXPLANATION OF PLATE 3

Figs. 1-16. *Kraussina rotundata* sp. nov. 1-5, holotype from Avontuur A-T3. BD6705. $\times 1.5$. 1 and 2, the complete shell viewed dorsally and ventrally showing the median ribbing. 3, the brachial valve interior with a virtually complete brachial support. 4, the shell viewed posterodorsally showing abrasion around the pedicle opening. 5, the pedicle valve showing the teeth. 6-9, a young shell from Avontuur. BD6706. $\times 1.5$. The shell is viewed dorsally, posteriorly, anteriorly slightly agape to show the brachial supports, and laterally; the ventral umbo is virtually unabraded. 10 and 11, a mature shell viewed laterally and anteriorly showing the extent to which the valves can open, and the lophophore supports. Avontuur, BD6707. $\times 1.5$. 12-14, a young shell displaying considerable growth distortion and abrasion (arrowed). Avontuur, BD6708. $\times 1.5$. 12 and 13, brachial and pedicle valve exteriors. 14, brachial valve interior showing the distorted growth of the brachidium, in which the two arms grew almost in contact medianly. 15 and 16, an almost fully grown but distorted and abraded shell. Avontuur, BD6709. $\times 1.5$. 15, the complete shell viewed dorsally; the ventral umbo had been abraded especially on the left side, as far as the tooth. 16, brachial valve interior showing the confined growth of the hinge line. 17 and 18, an adult, strongly abraded shell. Avontuur, BD6710. $\times 1.5$. 17, oblique lateral view showing severe abrasion at both umbos and flank of the pedicle valve. 18, dorsal view showing median abrasion to the extent that the dorsal median septum shows through the remaining shell (arrowed). 19 and 20, a brachial valve viewed externally and internally from the Carrington collection, Upper E. BD6711. $\times 1$. 21-24, an abraded (right side of the ventral umbo) and posteriorly bored (arrowed) shell viewed ventrally, dorsally and anteriorly. Avontuur. BD6712. 21-23, $\times 1.5$. 24, detail of the anterior margin showing tubercles through the gape. $\times 4$.



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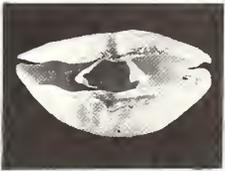
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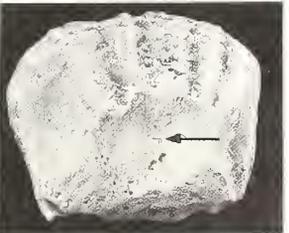
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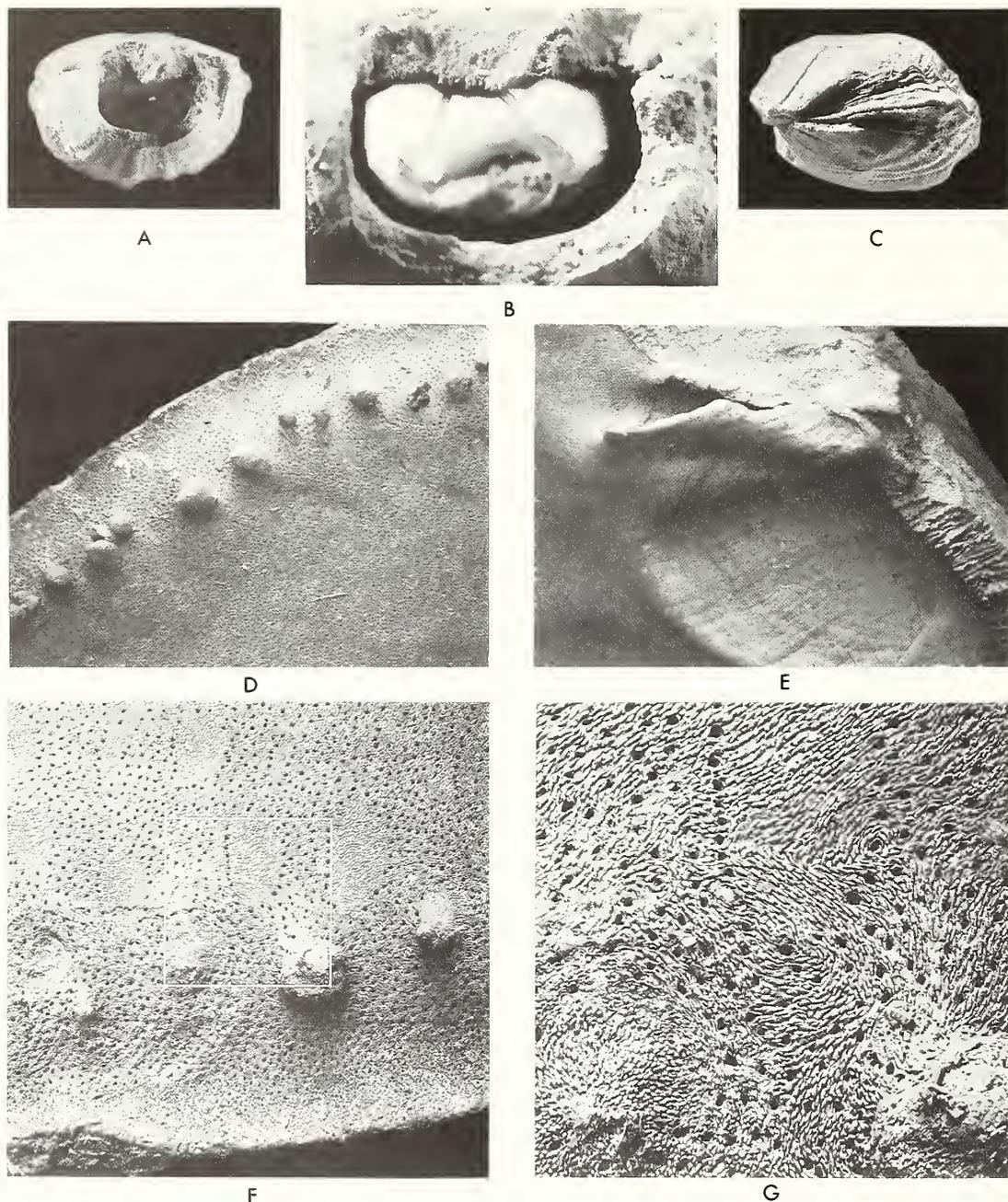
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TEXT-FIG. 6. *Kraussina rotundata* sp. nov. from Avontuur - T3. A, C, a large shell viewed posteriorly (A) and laterally (C) showing posterior abrasion and lateral growth distortion, BD6713, $\times 1.5$. B, enlarged posterior view of the pedicle aperture using bottom lighting to show the lophophore support within the shell, $\times 5$. D-G, scanning electron micrographs (not coated, environmental chamber) of the interior of a brachial valve, BD6714. D, tubercles at the posterolateral margin, $\times 19$. E, part of the cardinalia showing a socket, part of the radially ridged cardinal process and part of the pedicle adjustor muscle scar, $\times 12$. F, tubercles at the anterior margin displaying resorption and regeneration patterns, $\times 42$. G, detail from the centre of F showing the shell mosaic in an area of recent resorption and two current tubercles, $\times 130$.

Kraussina rotundata sp. nov.

Plate 3, figs. 1–24; Text-figs. 6–8

Diagnosis. Strongly biconvex *Kraussina* ornamented by relatively few, medianly developed, coarse costae.

Type. Holotype BD6705. Paratypes SAM PQ AV 609, AV 610; SAM PQ HB 217, HB 348, and eight figured shells, BD6706–BD6714 (excluding BD6711), from Avontuur A.

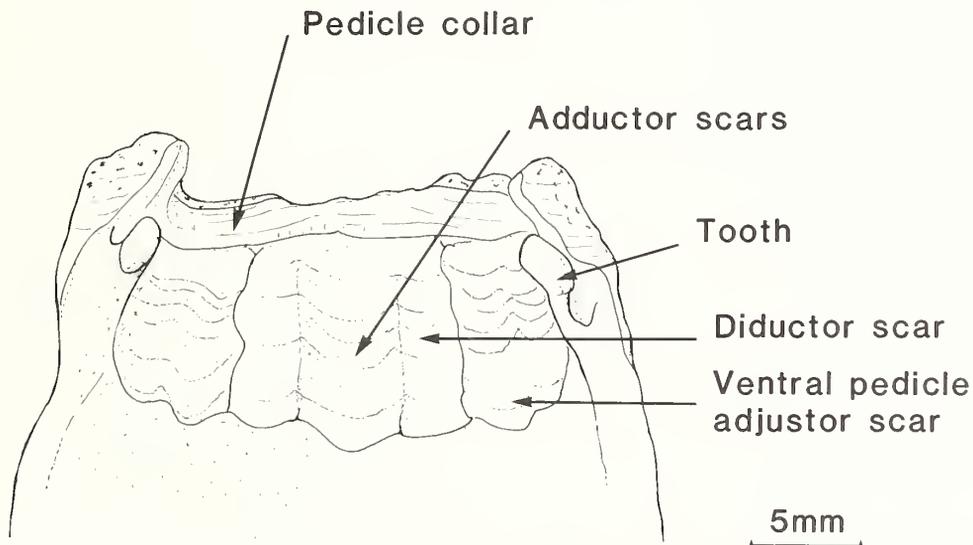
Name. Rotundus (L.) = round, spherical, referring to the strong biconvexity of the shell.

Material and horizon. Thirty-three conjoined valves, nine pedicle valves and eight brachial valves all from the 50 m Unit on Hondeklip and Avontuur A. Three shells and a few incomplete valves in the Carrington collection.

Description. Strongly biconvex shells with subcircular outlines; the length usually slightly greater than width, although shape can be variable. The hinge line is nearly straight, about four-fifths as wide as the valve. The anterior commissure is rectimarginate to broadly and gently sulcate. The beak is suberect with a very large submesothyridid foramen; posterior margins of shells are often abraded away by movement against hard substrates. The ornament consists of concentric growth lines and a few coarse subangular costae developed medianly. Ribs extend from the umbo but are often abraded from posterior portions of the valves; ribbing density of one to four ribs in one, twelve, four and one specimens at 5 mm medianly at the 10 mm growth stage, although a few shells show minimal ribbing; lateral areas are devoid of ribbing. Shell substance is thick, compared to *K. rubra*.

The pedicle valve is strongly convex in anterior and lateral profiles. Brachial valves are convex in lateral profile, and also in anterior profile but with a slight median flattening or incipient sulcus development.

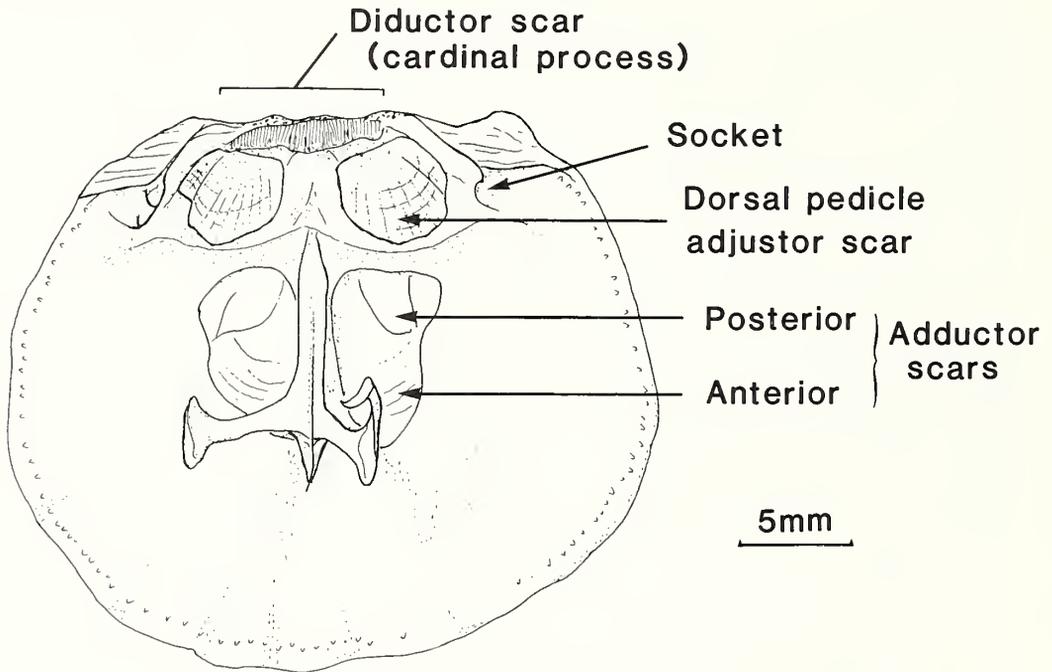
The pedicle valve interior has small, robust and strongly cyrtomatodont teeth. The pedicle collar is short, commonly sessile, but rarely free anteriorly resulting from anterior growth as a consequence of posterior abrasion. The ventral pedicle adjustor muscle scars are prominent, somewhat quadrate areas positioned posterolaterally, below the thickened shell of the teeth supports; they are commonly ridged concentrically (text-fig. 7). Between these scars is a slightly concave ovate area, somewhat thickened anteriorly and laterally, which extends forwards to a position just in front of the anterior edges of the adjustor scars; this is the scar



TEXT-FIG. 7. Drawing of the posterior internal region of a pedicle valve of *Kraussina rotundata* sp. nov. showing the dispositions of the muscle attachment areas.

of the relatively small adductor muscles which, unlike their dorsal ends, are a closely united pair. The diductor muscle scars are weakly impressed, but positioned between the adductor and adjustor scars. (This interpretation is based upon study of the muscles in Recent *K. rubra*, with very similar muscle scars to *K. rotundata*.) Within about 0.5 mm of the valve margins are small outwardly directed tubercles with a frequency of about sixteen per 5 mm of valve edge. Their preservation is variable, due largely to the periodic resorption and overgrowth of the tubercles during valve growth and thickening (text-fig. 6D, F, G).

The brachial valve interior has short, thick widely divergent socket ridges bounding small narrow sockets. The cardinal process is transversely elliptical, situated between the posterior ends of the socket ridges but often is partially removed by abrasion of the posterior shell margin. A broadly triangular notothyrial platform serves for the attachment of pedicle adjustor muscles, marked by a pair of ovoid to quadrate scars; from the anterior margin the low median septum extends to little more than one-half of the valve length (text-fig. 8). The distal end of the septum supports a pair of ventrally diverging brachial lamellae; the ventral end of each lamella widens as it bends posteriorly then narrows to a prong curving ventromedianly (Pl. 3, figs. 3 and 11). Elliptical to oblong adductor scars are impressed on the valve floor on either side of the median septum, between the notothyrial platform and the brachidium; small subcircular posterolateral elements of the scars are differentiated and show where the smaller posterior adductor muscles were attached. Submarginal tubercles are more strongly and commonly present than in pedicle valves.



TEXT-FIG. 8. Drawing of a brachial valve interior of *Kraussina rotundata* sp. nov. showing the morphology and main muscle attachment areas.

Dimensions. Examples of the dimensions of conjoined valves are (in mm):

	<i>Length</i>	<i>Width</i>	<i>Hinge w.</i>	<i>Thickness</i>	
Holotype	22.5	22.4	19.1	15.2	BD6705
Paratypes	16.3	17.5	13.6	9.2	BD6706
	19.4	20.7	17.1	10.8	BD6712
	22.5	21.9	16.1	15.4	BD6713
	23.0	19.6	c.12.0	12.5	BD6709
	24.0	23.0	17.0	17.0	BD6707

Discussion. The shells described here are immediately referable to *Kraussina* on the basis of their internal structures, but they differ from other species of the genus in several important respects. Their coarseness and distribution of ribbing immediately separates them from the living species *K. rubra*, *K. cognata*, *K. gardineri* and *K. crassicostata*. *K. mercator* from off the west African coast, is a form that does not develop any ribs and, although many of the present specimens are sparsely ribbed, the normal form of the shell is with ribs developed medianly and thus they can be separated from *K. mercator*, which is also smaller and with a coarsely tubercular valve interior.

Of the fossil species, only *K. lata* has a similar density of ribbing to *K. rotundata* sp. nov. but it has ribs strongly developed over the entire valve surface. In addition, *K. lata* has a flatter brachial valve and is usually wider than long with maximum width at or near the hinge line and rather acute cardinal angles (Haughton 1932).

Kraussina laevicostata sp. nov.

Text-fig. 9A-H

Diagnosis. Large, transverse, ventribiconvex *Kraussina* lacking persistent ribbing.

Types. Holotype: BD6730, an incomplete shell (text-fig. 9A-C). Paratypes: two pedicle valves and an incomplete brachial valve from Koingnaas. Five incomplete brachial valves and one pedicle valve from the 'E Stage', Carrington collection.

Name. Laevis (L.) = smooth or bald. Costa (L, f) = rib, referring to the scant ribbing.

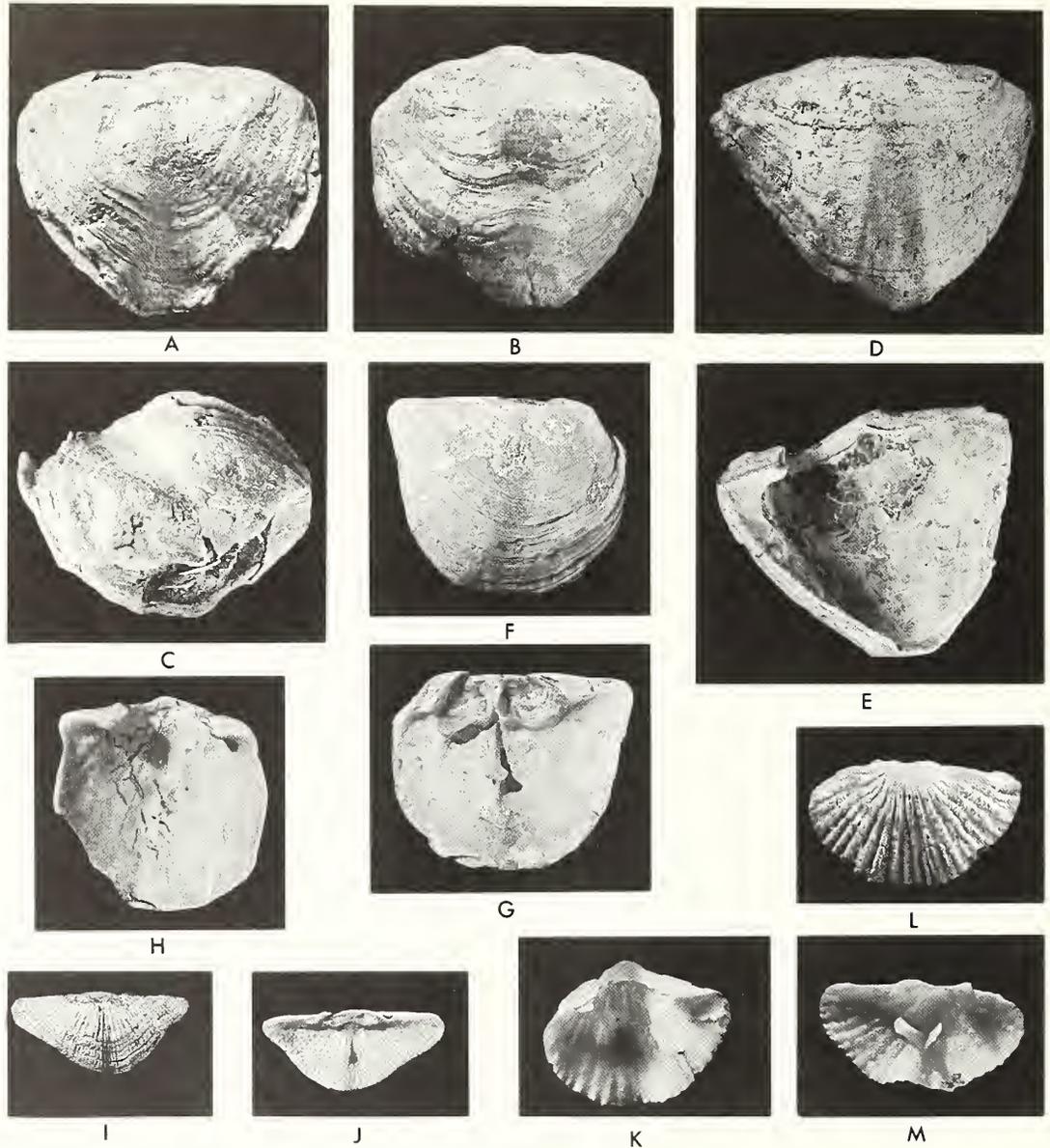
Description. The outline is very broadly obovate, with a hinge line almost reaching the maximum width. The lateral profile is ventribiconvex, the brachial valve being almost flat to gently convex, with a sulcus starting about 10 mm from the umbo. There is a complimentary fold on the pedicle valve producing a gently sulcate anterior commissure. The pedicle aperture is wide, abraded ventrally, and bordered by variably developed interareas. External ornamentation is of prominent growth lines, especially anteriorly, and irregular, impersistent occasional median ribs, developed only after about 30 mm in length.

Pedicle valve interiors have relatively small teeth, which in older specimens are supported by shell thickening below the interareas. There is a short pedicle collar which, in some specimens, is partially worn away. Muscle scars are typically kraussinid. In large shells they are slightly sunken into the valve floor; the laterally placed adjustor scars are more prominent. Brachial valve interiors are similar to those of *K. rotundata*, but in adults the prominent adjustor scars are less widely separated and elevated medianly. Both valves have submarginal tubercles with a frequency of ten to sixteen per 5 mm.

<i>Dimensions</i> (in mm)	<i>Length</i>	<i>Width</i>	<i>Hinge w.</i>	<i>Thickness</i>	
Holotype, shell	37.4	42.5	40.8	21.1	BD6730
Paratypes b.v.	28.0	33.6	32.6	—	BD6732
p.v.	30.5	30.4	26.6	—	BD6733
p.v.	35.8	47.4	44.8	—	BD6731
p.v.	40.6	38.9	c.37.6	—	BD6734

Discussion. This large species is comparable in size to the largest, wide example of *K. lata*, but the two differ in that the latter is strongly ribbed. *K. laevicostata* would seem to have had the same high degree of shape variation as is seen in the more numerous *K. rotundata*. The sulcate commissure developed early in life and the ventral fold may be accentuated by what resembles a pair of ribs (text-fig. 9D). However, these do not seem to be present on brachial valves.

In present-day waters off South Africa there is a ventribiconvex species, virtually lacking ribs, *K. cognata* (Sowerby), which is smaller and much less transverse than *K. laevicostata*. It is possible that size and relative width reduction may have transformed *K. laevicostata* into *K. cognata*.



TEXT-FIG. 9. A-H, *Kraussina laevicostata* sp. nov., A-C, Holotype viewed dorsally, ventrally and posterodorsally, Koingnaas, BD6730. D, E, a pedicle valve viewed externally and obliquely internally showing the pedicle collar and pedicle adjustor muscle scar flanking the diductor and median adductor scars, Koingnaas, BD6731. F, G, a smaller brachial valve exterior and interior with a distorted right ear. Carrington collection, E stage, BD6732. H, an incomplete pedicle valve interior. Carrington collection, E stage, BD6733. All $\times 1$. I-M, *Kraussina cuneata* sp. nov., from Koingnaas. I, J, a brachial valve exterior and interior, BD6738, $\times 1.5$. K-M, holotype, a complete shell with separated valves, BD3739, $\times 4.5$. K, pedicle valve interior showing the teeth and pedicle collar. L, M, brachial valve exterior and interior, showing the tuberculate interior and small inner socket ridges.

Kraussina cuneata sp. nov.

Text-fig. 9I-M

Diagnosis. Small, transverse, entirely finely ribbed *Kraussina* with persistent dorsal sulcus.

Types. Holotype BD6739 (text-fig. 9K-M) and ten other incomplete valves from the Carrington collection, E stage.

Name. Cuneatus (L.) = wedge-shape, or inverted triangle, referring to the shell's outline.

Description. These small shells (5–10 mm long) are broadly rounded triangular in outline, some reaching twice as wide as long. The greatest width is just anterior to the hinge line. The lateral profile is ventribiconvex. The dorsal sulcus is shallow, but originates close to the umbo. The ventral fold is less clear, but the anterior commissure is sulcate. The pedicle aperture is large and the interareas short but broad, small triangular deltidial plates may be preserved.

The external ornamentation is of periodical growth-halts plus fine, regular ribbing over the complete shell. Brachial valve costellae are added by intercalation. There are twelve to sixteen ribs per 5 mm width at 10 mm in three, one, two, five and one specimens. The pedicle valve interior has small cyrtomatodont teeth and a relatively long sessile pedicle collar. Muscle scars are ill-defined on the few available specimens, but appear to be as in *K. rotundata*.

Brachial valve interiors have small widely divergent sockets, almost confined to the thickened posterior margin of the valve. The cardinal process is very short, but wide and typically radially ridged. The notothyrial platform is short and wide, accommodating transversely elliptical pedicle adjustor muscle scars. The median septum is low posteriorly, reaching about one-half of the valve length, and branches ventrolaterally into the main V-shaped brachidium; the complete structure is unknown. Adductor muscle scars are positioned normally, but poorly differentiated.

The interiors of both valves display, to a variable extent, the form of the external ribbing and radial lines of tubercles following the rib interspaces. Close to the valve margins are more prominent tubercles with a frequency of between 9 and 13 per 5 mm length of margin.

<i>Dimensions</i> (in mm)	<i>Length</i>	<i>Width</i>	<i>Hinge w.</i>	
Holotype, shell	5.1	6.8	6.0	BD6739
b.v.	8.0	16.5	15.1	BD6738
b.v.	8.0	14.2	12.6	BD6740
p.v.	9.9	14.6	13.7	BD6741
p.v.	7.5	11.8	10.8	BD6771

Discussion. These small shells in some respects resemble *Megerlina*, but cannot be assigned to that genus because they show no sign of the pair of wing-like lateral extensions from the V-shaped part of the brachidium characteristic of *Megerlina*. The transverse outline, although much smaller, is comparable to the wide variety of *K. lata* from the Carrington collection. However, although some *Kraussina* specimens display an initial 4 mm of ribbing finer than that covering the adult valves, the ribbing covering the valves of *K. cuneata* is still finer than any seem on other *Kraussina* species in these faunas. The persistent dorsal sulcus and internally developed tubercles also differentiate this species.

Superfamily CANCELLOTHYRIDACEA Thomson, 1927

Family CANCELLOTHYRIDIDAE Thomson, 1927

Subfamily CANCELLOTHYRIDINAE Thomson, 1927

Genus CANCELLOTHYRIS Thomson, 1927

Cancellothyris platys sp. nov.

Plate 4, figs. 1–13; Text-fig. 10A–G

Diagnosis. Large, relatively broad, rectimarginate to uniplicate *Cancellothyris* with thickness just over one-half length of shell.

Types. Holotype, BD6742, from the 50 m Unit at Avontuur A. Paratypes, figured specimens from Avontuur A and Hondeklip.

Name. *Platys* (Gr.) = broad, wide.

Material. In addition to the type specimens, there are fourteen shells from Avontuur A, plus two pedicle valves and two brachial valves; from Hondeklip there are two pedicle and three brachial valves; and in the Carrington collection there are two small shells, three pedicle and three brachial valves, mostly marked 'B-1', all of which are somewhat eroded.

At the Koingnaas locality were recovered two shells, two pedicle and three brachial valves, all in an incomplete state of preservation, representing the large and wide sub-species, *C. p. petalos* nov. (See the discussion.)

Description. The outline is approximately five-sixths as wide as long, the greatest width being at about two-thirds the total length and the anterior margin being widely rounded. The lateral profile is biconvex, with a prominent ventral umbo truncated by the large pedicle foramen, commonly slightly widened by abrasion. Deltoidal plates are medianly joined and short. The lateral commissure rises slightly anteriorly, and the anterior margin is rectimarginate to gently uniplicate in specimens over about 30 mm long. Thus in brachial valves over about 28 mm long a slight marginal fold developed.

External ornamentation is of growth lines and a well developed fine ribbing, with 12–17 ribs in a width of 5 mm at 20 mm from the dorsal umbo in one, ten, six, six, two and one specimens. Even the larger uniplicate specimens show only the slightest folding or sulcation on their valves.

Internally the pedicle valve has strong cyrtomatodont teeth supported by shell thickening on the flanks of the umbonal cavity. There is a well developed pedicle collar, free anteriorly and capable of growth into a short tube (text-fig. 10F). Muscle scars are ill defined, but the diductors are large and spreading.

In the brachial valve umbo there is a narrow, ridged cardinal process from which sockets widen anterolaterally, with strong inner socket ridges overhanging the sockets posteriorly. The floor of the functional anterior part of the socket is supported by thickening from the inner surface of the valve (Pl. 4, fig. 9). From the anteromedian corners of the sockets crura extend anteromedianly, as if to meet at about two-thirds of the brachial valve length. They are, however, only a few mm long before branching to form the complete ring of the brachidium (Pl. 4, figs. 4 and 5). The anterior transverse band is relatively wide, ventrally arched and convex anteriorly. Muscle scars are not clearly differentiated. The median diductor scars are oblong, with rounded anterior margins, and flanked by widely spreading pedicle adjustor scars.

Dimensions (in mm). (All but one being from complete shells)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>	
Holotype	33.5	29.7	18.9	BD6742
Paratypes	36.2	29.9	20.6	BD6745
	34.3	29.1	18.6	BD6743
	37.9	28.3	19.4	BD6744

EXPLANATION OF PLATE 4

Figs. 1–14. *Cancellothyris platys platys* sp. et subsp. nov. 1–5, holotype, the complete shell viewed ventrally and dorsally. The separate pedicle valve internally and the brachial valve internally and oblique internally. Avontuur. BD6742. $\times 1$. 6–10, a complete shell from Hondeklip. BD6743. 6–8, viewed ventrally, dorsally and laterally. $\times 1$. 9, the cardinalia and pedicle valve umbo (above). $\times 3$. 10, the umbos of the shell externally showing the deltoidal plates and slightly abraded pedicle aperture. $\times 6$. 11, lateral view of a shell with growth distortion (arrowed) at its lateral commissure. Avontuur. BD6744. $\times 1$. 12–14, a complete shell with, internally, its loop and some of the associated spiculation preserved and protruding from the sand which filled the shell. Avontuur. BD6745. 12 and 14, the open shell viewed anterolaterally and closed, from the other side. $\times 1$. 13, a detail from fig. 12 showing the anterior portion of the brachial loop (arrowed) and, anterior to that, a large remnant of the spicular skeleton that helped support the lophophore beyond the loop. $\times 10$.



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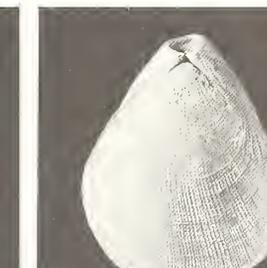
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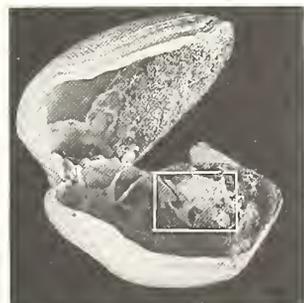
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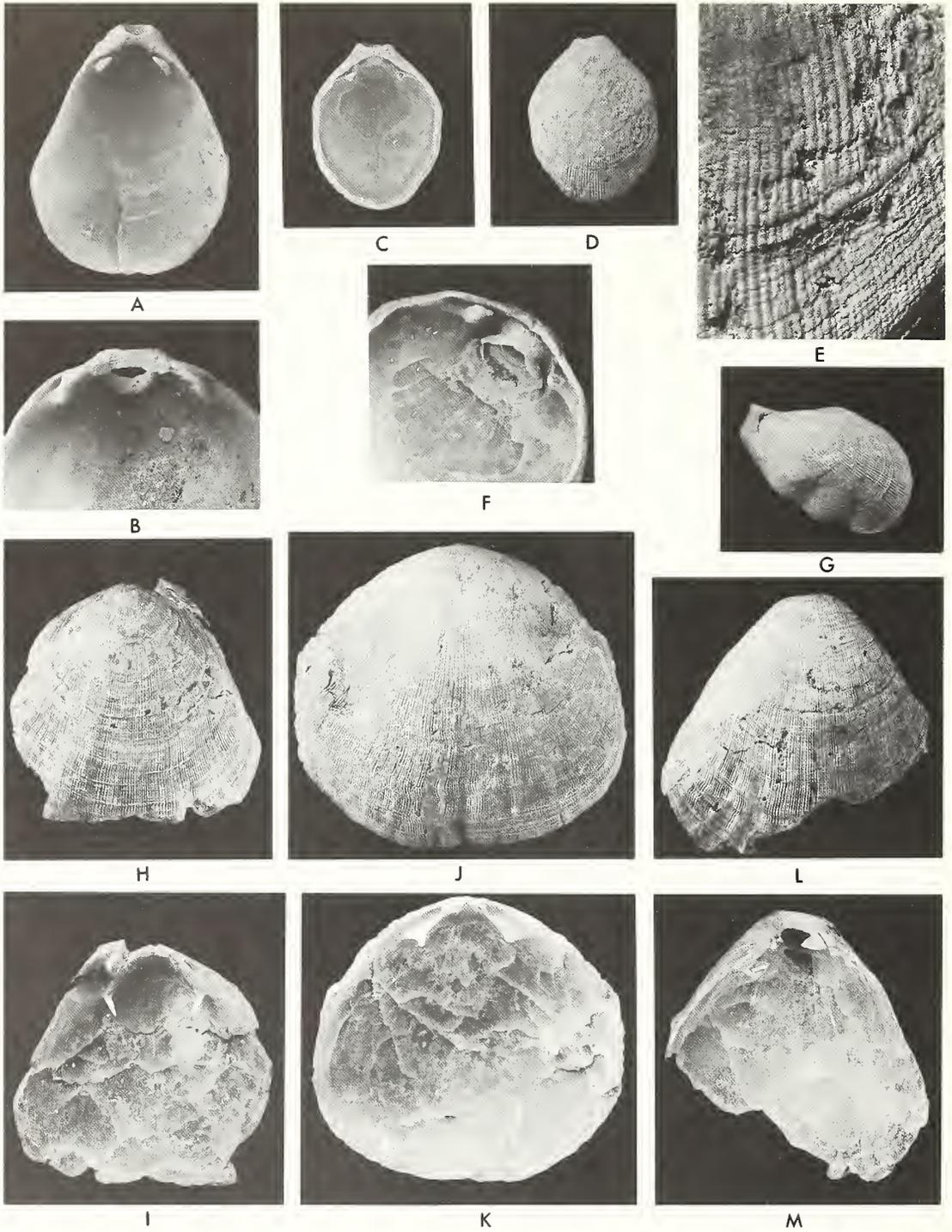
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TEXT-FIG. 10. For legend see opposite.

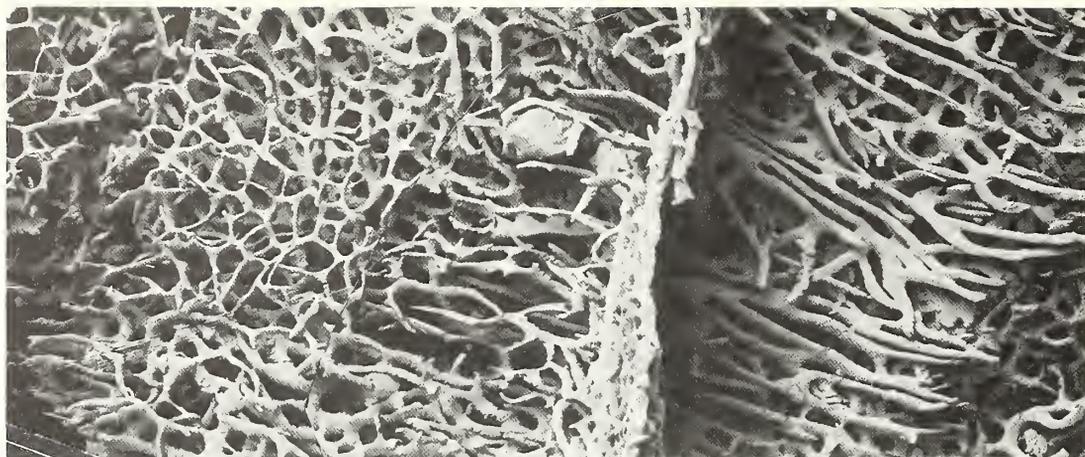
p.v.	37.9	30.4	—	BD6746
	36.8	31.6	21.5	BD6751
	30.5	30.4	16.7	BD6752
	32.4	27.5	15.3	BD6753
	28.8	26.3	13.0	BD6754
	15.8	13.9	10.7	BD6755
	16.0	14.8	8.3	BD6756

Discussion. Living *Cancellothyris* appears to be restricted to Australian waters and taxonomically the nearest species now living in South African waters are *Terebratulina abyssicola* (Adams and Reeve), *T. meridionalis* Jackson 1952 and *Terebratulina* species of Cooper (1973*b*), Hiller (1986) and Jackson (1952). The main distinction between *Cancellothyris* and *Terebratulina* is the conjunct deltidial plates in the former, but Cooper (1973*a*) has commented that *T. abyssa* [error for *abyssicola*] from off South Africa may occasionally have united deltidial plates. Cooper's observation raises a question of validity of these two genera, and also provides a clue that this cancellothyrid morphology of conjunct plates may be retained in the South African populations. *C. platys* differs from *T. abyssicola*, as originally described, by being very much larger. However, as pointed out by Jackson (1952), the original Adams and Reeve (1850) specimen is probably young and those figured by Jackson reached 28.4 mm long. Apart from the non-conjunct deltidial plates, Jackson's *T. abyssicola* specimens have a prominent dorsal sulcus, producing a sulciphate anterior commissure. The loops of Jackson's examples and those of *C. platys* are very similar.

C. platys is most abundant at the Avontuur A locality. Shape variation is not extreme, but a few specimens did grow in confined conditions, leading to growth distortions (text-fig. 10G). Most of these distortions affected relatively short lengths of the valve margins and in one shell (Pl. 4, fig. 11) possibly led to its shift in position away from the confining object and consequential extra abrasion at the left side of the pedicle aperture. We believe it more likely that these distortions resulted from growth against hard substrate rather than against other specimens. An unusual feature in some pedicle valves is the extent of anterior growth of the pedicle collar (text-fig. 10C, F). This does not seem to be associated with particularly severe abrasion of the pedicle aperture, as might be expected.

Within the coarse sands and fine shelly debris filling specimens of *C. platys* we have recovered some small fragments of the original spicular skeleton which supported the lophophore. The complexity and stability of these structures are to be expected in this species, in view of the spicules studied in living *Terebratulina* by such authors as Deslongchamps (1860), Blochmann (1912) and Schumann (1973). Spicules have been described previously from fossil brachiopods, for example by Steinich (1963) from the Cretaceous and by Rowell and Rundle (1967) in Eocene *Terebratulina*, but seldom with as good preservation or articulation as here. In one specimen the entire mesodermal spicular skeleton has slipped anterolaterally from its original position on the loop and lies, somewhat crushed, within the sediment; those parts from the loop area and one side arm of the lophophore can be seen (Pl. 4, figs. 12 and 13). The features which strikingly differentiate these spicules from those previously figured from *Terebratulina* are their length and intricate intermeshing, each part of the skeleton being made up of many layers of interlocked spicules (text-fig. 11).

TEXT-FIG. 10. A-G, *Cancellothyris platys platys* sp. et subsp. nov. from Avontuur, A, B, a pedicle valve interior showing conjoined deltidial plates and teeth ($\times 1$) and a detail of the umbo internally showing the pedicle collar ($\times 2.5$) BD6746. C-F, a pedicle valve, BD6747. C, viewed internally showing the well differentiated muscle field, $\times 1$. D, external view, $\times 1$, E, part of the external view enlarged to show the effect of surface borings, $\times 5$. F, the internal posterior region showing the unusually lengthened pedicle collar, the teeth, and the wide adductor and diductor muscle scars, $\times 2$. H-M, *Cancellothyris platys petalos* sp. et subsp. nov. from Koingnaas, $\times 1$. H, I, an incomplete brachial valve exterior and interior with the tooth from the pedicle valve remaining in position on one side, BD6749a. J, K, holotype of the subspecies, a brachial valve viewed externally and internally, BD6750. L, M, the pedicle valve, viewed externally and internally, belonging to the brachial valve figured H, I. Deltidial plates have mostly been broken away when the shell was slightly crushed within the sediment, BD6749b.



TEXT-FIG. 11. Scanning electron micrographs of part of the spicular lophophore support recovered from an example of *Cancellothyris platys* sp. nov. from Avontuur. This area is thought to have been associated with the anterior transverse band of the loop, the long elements on the right being associated with the lophophore canals and the reticulated area on the left being part of the central support between the lophophore arms. BD6767. $\times 75$.

At the Koingnaas locality there are several incomplete specimens which are larger (around 50 mm long) and relatively wider (the length and width being approximately equal) than the normal *C. platys*. Growth lines indicate that this shape was more or less consistent throughout life and that this extra width is not simply a gerontic feature. The rib density is comparable to the other specimens. Since these specimens became broader than true *C. platys* at an early stage of life it is not surprising to find the relative width of the crural bases (text-fig. 10t) is greater than in *C. platys*. We treat these specimens as a subspecies, *C. platys petalos* (text-fig. 10H–M)

Dimensions (in mm)	Length	Width	Thickness	
Holotype b.v.	48.0	53.0	—	BD6750
Paratypes p.v.	c.53.9	c.51.5	—	BD6764
shell	51.5	46.4	c.23.8	BD6765
shell	50.3	c.46.3	28.6	BD6766

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EARLY MISSISSIPPIAN HYOLITHA FROM NORTHERN IOWA

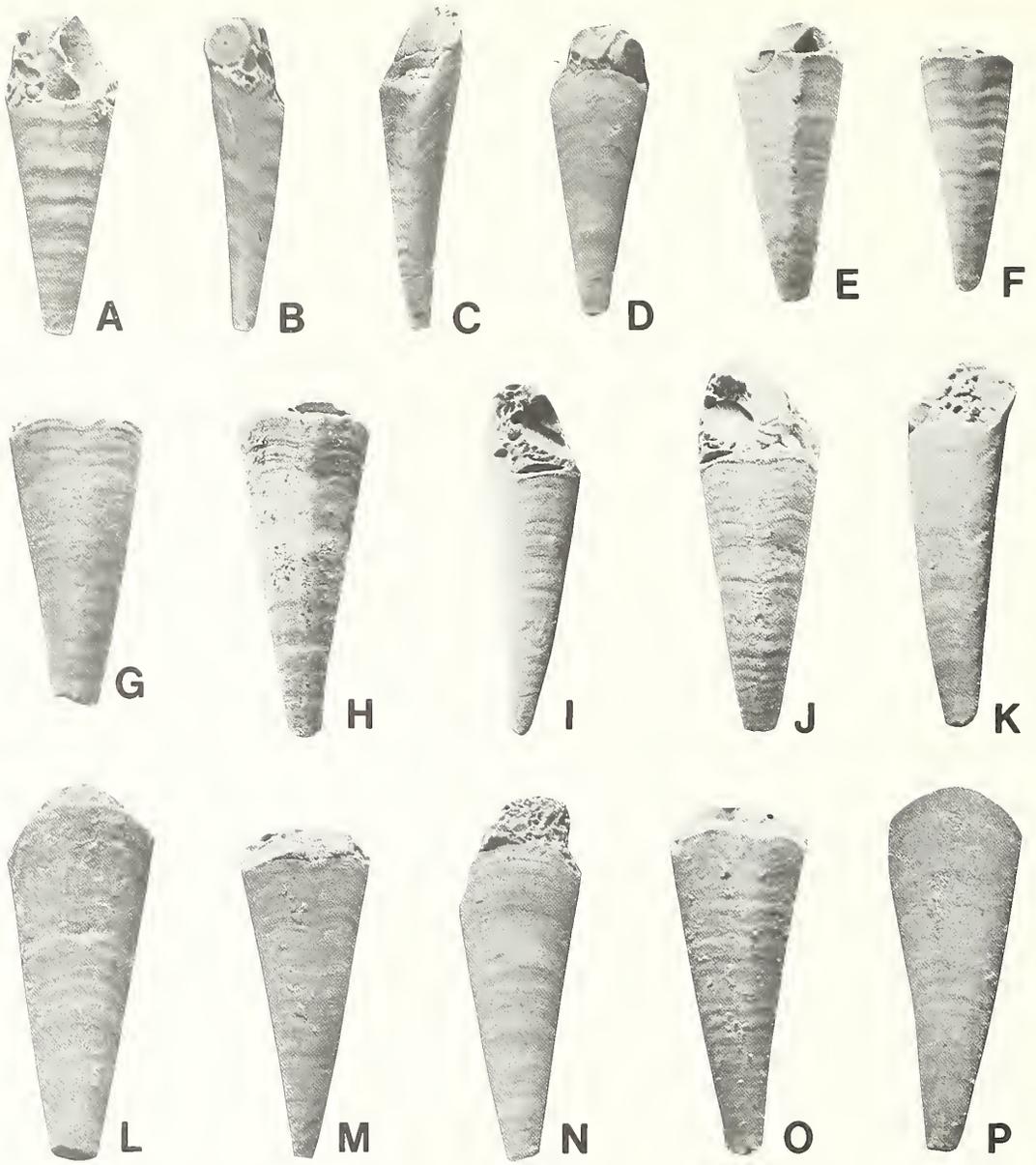
by JOHN M. MALINKY and SHIRLEY SIXT

ABSTRACT. The exceptionally fine preservation and large number of specimens from a single late Palaeozoic locality makes the hyoliths in the Humboldt Oolite (Osagean, lower Mississippian) unique. All specimens are assigned to *Gerkella humboldti* n. gen., n. sp., family Hyolithidae, order Hyolithida. There is considerable variation in certain morphological features, such as transverse shape, nature of ornament and apical curvature; however, these differences are judged to be gradational. This indicates that certain features may be variable within one species and shows that establishment of hyolith species should be based upon a variety of features. Other North American late Palaeozoic hyoliths include *Hyolithes carbonaria* Walcott, *H. milleri* Sinclair, *H. parvulus* Girty and *H. waverliensis* Hyde. Their types lack important morphological features, which makes their generic identifications uncertain. Their names should not be used for any further material until better preserved topotypes become available for study.

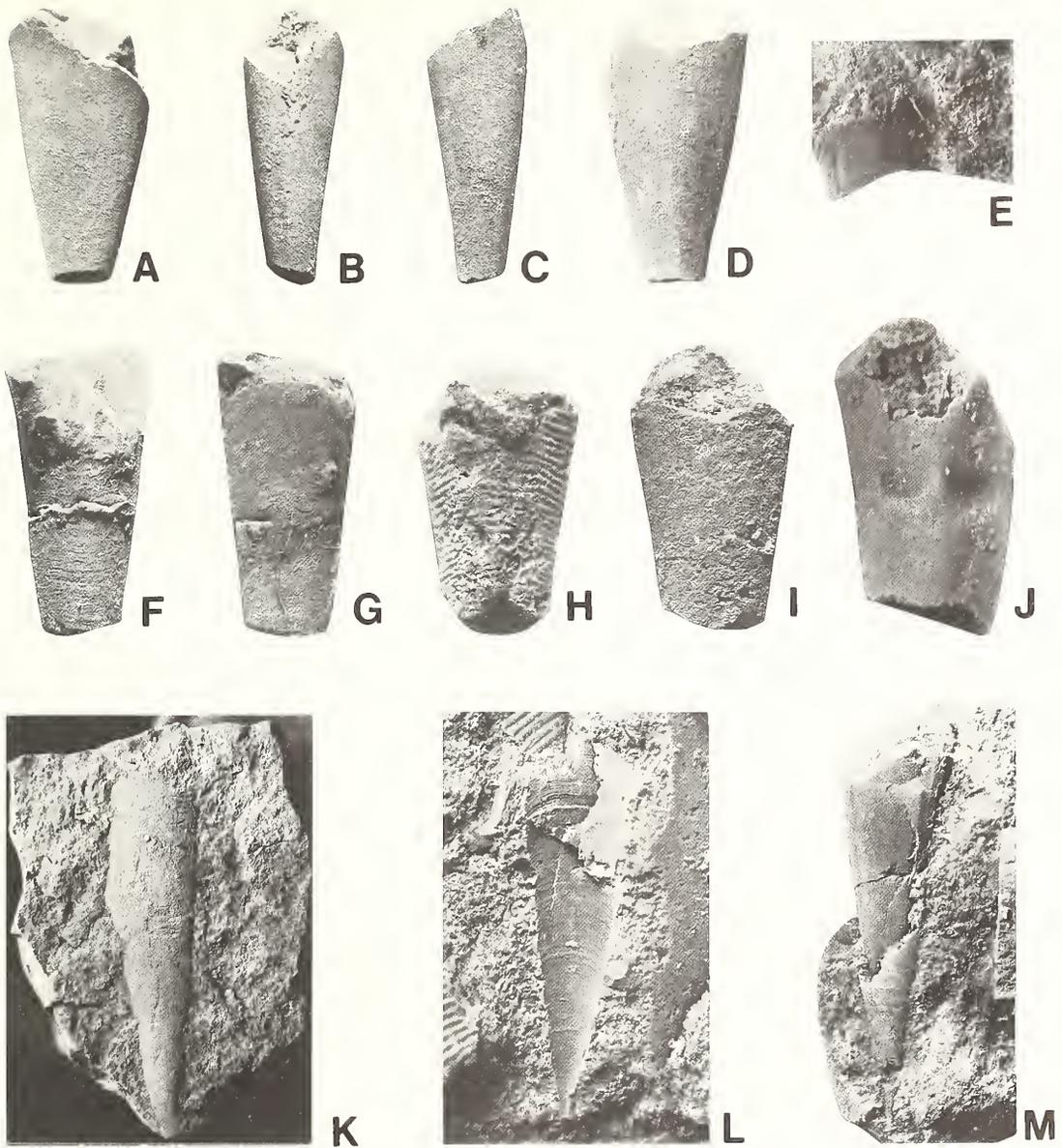
EARLY Palaeozoic hyoliths are currently under intensive investigation in the Soviet Union, China and North America. However, late Palaeozoic hyoliths have received much less attention largely because of rare occurrence. Only six late Palaeozoic species, represented by fewer than ten specimens, have been reported in North America since the mid-nineteenth century (Sinclair 1946). The number of late Palaeozoic specimens drastically increased with the discovery of approximately forty specimens from the Missourian (Pennsylvanian) Eudora Shale of southeastern Kansas (Malinky and Mapes 1983) and more than 1000 specimens from the Pennsylvanian of Kansas, Oklahoma and Texas (Malinky *et al.* 1986). Unfortunately, only a small number of those specimens can be identified to genus; most are poorly preserved steinkerns and cannot be assigned to genus or species. Therefore the discovery of seventy-six well preserved hyoliths from the lower Mississippian of northern Iowa is unique among late Palaeozoic occurrences because of the large number of exceptionally well preserved specimens from one late Palaeozoic locality. Morphology of these specimens indicates that all represent the same species; they are assigned to *Gerkella humboldti* n. gen., n. sp., in the family Hyolithidae and order Hyolithida (text-fig. 1A-P).

Finding these specimens permits a survey of the range of morphological variation within a hyolith species. This further allows assessment of the taxonomic significance of features such as transverse shape and curvature of the apical end of the shell. Transverse shape in particular was used as the ruling criterion for establishing hyolith species in the nineteenth and early twentieth century (Barrande 1867; Novak 1891; Holm 1893; Walcott 1886, 1889, 1890; Resser 1938). It formerly served as the sole distinguishing feature between *Hyolithes* Eichwald, 1840, and *Orthotheca* Novak, 1886, the only two generic names in use for hyoliths until recently (Sysoiev 1958, and many other Soviet and Chinese publications). These genera now form the basis for the orders Hyolithida Matthew *vide* Fisher, 1962, and Orthothecida Marek, 1966, within the class Hyolitha Marek, 1963. Recent studies by Marek (1963, 1967) suggested that while transverse shape remains a characteristic to be considered for diagnosis and recognition of hyolith taxa, other features of the conch and operculum must also be used when available. The gradational nature of transverse shape and other morphological features, such as prominence of growth lirae on the shell, indicates that all specimens from the Humboldt Oolite belong to one species.

In addition to *G. humboldti*, other North American late Palaeozoic hyoliths are the Mississippian species *Hyolithes aculeatus* (Hall, 1860) from Indiana, *H. milleri* Sinclair, 1946 from Missouri, *H.*



TEXT-FIG. 1. *Gerkella humboldti* n. gen., n. sp., Osagean, northern Iowa, USA. A-D paratype USNM 390573, dorsal, left lateral, right lateral and ventral views respectively, $\times 6.4$. E, paratype USNM 390521, dorsum (note apical curvature toward right), $\times 7.4$. F, paratype USNM 390554, dorsum (note apical curvature toward left), $\times 6.3$. G, paratype USNM 390543, dorsum (note apical curvature toward left), $\times 7.2$. H, paratype 390532, dorsum (note curvature toward right), $\times 8.3$. I, J, N, holotype USNM 390504, left lateral, dorsal and ventral views respectively, $\times 4.5$. K, L, paratype USNM 390531, left lateral and ventral views respectively, $\times 5.7$. M, paratype USNM 390552, dorsum, $\times 7.5$. O, P, paratype USNM 390545, dorsal and ventral views respectively, $\times 5.8$.



TEXT-FIG. 2. A–D, *Hyolithes waverliensis* Hyde, holotype OSU 19895, ventral, right lateral, left lateral and dorsal views respectively, $\times 5.3$. E, J, L, M, *H. carbonaria* Walcott, USNM 14426. E, shell at anterior edge of ligula, $\times 5$. J, internal mould of dorsum, $\times 8$. K, external mould of venter, $\times 10$. L, internal mould of venter with some shell near apical end, $\times 10$. F–I, *H. parvulus* Girty. F, G, lectotype USNM 121196, dorsum and venter respectively, $\times 7.2$. H, I, paralectotype USNM 122195, dorsum and venter respectively, $\times 7.5$. K, *H. milleri* Sinclair, lectotype UCGM 3900A, venter, $\times 2$.

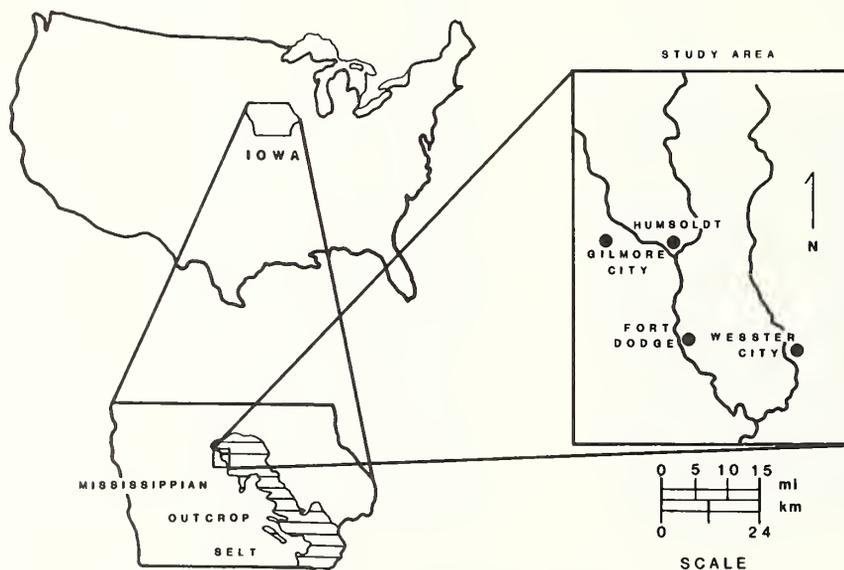
parvulus Girty, 1926 from Texas and *H. waverliensis* Hyde, 1953 from Ohio, and the Pennsylvanian species *H. carbonaria* Walcott, 1884 from Nevada (text-fig. 2A–M). The types of *H. carbonaria*, *H. milleri*, *H. parvulus* and *H. waverliensis* are incomplete, hence their generic identifications may be doubted. The names of these species should not be used for any further material until better-

preserved topotypes become available for study. The type or types of *H. aculeatus* (Hall, 1860) cannot be located at present; however, the published description of that species indicates that few morphological features are preserved, so that its generic identification is uncertain.

Three other Carboniferous species, *H. roemeri* Koenen, 1879, *H. sicula* Koninck, 1883 and *H. sturi* Klebelsberg, 1912 were reported from western Europe. Although these specimens have not been examined, published descriptions and illustrations of the types indicate that preservation is poor, again rendering generic identifications doubtful. Preservation of more recently-discovered specimens considered to be hypotypes of those species (Zakowa 1971) from the *Goniatites granosus* zone of eastern Europe is not sufficiently good confidently to identify those specimens.

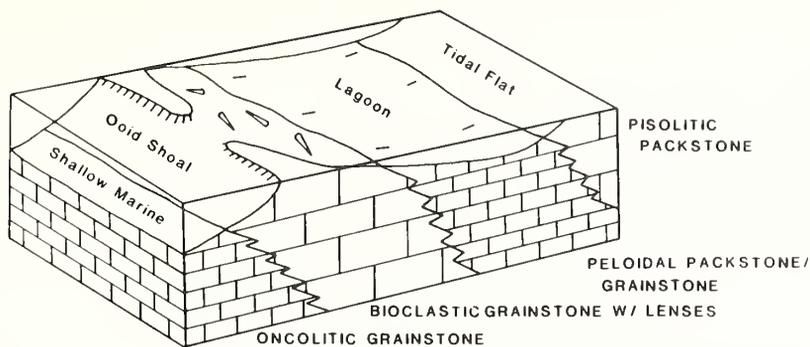
PALAEOECOLOGY AND MORPHOLOGICAL VARIATION

Stratigraphic setting and palaeoenvironment. *G. humboldti* was discovered in the Osagean (Early Mississippian) Humboldt Oolite near Humboldt in northern Iowa (text-fig. 3). The palaeoenvironment of this unit was studied in detail by Gerk and Levorson (1982) and Glenister and Sixt (1982); detailed stratigraphic sections of that locality showing distribution of fauna were given by Glenister and Sixt (1982) and by Brenkle and Groves (1985). Previous studies of fauna were summarized by Glenister and Sixt (1982). More recent taxonomic studies of the trilobites and foraminiferans are those of Brenkle and Groves (1985) and Brezenski (1988) respectively. The hyoliths described herein were only previously mentioned once in an unpublished study of the gastropods of this unit (Harper 1977).



TEXT-FIG. 3. Locality map of *Gerkella humboldti* n. gen., n. sp.

The hyoliths occur within the bioclastic grainstone facies of the Humboldt Oolite (text-fig. 4). That facies includes a series of poorly-indurated, friable, ooid grainstone lenses, 50–200 mm thick which are most common near the middle of the section. The lenses also contain abundant, small, apparently size-sorted gastropods, brachiopods, bivalves, rostroconchs, ostracods and calcareous algae, all of which are exquisitely preserved. According to Gerk and Levorson (1982), the Humboldt Oolite is thought to represent a shallow to marginal marine deposit which originated in an arid climate. More normal marine deposits occur at the base of the section with environmental and facies



TEXT-FIG. 4. Reconstruction of facies during deposition of Humboldt Oolite. Hyolith shells (\triangleleft) accumulated in lenses on bars or shoals (bioclastic grainstone) which sheltered a lagoon (peloidal packstone/grainstone).

restriction progressively increasing toward the top. The bioclastic grainstone represents a series of bars or shoals that sheltered a lagoon in which the sparsely fossiliferous peloidal packstone facies originated. Gerk and Leverson (1982) suggested an analogy between the hyolith-bearing lenses and recent shell beds in protected back-beach areas of the Bahamas. These modern shell deposits resemble the Humboldt lenses in size, lithofacies association and faunal diversity. The Bahamian deposits are thought to have originated from a coincidence of high tide and a south-west wind, rather than from fair weather wave agitation or reworking associated with storms. Movement of water at high tide transports shells to back-beach areas where they are protected from further reworking. Under these circumstances chances of preservation are greater. Conditions resulting in such deposits are unusual and occur only several times a year. A similar origin was suggested by Gerk and Leverson (1982) for the lenses in the Humboldt Oolite.

Hyolith palaeoecology and taphonomy. Various aspects of hyolith palaeoecology were summarized by Fisher (1962) and by Marek and Yochelson (1964, 1976) and will not be reviewed in detail here. However, the unusual lithologic and environmental setting of *G. humboldti* requires additional comment. Because the hyoliths are relatively small they cannot be observed directly on outcrop and their distribution and orientation within the matrix are unknown. None the less, some generalizations on the palaeoecology and taphonomy of this species are still possible.

Late Palaeozoic hyoliths in North America occur in a wide variety of facies from shallow normal marine to offshore, oxygen-poor facies, however they only seem to be abundant in facies which originated in stress environments. Hyoliths have been discovered in normal marine facies such as sandstone (*H. waverliensis* Hyde, 1953 from Ohio), shale (Malinky, unpublished data), and limestone (all remaining Mississippian occurrences and the Pennsylvanian *H. carbonaria* Walcott, 1884). This indicates that they were widespread in the marine environment despite their relatively low abundance at any single locality. However, the taxa from normal marine environments are represented by only one or two individuals each. In contrast, in late Palaeozoic facies from stress environments assemblages of hundreds of hyoliths are known. More than 1000 specimens from fourteen different shale units have been discovered in offshore marine though oxygen-poor shales (Heckel 1977) from the Pennsylvanian of the southern Midcontinent (Malinky *et al.* 1986). Kammer *et al.* (1986) suggested that this type of environment served as a refuge for hyoliths and other 'archaic' taxa such as monoplacophorans which were abundant in the lower Palaeozoic but uncommon in middle and upper Palaeozoic strata. In the oxygen-stressed Pennsylvanian marine environment dysaerobic conditions would have excluded all benthos except those forms such as the hyoliths which seem to have been specially adapted to it. The relative scarcity of other organisms owing to oxygen stress would have decreased competition with the mechanically inefficient hyoliths (Yochelson 1984).

The environment represented by the Humboldt Oolite includes a number of microenvironments, and therefore it is heterogenous or 'coarse-grained' (Ricklefs 1979) for slightly mobile, benthic organisms with regard to water depth, amount of agitation and suspended sediment in the water, and salinity fluctuation. Because the bioclastic grainstone facies was deposited nearshore, environmental stress during deposition would have been caused by these factors rather than by low oxygen. Most stenotopic organisms would have been excluded from an environment such as this except for those specially adapted to it. Even though *G. humboldti* may not have lived in the lenses where it was discovered, the fine preservation of specimens indicates that the amount of transport was minimal and that this form was without question a shallow marine, nearshore species. The relative abundance of this species in the Humboldt Oolite (compared to other Mississippian units) suggests that the species was well adapted and even opportunistic in this particular environment. Yet compared to other invertebrates normally seen in late Palaeozoic marine strata, hyoliths constitute only a small portion of the fauna in the Humboldt Oolite.

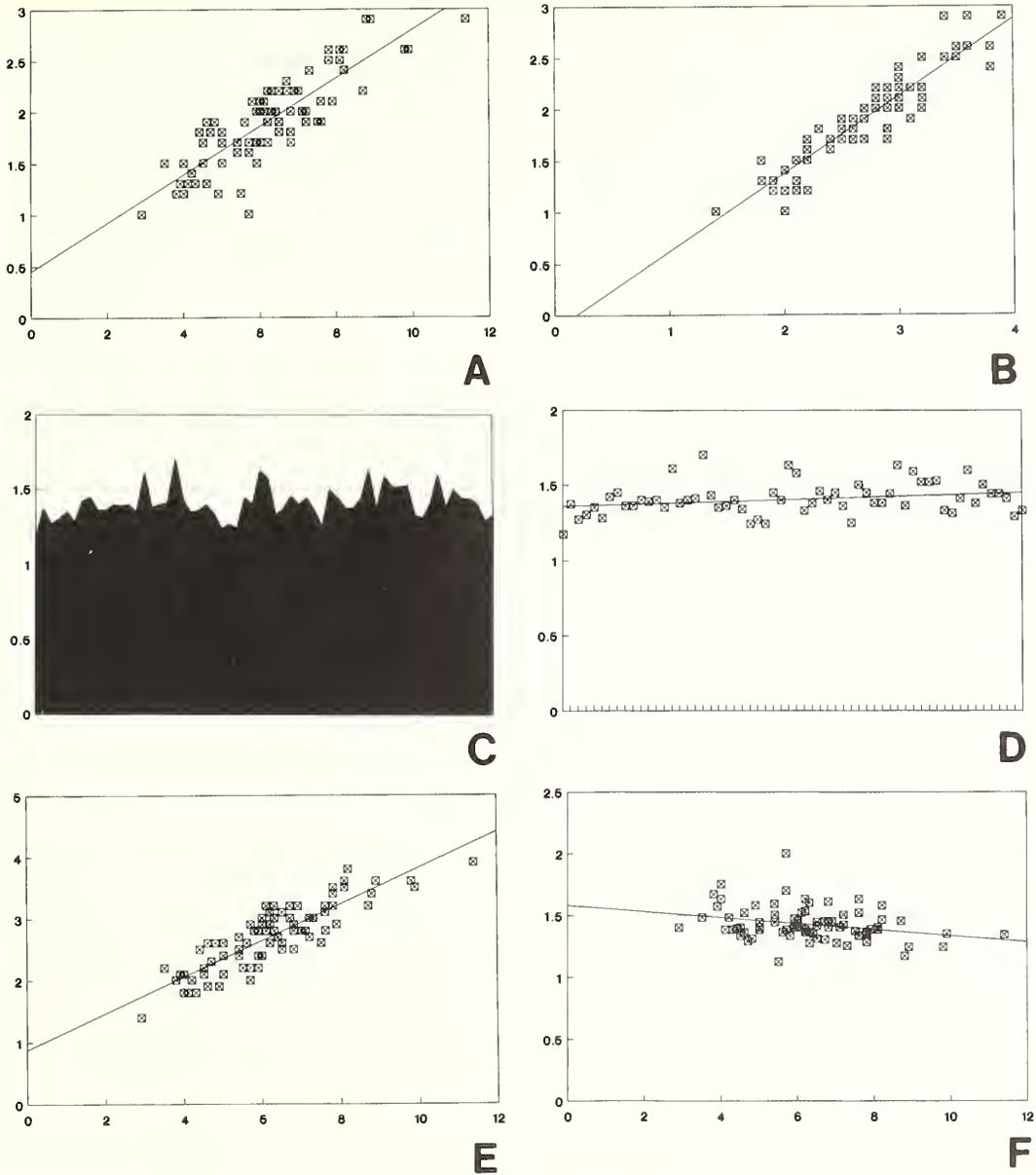
All ontogenetic stages seem to be represented among the Humboldt hyoliths although the larger, and presumably adult, individuals seem to predominate. This may be partly a function of winnowing in which smaller individuals were removed, or it may reflect normal mortality within a breeding population. Individuals dying in old age will normally disarticulate, and the operculum and helens may be lost. Hyoliths buried alive by a sudden influx of sediment might be articulated (Yochelson, pers. comm. 1984). Most of the hyoliths in the Humboldt Oolite may have died from old age, although if any were rapidly buried while alive, winnowing has caused disarticulation of hard parts for those individuals as well.

Following burial, the hyolith conchs in the Humboldt Oolite filled with sediment and small skeletal debris. The sediment and the shells neomorphosed into blocky calcite spar causing all traces of original shell structure to be destroyed. The boundary between the inner shell wall and the spar is distinct, but it is impossible to separate the two to search for muscle scars or other features on the interior of the shell. Calcite spar readily separates from the outer shell wall, suggesting some microenvironmental differences in diagenetic conditions between the interior and exterior of the shell. Lack of oncolitic coatings on the hyoliths suggests either sufficient turbidity to block out sunlight or rapid burial of shells following winnowing.

Morphological variation. Morphological criteria by which species may be recognized among hyoliths were listed by Syssoiev (1958) and Marek (1967). They specifically mentioned: length of shell (L), shell thickness, width (W) and height (H) of aperture, details of growth lirae and other ornament, apical curvature, and various angular measurements of the aperture and apex. Marek (1967) also listed many features of the operculum, but these are not considered here because the operculum of *G. humboldti* is unknown at present. Based upon the number of specimens used by these authors in naming new taxa, neither Marek nor Syssoiev had access to as many individuals as are used in this study. Presumably for these authors, morphological gaps existed between specimens from different horizons or different localities, thereby suggesting taxonomic status.

The hypothesis proposed herein is that all hyoliths from the Humboldt Oolite represent the same species. They occur at the same stratigraphic position and in the same facies, but by themselves these criteria are not conclusive. An examination of selected morphological features must be undertaken either to separate specimens into discrete species, or to survey the range of variation among selected features within the same species. The criteria selected to test the species hypothesis are length of shell, apical curvature, and width and height of the aperture (= transverse shape). These features were chosen specifically because they allow accurate measurement. Other features, such as length of the ventral ligula and nature of growth lirae cannot be used with the same degree of certainty as the features listed above. On many of the Humboldt specimens the ligula is incomplete and variation among growth lirae may reflect partial dissolution of the outer shell wall. Apical and lateral angles are not used because they are directly proportional to the width and height of the aperture, and their distribution will follow that of the apertural parameters.

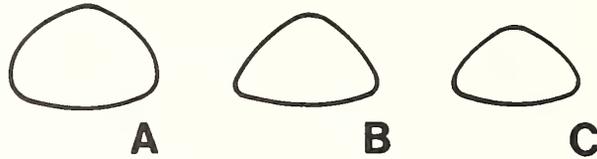
Bivariate plots of the apertural characteristics and a visual comparison of apical curvature



TEXT-FIG. 5. A, apertural width (W) plotted against apertural height (H). B, H plotted against length of shell (L). C, distribution of W/H among Humboldt hyoliths. D, trend in W versus H. E, H plotted against L. F, L plotted against W/H. Absence of clusters among points demonstrates that, based upon these selected characteristics of the shell, all specimens studied herein belong to the same species.

strongly support the notion that all Humboldt hyoliths belong to the same species (text-fig. 5). These results suggest that caution should be used when erecting hyolith taxa based upon relatively few characteristics. Even at present, transverse shape remains the major criterion for some workers when naming and recognizing hyolith species (Sysoiev 1962, 1968; Landing 1988; and many others). Had only the specimens from each end of the range of variation been discovered, the case

for more than one species based upon transverse shape would have been strong because of the large morphological gap between specimens (text-fig. 6). Conversely, different species established on features such as growth lirae or apertural morphology including lateral sinuses or an apertural flare may have similar transverse shapes. In this case, the large population of hyoliths demonstrates that the selected characteristics are gradational among specimens, although the amount of variation seen here may not be typical of all hyolith populations. The adaptive significance in this environment, if any, for the characteristics mentioned above is unknown.



TEXT-FIG. 6. Transverse sections of *Gerkella humboldti* n. gen., n. sp. A, holotype USNM 390504. B, paratype USNM 390521. C, paratype USNM 390545. All $\times 10$.

SYSTEMATIC PALAEOLOGY

Class HYOLITHA Marek, 1963

Order HYOLITHIDA Matthew *vide* Fisher, 1962

Family HYOLITHIDAE Nicholson *vide* Fisher, 1962

Genus GERKELLA gen. nov.

Etymology. The genus is named in honour of Arthur J. Gerk, who discovered these specimens.

Type species. *Gerkella humboldti* n. gen., n. sp.

Diagnosis. Hyolithid which has rugae on the exterior of the shell. Apertural rim is orthogonal without a flare, and the ligula is short.

Included species. *G. humboldti* n. sp. and possibly *H? centennialis* (Barrett, 1876) from the Devonian of New York.

Remarks. This genus is distinguished from others included under the Family Hyolithidae (see Malinky 1988 for list of genera) by the presence of rugae on the shell and other details of ornament and apertural characteristics. *Hyolithes* Eichwald, 1840, *Carinolithes* Syssoiev, 1958, *Sololites* Marek, 1967, *Maxilites* Marek, 1972, *Cavernolites* Marek, 1974, *Nervolites* Marek, 1974, and *Dilytes* Marek, 1974 possess longitudinal sculpture on the shell which *Gerkella* lacks. In addition, *Eumorpholites* Marek, 1967, *Lirotheca* Malinky and Mapes, 1983, and *Darwinites* Malinky, Mapes and Broadhead, 1986 possess a distinct apertural flare which *Gerkella* lacks. *Elegantilites* Marek, 1967, and *Joachimilites* Marek, 1967 have a small apical angle and fine, closely spaced, transverse ribs which anastomose in some places; *Gompholites* Marek, 1966, and *Buchavilites* Marek, 1975 have a tubular shell with a rounded transverse section. *Nevadotheca* Malinky, 1988 has nearly angular lateral margins and inflated slopes on the dorsum which *Gerkella* lacks.

Hyolithes? centennialis Barrett, 1876, from the Devonian of New York may represent this genus; the types of that species are covered with prominent rugae, making it the only recorded species from the middle Palaeozoic of North America to have rugae. The generic identification of this species is uncertain (Malinky, Linsley and Yochelson 1987) because the venter is unknown. Until complete specimens become available for study, that species is tentatively retained under *Hyolithes*.

Stratigraphic range. ?Middle Devonian; Osagean, Lower Mississippian.

Gerkella humboldti n. sp.

Text-fig. 1A-P

Etymology. The species is named after the locality where it was discovered.

Diagnosis. *Gerkella* which has a shallow sinus along the apertural rim of the dorsum.

Description. The shell of this species has a broad, nearly flat to slightly inflated venter, which grades into narrowly rounded lateral margins. The dorsum is inflated with a narrowly rounded longitudinal axis and the adjacent slopes vary from nearly flat to slightly inflated. The ligula along the ventral apertural margin is short, and the anterior edge is straight. The dorsal apertural rim lacks a flare, but a shallow sinus occurs in the rim along each lateral margin and in the middle of the dorsum. The apertural rim is orthogonal (perpendicular to the venter). The apical angle of the shell is small, and the apical end curves either to the left or right when viewed dorsally, and on some specimens it also curves toward the venter. The transverse section of the shell is subtriangular (text-fig. 6).

The exterior of the shell is covered with widely spaced rugae. On the venter, the rugae curve to follow the outline of the anterior edge of the ligula. The rugae curve on the lateral margins to form a shallow sinus, parallel to that in the apertural rim, and on the dorsum the rugae are nearly transverse except for a shallow median sinus which follows that of the apertural rim. The operculum and helens are unknown.

Remarks. This species is currently known from seventy-six specimens; specimen USNM 390504 is selected as holotype because it is the most complete and best preserved. That specimen is 8.8 mm long, and has an apertural width and height of 2.6 mm and 2.3 mm respectively. Neither the holotype nor any paratype is operculate, and no disarticulated opercula or helens have been found for this species. All specimens are free of matrix, although the interiors of the shells contain blocky calcite spar which cannot be removed without destroying the specimens. Details of the interior are unknown.

The specimens upon which this species is based were collected over a twenty year period by A. J. Gerk of Mason City, Iowa. These hyoliths were mentioned in a study of the Gastropoda of the Humboldt Oolite by Harper (1977), who regarded them as conspecific with *Hyolithes? waverliensis* Hyde, 1953 from the Mississippian of Ohio. That species is based upon a steinkern which lacks most taxonomically important characteristics such as all features of the apertural end. No meaningful comparison between that species and *G. humboldti* is possible, and the two are herein treated as separate species.

Material. Holotype USNM 390504 and seventy-five paratypes under 390505 through 390580.

Occurrence. P. & M. Hodges quarry, sec. 32, T92N, R28W, northeast of Humboldt, Humboldt County, north-central Iowa, from the Humboldt Oolite, Osagean (lower Mississippian) (text-fig. 3).

Stratigraphic range. Osagean.

Class HYOLITHA *incertae sedis**Hyolithes? aculeatus* (Hall, 1860)

- 1860 *Pugiunculus? (Theca) aculeatus* Hall, p. 107.
- 1862 *Pugiunculus? aculeatus* Hall; Winchell, p. 423.
- 1865 *Pugiunculus? aculeatus* Hall; Winchell, p. 131.
- 1898 *Hyolithes aculeatus* (Hall); Weller, p. 311.
- 1946 *Hyolithes aculeatus* (Hall); Sinclair, p. 73.
- 1967 *Hyolithes aculeatus* (Hall); Yochelson and Saunders, p. 9.

Description. 'Elongate, obtusely triangular bodies, having one side nearly flat, and the other two sides meeting at a very obtuse angle, and slightly incurved towards the angle, the flat side being convex in the direction of the length. Aperture obtusely triangular, and a little thickened on the straight side of the lateral angles' (Hall 1860, p. 107).

Remarks. This species was named and described but not illustrated by Hall (1860, p. 107). To date, this species apparently has never been illustrated, yet the name has been used for other specimens by later workers (see below). Hall (1860) did not select a holotype for this species, and the type or types cannot be located at present. Hall's description, and indeed, the fact that he was uncertain of the generic identification, leaves little doubt that preservation of the type material was poor. Because so few characteristics of this species are known, its name should not be used for any additional specimens.

Winchell (1862, 1865) referred hyoliths which he described as casts 'without external markings' to *P.?* *aculeatus*, but he provided no additional details of those specimens or their occurrences. Weller (1898), Sinclair (1946) and Yochelson and Saunders (1967) listed the species name in their respective compilations of hyolith species without reporting any specific occurrences other than that of the type. Weller (1898) listed the species under *Hyolithes* because by that time, both *Pugiunculus* Barrande (1847), and *Theca* (Sowerby *vide* Morris 1845) were regarded as junior synonyms of *Hyolithes*.

Occurrence. Hall (1860, p. 107) discovered this species in the 'Goniatite limestone near Rockford, Indiana.' That unit is now called the Rockford Limestone (lower Mississippian, Osagean; Gray 1979). Winchell's (1865) specimens were discovered in the Marshall Formation (Osagean; Ellis 1979) in the SE 1/2 SW 1/2 sec. 23, Adam, Hillsdale County, Michigan and in 'Alan's and Germain's quarries, Hillsdale,' Michigan (Winchell 1862).

Hyolithes? *carbonaria* Walcott, 1884

Text-fig. 2E, J, L, M

- v* 1884 *Hyolithes carbonaria* Walcott, p. 264, pl. 23, fig. 3.
- v* 1892 *Hyolithes carbonaria* Walcott, p. 333.
- v* 1946 *Hyolithes carbonaria* Walcott; Sinclair, p. 74.
- v* 1967 *Hyolithes carbonaria* Walcott; Yochelson and Saunders, p. 9.

Description. The venter of this species is flat, but curves slightly to grade into narrowly rounded lateral margins. The dorsum is low, and the longitudinal axis is narrowly rounded. The slopes adjacent to the axis are nearly flat. The ligula along the ventral apertural margin seems to be short, and the anterior edge appears to have been flat. The ligula appears to curve slightly toward the venter.

The shell on the venter is covered with fine, closely-spaced lirae which follow the outline of the anterior edge of the ligula. Two longitudinal sulci are located at each edge of the venter and they extend for the entire length of the venter. The sulci are prominent near the apertural end, but become shallower toward the apical end. The dorsal internal mould is smooth except for a prominent indentation located near the apertural end on each slope. The operculum, the shell on the dorsum and the complete aperture are unknown.

Remarks. The holotype and only known specimen of this species is 9.5 mm long, and has an apertural width of 2.3 mm. The holotype exists as several counterparts; an external mould furnishes details of the venter, a portion of the internal mold provides some detail of both dorsum and venter, and a fragment of internal mould with shell embedded in matrix furnishes further details of the venter and interior of the shell. Unfortunately, the dorsal apertural rim and the shell on the dorsum are unknown. This specimen lacks an operculum, and no disarticulated opercula were included in this species.

The indentations on the dorsal internal mould resemble those of *Lirotheca wilsoni* Malinky and Mapes, 1983, from the Pennsylvanian of Kansas. *Maxilites maximus* (Barrande, 1867) from the Caradocian of Czechoslovakia also has two crescent-shaped indentations on the dorsum which may represent muscle scars (Marek 1967), but these are smaller and narrower than the indentations on *H. carbonaria*. Walcott (1884) also compared this species to *H. acilis* Hall, 1876, from the Devonian of New York, but the apertural rim on that form is flared, whereas the apertural rim of *H. carbonaria* is unknown.

Material. Holotype USNM 14426, National Museum of Natural History.

Occurrence. Walcott (1884, p. 264) reported that this species was discovered in the 'Lower portion of the Lower Carboniferous limestone, in canon directly south of a small conical hill on the east side of Secret-canon-road Canon, Eureka District, Nevada.' This locality is probably in the NW 1/4, SE 1/4, sec. 36, T19N, R53E, Pinto Summit (15 minute) quadrangle. The 'Lower Carboniferous' limestone is probably the Ely Limestone, now recognized as Morrowan (early Pennsylvanian) in age (Larson and Langenheim 1979).

Hyolithes? milleri Sinclair, 1946

Text-fig. 2k

v* 1894 *Hyolithes lanceolatus* Miller, p. 317, pl. 19, figs. 35, 36.

v* 1946 *Hyolithes milleri* Miller; Sinclair, p. 73.

v* 1967 *Hyolithes milleri* Miller; Yochelson and Saunders, p. 9.

non 1845 *Hyolithes lanceolatus* Morris, p. 289, pl. 18, fig. 8.

Description. The conch of this species has a small apical angle, and the apical end appears to be straight. The venter is nearly flat, and that side is smooth without any lirae or other ornament. The ligula is short and the anterior edge appears to be straight. All other features, such as the aperture and operculum are unknown.

Remarks. Characteristics attributed to this species by Miller (1894) were derived in part from about two dozen phosphatic tubes which Miller (1894) mistakenly included under this species. *H. milleri* is unequivocally represented by one specimen (UGGM 3900A) and possibly by a second (UCGM 3900B); the phosphatic tubes were transferred to *Enchostoma* by Miller and Gurley (1896). Miller's illustration of *H. milleri* is a line drawing of a phosphatic tube that bears no resemblance to any authentic hyolith. Until now, these hyoliths have never been illustrated with photographs.

Specimen UCGM 3900A is here designated the lectotype; it is 19.5 mm long, and has a width of 4.4 mm. Only the venter is exposed; the dorsum is embedded in matrix from which extraction intact would probably be impossible. Whether that specimen has a shell or is an internal mould is not known with certainty. If shell is preserved, it appears to be smooth and featureless. The presence of an operculum cannot definitely be ascertained because the apertural end is concealed by matrix. Miller (1894) named this species *lanceolatus*, but Sinclair (1946) renamed it because the name *lanceolatus* was preoccupied (Morris 1845).

Material. Lectotype UCGM 3900A and possible paralectotype under 3900B deposited at University of Cincinnati Geology Museum.

Occurrence. Miller (1894) reported that these specimens were discovered in the Chouteau Limestone (Kinderhookian, lower Mississippian, Thompson 1979) 'near Sedalia, Missouri'. No other details of the occurrence are known.

Hyolithes? parvulus Girty, 1926

Text-fig. 2F-I

v* 1926 *Hyolithes parvulus* Girty, p. 38, pl. 6, figs. 18a-18e, 19a-19d.

v* 1946 *Hyolithes parvulus* Girty; Sinclair, p. 79.

v* 1967 *Hyolithes parvulus* Girty; Yochelson and Saunders, p. 9.

Description. The venter of this species is nearly flat and grades into narrowly rounded lateral margins. The dorsum is high and the longitudinal axis is narrowly rounded. The apical end of the shell appears to be straight, and the apical angle seems to be small. The conch is covered with fine lirae; they are nearly transverse on the dorsum but curve on the venter to follow the outline of the ligula. The ligula is short and broadly rounded at the anterior edge. The complete aperture and operculum are unknown.

Remarks. Two specimens were assigned to this species by Girty (1926); specimen USNM 121196 is herein designated the lectotype. That specimen is 5.4 mm long, and has an apertural width and height of 2.9 mm and 2.0 mm respectively. The lectotype retains a shell although both ends are broken, so that the complete aperture, as well as the operculum are unknown. Preservation of a

possible paralectotype (USNM 121195) of similar size is comparable to the lectotype although that specimen is covered with coarse ribs; whether it represents the same taxon as the lectotype is uncertain.

Material. Lectotype USNM 121196 and paralectotype USNM 121195, National Museum of Natural History.

Occurrence. Girty (1926, p. 38) reported these specimens from 'station 2623, about 5.0 km (3.0 miles) east of San Saba County courthouse' in San Saba County, Texas. The labels associated with the specimens give more information: 'on the SW side of the road to Chappel, about 3 miles SE of San Saba courthouse, at first sharp turn well uphill.' The unit which yielded the hyoliths is 'a thin limestone above the Ellenburger and below the Barnett Shale': this is the Chappel Limestone of late Kinderhookian to early Osagean (early Mississippian) age (Kier *et al.* 1979). A recent visit to that locality by J. M. M. showed that the limestone remains exposed on the southwest side of Chappel Road, but no additional hyolith material was discovered.

Hyolithes? waverliensis Hyde, 1953

Text-fig. 2A-D

v* 1953 *Hyolithes waverliensis* Hyde, p. 335, pl. 53, figs. 10-15.

v* 1967 *Hyolithes waverliensis* Yochelson and Saunders, p. 9.

Description. The conch of this species has a broadly rounded venter which grades into narrowly rounded lateral margins. The dorsum is low and narrowly rounded along the longitudinal axis; the adjacent slopes are slightly inflated. The apical angle is small, and the apical end curves slightly toward the dorsum.

The lateral margins of the internal mould are covered with faint transverse growth lirae, and along each lateral margin faint longitudinal lirae are present. The shell, complete aperture and operculum are unknown.

Remarks. This species is known from a steinkern and a fragmentary external mould, both of which are counterparts of the holotype. The steinkern is 8.0 mm long, and has an apertural width and height of 5.0 mm and 3.0 mm respectively. Both ends of the steinkern are broken, and no apertural detail is preserved. The steinkern has no operculum, and no disarticulated opercula have been identified for this species.

The appearance of the steinkern closely matches the line drawings of figures 13 and 14 on plate 53 (Hyde 1953); figures 10-12 on that plate seem to be restorations for no available specimens of this species match those illustrations, and there is no evidence for the apertural detail shown.

Material. Holotype OSU 19895, Orton Museum of Geology, Ohio State University.

Occurrence. Hyde (1953, p. 336) discovered this specimen in Bed 1, Byer Member of the Logan Formation (Kinderhookian, lower Mississippian, Collins 1979), near Sciotoville, Scioto County, Ohio.

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PSEUDOPLANKTON

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ABSTRACT. All attached epifaunal species have the potential to colonize floating substrates such as driftwood, externally shelled cephalopods, *Sargassum*-like algae and marine vertebrates. Such pseudoplankton are preserved in a much wider range of facies than their benthic relatives. However, they are never as abundant as benthos due to the rarity of attachment sites. Pseudoplanktonic species utilize five attachment strategies: cemented, adpressed, pendent, boring and clinging. Overcrowding appears to be a common problem on floats and consequently the pendent strategy, with its limited attachment area relative to the size of the organism, appears to have been favoured by obligate pseudoplankton. However many species are facultatively pseudoplanktonic, making palaeoecological interpretations difficult. Most reported examples of pseudoplankton, particularly those from black shale facies, are too abundant to be attributed to this group and, in the majority of cases, a benthic mode of life is more plausible. The fossil record of pseudoplankton is thought to be considerably poorer than has hitherto been suggested. Evaluation of the literature reveals a low, although variable diversity of pseudoplanktonic populations through the Phanerozoic. High diversity in the mid-Palaeozoic is due to the presence of large orthoconic nautiloids which provided ideal floating substrates for a number of groups. Unexplained diversity minima occurred in the Permian and Cretaceous.

IN any palaeoecological work it is essential to distinguish between benthic and pelagic elements of the fauna since each provides evidence of their fundamentally different environments. In most instances it is relatively easy to discern the general mode of life of an organism from the morphology of the hardparts or from comparison with extant relatives. In particular, the constraints on morphology of benthic organisms differ greatly from those of free-swimming (nektonic) and drifting (planktonic) organisms. However, a few species have the morphological adaptations of epifaunal benthos yet they pursue a mode of life attached to floating objects (either organic or inorganic) in the water column and hence are effectively planktonic; these are termed pseudoplanktonic forms (alternatively known as epiplanktonic or pseudopelagic forms in some studies). Excluded from this definition are those organisms which secrete their own float, for these are more properly classified with the true plankton. The basic morphology of pseudoplankton means that, should they become detached from their floating substrate before burial, it may be difficult to deduce their original mode of life. As a result, conflicting palaeoecological interpretations have arisen frequently in the literature.

The aim of this paper is to provide criteria for the recognition of pseudoplankton in the fossil record and to discuss some of the biological constraints and consequences of this unusual mode of life. A tripartite classification scheme is then proposed for pseudoplanktonic forms. Finally the moderately diverse, though patchy, history of pseudoplankton in the Phanerozoic is reviewed.

A large proportion of fossil pseudoplankton described in the literature is recorded from black shales. The depositional conditions of this facies undoubtedly provide excellent potential conditions for the preservation of pseudoplankton, but in many cases the rationale behind such reports lies in the assumption that black shale environments are inimical to benthic life. Therefore, by default, any apparently benthic fossils are considered to have fallen on to the sea floor from floating substrates higher in the water column. Taphonomic and functional morphological evidence have rarely been cited to support such interpretations and, as will be discussed below, many examples of so-called black shale pseudoplankton were probably truly benthic.

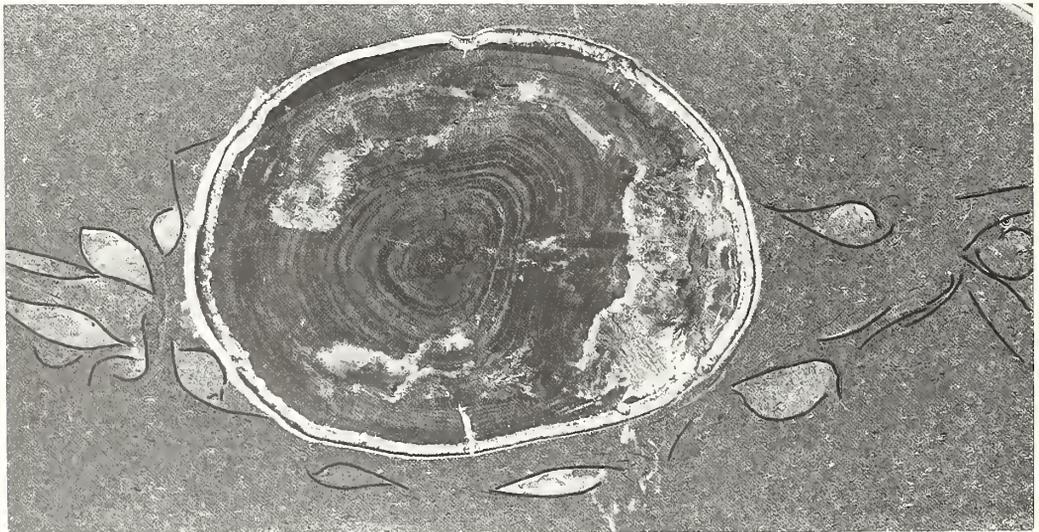
THE RECOGNITION OF FOSSIL PSEUDOPANKTON

Virtually every aspect of the biology, taphonomy and facies distribution of pseudoplanktonic species differs from that of benthic species. Thus a number of features can be used to identify pseudoplankton in the fossil record.

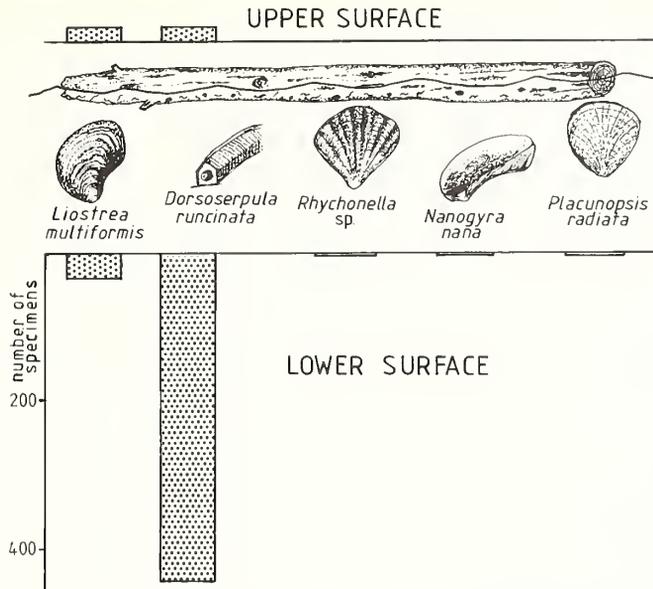
Association with floating objects

Pseudoplanktonic forms are most readily identified when they are preserved together with their floating substrate. The frequency with which this occurs is partially dependent on the style of attachment; for example, cemented bivalves are more likely to remain fixed than byssate forms which readily become dislodged after death. The energy of the depositional environment is also important – quiet conditions, such as those leading to organic-rich shale accumulation, are particularly favourable for the preservation of intact pseudoplanktonic colonies. A range of floating attachment sites was and is available in the marine realm.

Driftwood. Floating logs have been available for colonization by pseudoplankton since the appearance of trees in the late Devonian. Estimates for the maximum floating duration of driftwood range from less than one year (Kauffman 1981) to ten years or more (Simms 1986). The actual time will depend on a combination of factors, such as the nature of the wood, its size, and the influence of osmosis and bacterial sealing (Simms 1986). In general the carrying capacity of wood appears to be high. However, logs can become colonized both while they are afloat and after sinking to the substrate. Pseudoplanktonic colonies are generally found beneath driftwood or alongside the wood if it sank to the substrate at an oblique angle (e.g. Seilacher *et al.* 1968; text-fig. 1). Most pseudoplanktonic colonies on driftwood have been recorded from organic-rich shales (e.g. Withers 1928; McIntosh 1978; Simms 1986) but they are also known from more normal marine mudrocks. Thus Davis and Elliot (1958) record colonies from the Eocene London Clay, whilst a log with abundant epibionts on its lower surface has been examined from aerobic biofacies of the Kimmeridge Clay (text-fig. 2). Lepadomorph barnacles are the dominant driftwood colonizers in modern seas (Schäfer 1972).



TEXT-FIG. 1. Section through a nodule from the Obtusum Zone (Sinemurian, Lower Jurassic) of Stonebarrow Cliff, Charmouth, Dorset, illustrating driftwood, partially calcitized, with individuals of *Cuneigervillia* (outlined) occurring beneath and alongside the wood. Field of view is 100 mm wide.



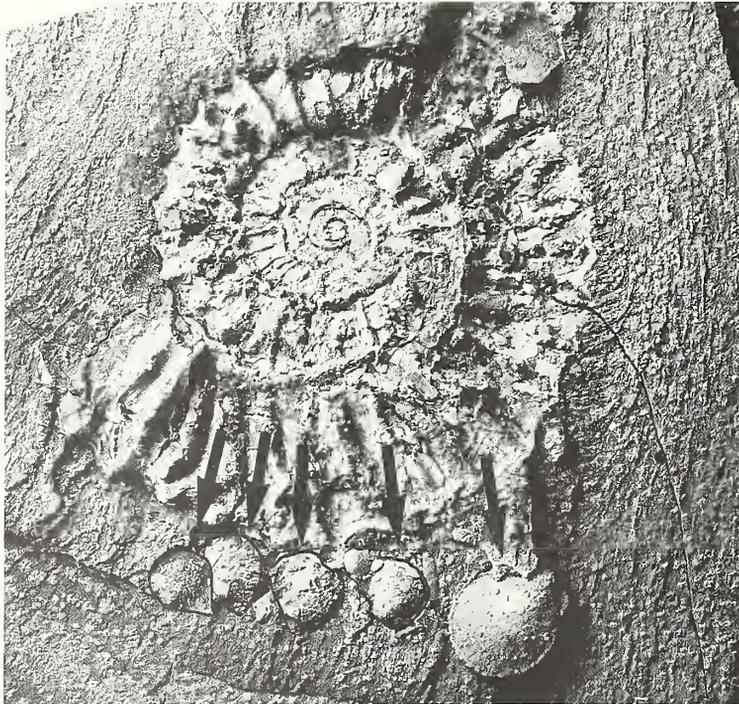
TEXT-FIG. 2. Epizoan abundance measured on a 3.5 m long piece of driftwood from the lower Mutabilis Zone (Lower Kimmeridge Clay, Upper Jurassic) at Wyke Regis, Weymouth, Dorset. The majority of encrusters is found beneath the wood whilst the specimens located towards the edges on the upper surface were probably originally on the flanks of the log. The occurrence of '*Rhynchonella*' *subvariabilis*' beneath this log supports Ager's (1962) contention that this species was, at least occasionally, pseudoplanktonic. Several branches on the log would have inhibited it from rolling on the sea floor, thereby discounting the possibility that the log was overturned to cause the smothering of the epizoans.

Externally shelled cephalopods. Nektonic or nektobenthic cephalopods have been available as hosts for pseudoplankton since the Ordovician. The earliest colonizers were bryozoans and inarticulate brachiopods found on large orthoconic nautiloids in the Upper Ordovician (Havlíček 1972; Lockley and Antia 1980; Baird *et al.* 1989). Goniatites, the dominant Upper Palaeozoic cephalopods, were generally too small to support any significant epifauna although they may also have been able to defend themselves from colonization (Boston *et al.* 1988). Large ammonites became common in the Mesozoic and many examples of oyster encrustation are known (e.g. Meischner 1968; Heptonstall 1970; Riccardi 1980; Seilacher 1982a; Tanabe 1983).

There has been considerable debate about whether ammonite colonization occurred during life (Seilacher 1982a, b), after death but whilst the ammonite was drifting (Palmer 1987; Tanabe 1983), or after the ammonite settled to the bottom to form a localized hard substrate (Kauffman 1981). In the last case, ammonites lying on the sea floor should be encrusted on the upper surface only, although this is not always easy to determine if aragonite dissolution has occurred at an early stage of burial. However, if the ammonite was overturned by foraging organisms then it would be possible for both sides to become encrusted while it lay on the sea floor. Other distinguishing criteria have been discussed by Seilacher (1982a). In-life colonization is thought to be characterized by orientated growth, commonly towards the aperture of the cephalopod. Individual ammonites may be heavily encrusted whilst other specimens, from the same horizon, totally lack epibionts. Typically the encrustation is host-specific with heavily ribbed ammonite species being preferentially colonized (Seilacher 1982a; Doyle and Whitham, in press). Such patterns are only likely to occur if infestation occurred in the water column where some ammonites may have defended themselves against infestation while others positively encouraged epibionts as a form of camouflage. This implies that most ammonite colonization occurred during life. Defence against unwanted epizoans may have been through active cleansing using tentacles. Alternatively, the possession of a thick

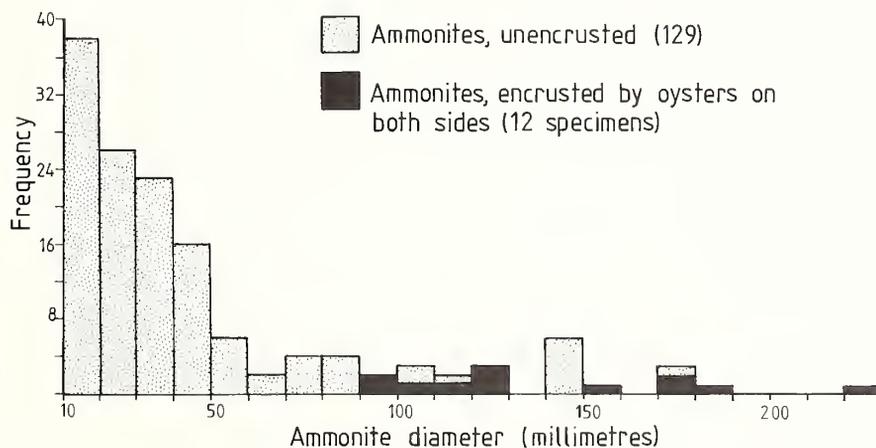
periostracum may inhibit boring and encrustation (Bottjer 1981). In rare cases ammonites have been observed to deviate from their normal planispiral growth pattern due to the presence of large oysters on one flank (Merkt 1966; Heptonstall 1970). Similarly, serpulids growing on the ventral margin of ammonites have been distally overgrown by the later whorls of the ammonite, providing unequivocal evidence of in-life colonization (Merkt 1966).

Nekroplanktonic colonization of dead ammonites floating at the surface cannot always be distinguished from in-life colonization. Diagnostic features include the presence of epibionts within the body chamber of ammonites. The uppermost flanks would project above the surface of the water after death and so these areas would be free of epizoans. Such distributions have rarely been recorded. Data from Recent *Nautilus* suggest that hydrostatic pressure rapidly fills the phragmocone with water following death and thus precludes significant nekroplanktonic drifting (Chamberlain *et al.* 1981). Ammonites were probably less robust than *Nautilus* and hence even less likely to remain afloat for long after death (Seilacher 1960). In general the majority of pseudoplankton associated with ammonites appears to have colonized the ammonite whilst it was alive. Ammonites with apparently *in situ* populations of byssally attached bivalves have been encountered in organic-rich facies from the Lower Jurassic. Seilacher (1982a, fig. 9) illustrated a colony of *Gervillia lanceolata* clustered around the venter of an ammonite close to the aperture. A similar distribution has been noted for specimens from the Sinemurian (Lower Jurassic) of Dorset; *Plagiostoma* has been found associated with *Arnioceras* from the Turner Zone, *Cuneigervillia* with *Asteroceras* from the Obtusum Zone, and *Oxytoma inequivalve* attached to *Echioceras* from the Raricostatium Zone (text-fig. 3).



TEXT-FIG. 3. Five specimens of *Oxytoma* (arrowed) close to the apertural margin on the venter of a specimen of *Echioceras*. Collected from the Raricostatium Zone (Sinemurian, Lower Jurassic) of Charmouth, Dorset, by C. E. Savrda. The bivalves were probably suspended from beneath the ammonite during life. Benthic colonization would have been expected to produce a more random association. Ammonite is 19 mm in diameter.

In an unusual case of ammonite encrustation, documented by Cope (1968) from the Kimmeridge Clay, oysters were only found cemented to the lower side of ammonites, mainly in the umbilical region. This he attributed to a photonegative response of the oyster larvae settling under ammonite shells lying on the sea floor. However, extensive collecting from the same succession revealed that, of 20 oyster-encrusted ammonites, 14 had oysters on both flanks, 5 had oysters on the upper surface only and only a single specimen was found to have oysters restricted to its lower surface. These data suggest that most oyster-encrustation occurred while the ammonites were still in the water column. The five examples with colonization on the upper surface tended to have oyster nests nucleated anywhere on the shell with little preferred growth orientation. Examples with oysters on both sides of the ammonite tended to show a radial growth orientation centred on the umbilical region. This pattern may have been caused by the oyster spat seeking out the most sheltered region of the ammonite shell although it could also reflect the greater age of the umbilical region compared to the outer whorls. In support of this, all 14 of the Kimmeridge Clay ammonites with oysters on both flanks are large, old specimens greater than 90 mm in diameter (text-fig 4). Similarly, in-life encrustation of ammonites in the Lower Jurassic is mainly restricted to adult examples of large, presumably long-lived individuals. The radial orientation is caused by the competitive growth of the oysters with each individual being forced outwards from the umbilicus by the presence of its neighbours, causing the growth of wedge-shaped morphologies.



TEXT-FIG. 4. Size-frequency histogram illustrating the proportion and abundance of oyster-encrusted pectinatitid ammonites from the Upper Kimmeridge Clay (Upper Jurassic) of the Dorest coast. The over-representation of large and oyster-encrusted specimens in this sample is a collecting artifact. All specimens in the P. B. Wignall collection.

Vertebrates. For most marine vertebrates the presence of pseudoplankton is undesirable since it causes a drastic increase in drag. Precautions against such colonization include the ability to shed scales and the development of a skin surface unsuited to settlement. Only in large or slow moving vertebrates, such as whales and turtles, is the addition of large species of pseudoplankton unlikely to alter the hydrodynamic properties. Whales are commonly infested with large numbers of barnacles (*Xenobalanus* and *Coronula*), copepods and a diverse meiofauna including diatoms (e.g. Holmes 1985). Turtles are commonly host to an even greater range of epizoans, including gastropods, bivalves, hydroids, crabs and barnacles (Frazier *et al.* 1984). Due to the rarity of soft tissue preservation in the fossil record, no examples of pseudoplankton on vertebrates are known, though it is possible that suitably enlightened investigation of the immediate surrounds of large intact vertebrates in anoxic sediments may reveal their presence.

Conulariids. A diverse pseudoplanktonic fauna, including punctate brachiopods and bryozoans, has been found attached to conulariids in the Carboniferous, Bear Gulch Limestone of Montana (Williams 1983), whilst inarticulate brachiopods are considered to have attached to conulariids in the Ordovician (Havlíček 1972). Such occurrences are surprising considering the small, delicate nature of these organisms.

Chondrophorines. The fragile chitinous floats of these jellyfish-like organisms have only recently been identified in the fossil record, many examples previously having been misidentified as patellid gastropods (Stanley and Kanie 1985). As with conulariids, the chondrophorines were probably too fragile to support epizoans commonly, although an exception is the attached fauna found on chondrophorines in the early Devonian Hunsrückschiefer of Germany (Yochelson *et al.* 1983).

Algae. Vesicular algae, such as *Sargassum*, are one of the most common attachment substrates for pseudoplankton at the present day. Brown algae are commonly invoked as attachment sites for ancient epizoans, but such soft material has a very low preservation potential (see Jerzemska and Kotlarezyk (1976) for an exception). Ruedemann (1934) has illustrated examples of so-called algae from Palaeozoic black shales. Many of these are probably trace fossils but a number of carbonaceous branching structures (e.g. Ruedemann 1934, pls. 2–3) remain unexplained. Rickards (1975) suggested that they may be the extrathecal tissue of graptolites.

Pumice. Pumice, which is probably the only naturally occurring non-organic substrate for pseudoplankton, has been available throughout the Phanerozoic. Its floating duration is dependent on size, initial density, temperature upon entering water and the size distribution and connectivity of the vesicles (Whitham and Sparks 1986). Their experiments showed that some pumice remained afloat for more than 18 months. Extrapolation from their observations suggested that large, low density masses up to 1 m across may remain afloat for more than 10 years. Jokiel (1984) also inferred, from the size of a coral colony attached to floating pumice, that pumice could remain afloat for two to three years at least. Despite such observations, examples of pseudoplankton attached to pumice are very rare in the fossil record, although Doyle and Whitham (in press) have recorded oxtomid bivalves associated with pumice from the Upper Jurassic.

Abundance and facies distribution

In many instances pseudoplankton may become detached from its floating substrate before burial or, in the case of epizoans attached to floating seaweed, their attachment site may not be preserved. In such situations less direct methods of taphonomic analysis must be used to determine their original mode of life.

Pseudoplankton today only constitutes a tiny fraction of the total abundance of epizoans due to the rarity of floating attachment sites compared to the abundant sites available in the benthic environment. Conditions are unlikely to have been significantly different in the past and consequently pseudoplanktonic species should generally be a rare component of fossil assemblages. For examples modern-day lepadomorph barnacles are an important pseudoplanktonic group but their plates are only found in very small numbers, scattered through a wide range of marine sediments (Schäfer 1972). Only under slow sedimentation rates, such as those commonly found in the depositional environments of organic-rich shale (Tyson 1987), will pseudoplankton ever occur in anything approaching moderate numbers. Even under such conditions, pseudoplanktonic forms should not occur as more than a few individuals scattered across bedding planes. Exceptionally slow sedimentation rates may lead to greater abundances although in these instances the pseudoplanktonic species should be accompanied by high concentrations of truly pelagic forms such as fish and marine vertebrates. Epizoans attached to brown algae may reach moderate abundances but do not contribute more than a few percent to the total skeletal carbonate content of modern sediments (Pestana 1985).

Pseudoplanktonic drifting causes species to be preserved in a wide range of benthic environments.

Examples of surprising facies distributions include the rare occurrence of sponges, crinoids and corals in organic-rich shales (e.g. Ruedemann 1934; Bulman 1964; Simms 1986, 1988*b*; Baird *et al.* 1989) where depositional conditions were oxygen-restricted. These groups are known to be particularly intolerant of such conditions at the present day (e.g. Webster 1975) and they are unlikely to have been true benthos in the ancient examples. This is not to say that all apparently benthic species in black shales were pseudoplanktonic, as has been tacitly assumed in many studies, for many groups of organisms, particularly molluscs, are able to live under conditions of very low oxygen (Sageman *et al.* in press).

Rafts of sunken *Sargassum* and their attached fauna have been recorded from modern benthic environments ranging from the intertidal zone down to abyssal depths (Schoener and Rowe 1970; Pestana 1985). Such a wide ranging facies distribution can also be expected for fossil pseudoplankton; indeed, a facies-crossing pattern is one of the most reliable, and widely used criteria for detecting ancient examples (e.g. Ager 1965; Tchoumatchenco 1972). Similarly, pseudoplanktonic species have a widespread geographic distribution when compared to their benthic relatives giving them a good potential for correlation (Schäfer 1972). For example, the pseudoplanktonic genera *Seiocrinus* and *Pentacrinites* are the only Lower Jurassic crinoids known from both the Boreal and Tethyan realms of the Lower Jurassic (Klikushin 1982).

Attachment Strategies

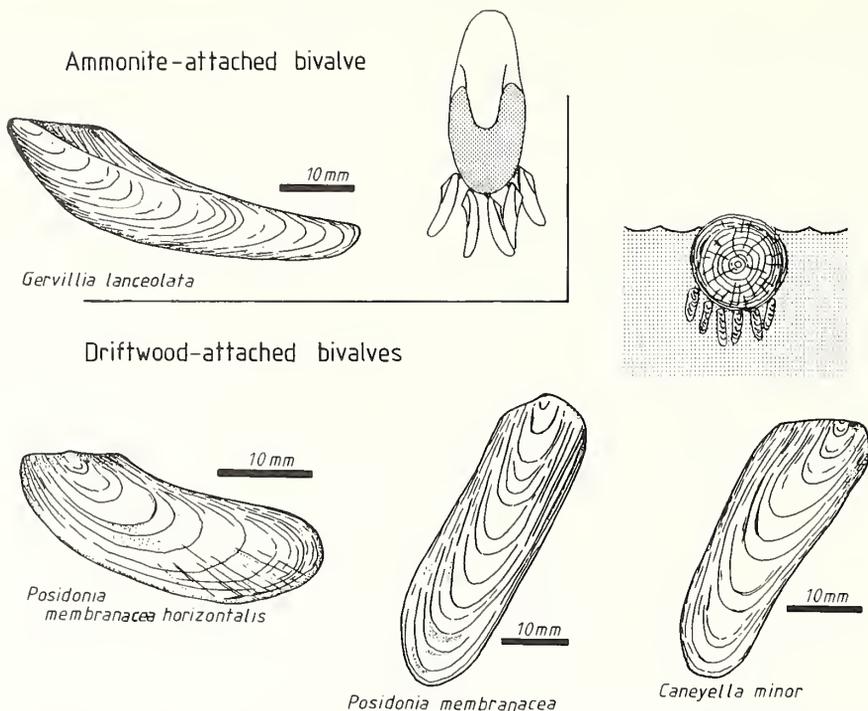
A precondition for all pseudoplanktonic species is the ability to attach to a floating substrate. Five attachment strategies can be recognized.

Cemented. Cementation provides one of the most secure means of attachment but it has the disadvantage that it requires a relatively large attachment area on a substrate where there might be intense competition for space. Oysters, bryozoans and serpulids are amongst the most frequently encountered cemented pseudoplankton in the fossil record, whilst acrothoracian barnacles are common cementers today (e.g. Landman *et al.* 1987); cnidarians and corals are less frequent cementers (Jokiel 1984).

Pendent. Pendent forms have a relatively small attachment area and dangle at some distance beneath their float. This strategy has the advantage of minimizing the area required for attachment on a floating substrate where crowding may be a serious problem. Crinoids (Simms 1986), certain lanceolate bivalves (text-fig. 5), lepadomorph barnacles (Moore 1867) and, more rarely, articulate brachiopods (text-fig. 2) all belong in this category.

The pseudoplanktonic adaptations of lanceolate bivalves include a short hinge line and weak dentition. Both factors tend to reduce the articulation strength, though this is not detrimental since the ligament does not have to operate against the confining pressure of the sediment such as is experienced by endobysate bivalves. The byssus emerges ventrally to a sharp anterodorsal angle of an equivalve shell. Consequently the attachment area is effectively reduced to a point. In benthic epibysate bivalves, such as *Mytilus*, the byssus emerges more centrally along the ventral margin and the contact area with the substrate is greater. The lanceolate bivalve morphology is also adapted to a reefal environment (Fürsich and Wendt 1977) where such forms may be able to hang beneath crevices or from branching corals. However, such reef dwellers are typically much thicker-shelled than their thin, fragile pseudoplanktonic relatives.

Few generalizations can be made about the morphology of pseudoplanktonic crinoids since very few are considered to have adopted this mode of life. Both the early Jurassic *Pentacrinidae* and the late Devonian *Melocrinites* have an endotomous pattern of arm branching (Simms 1986), though this is by no means unique and is also found in many benthic taxa. The stem of pentacrinitids differs from other articulates in showing an apparent increase in flexibility distally, as might be expected for a pseudoplanktonic crinoid (Seilacher *et al.* 1968), but this has not been documented for melocrinitids. The dense spacing of cirri on the proximal and distal parts of pentacrinitid stems may also be specifically adapted for a pseudoplanktonic mode of life, though



TEXT-FIG. 5. Lanceolate bivalve genera inferred to have been pseudoplanktonic. *Gervillia lanceolata* is from the Lower Toarcian and is commonly associated with ammonites. The species of *Posidonia* and *Caneyella* are from the lower Namurian of northern England and are inferred to have attached to driftwood which was fairly common at this time.

again this cannot be confirmed from observation of melocrinitids which have a cemented type of attachment at the base of the stem.

Addressed. Addressed forms attach themselves by organic tissue or threads and hold tight to the substrate. This has the advantage over the pendant strategy of reducing the chances of dislodgement but, as in cementing forms, the attachment area is relatively large. This mode of life is common in many benthic groups such as mytiliform bivalves, including many inoceramids, and the inarticulate brachiopod genera *Discinisca* and *Orbiculoidea*, of which some individuals may have been pseudoplanktonic (e.g. Tanabe 1983; Seilacher 1982a, b).

Boring. Tunnelling into the floating substrate is the most secure strategy against dislodgement but has the detrimental effect of reducing its floating properties. Boring bryozoans and acrothoracian barnacles have been reported from belemnites and *Nautilus* (Landman *et al.* 1987; Seilacher 1968). Seilacher (1968) argued that the consistent orientation of barnacle borings in the distal portion of a belemnite guard indicated that such infestation occurred during life. The majority of belemnite encrustation and boring is, however, random and probably occurred after death. Wood is commonly bored by isopods and, more importantly for the fossil record, teredinid bivalves. Boring bivalves appear to utilize wood either as a dwelling, from which to filter feed, or as the source of food itself (Kelly 1988b). The latter strategy severely reduces floating duration; consequently wood-eating bivalves are unlikely to be pseudoplanktonic for long.

Clingers. These are species which are able to move about their float, often in search of prey;

Friedrich (1969) referred to them as haptic forms. Only Recent examples are known with certainty. They include pycnogonids, flatworms and gastropods attached to *Sargassum* (Morris and Mogelberg 1973), gastropods and crabs attached to turtles (Frazier *et al.* 1984) and an isopod, *Idotea metallica*, which clings to blobs of crude oil (Herring 1969). The possibility that ancient, vagrant epifaunal forms, such as gastropods, may represent pseudoplankton does not appear to have been appreciated, although they are never likely to be common.

A number of supposed pseudoplanktonic forms from the fossil record cannot be assigned to any of the above five categories. These examples all occur in finely laminated shales of mid-Palaeozoic age and include the praecardioid bivalve genera *Manullicula*, *Butovicella*, *Cardiola*, *Slava* and *Dualina* (Watkins and Berry 1977; Watkins 1978) and lingulid brachiopods (Barron and Etensohn 1981). *Butovicella* possibly utilized an epibyssate, adpressed strategy (Kriz 1969) but the remaining bivalves are all endobyssate forms (Pojeta *et al.* 1976) which are unlikely to have been able to attach to floating objects. Lingulids are infaunal benthic forms which could not have led a pseudoplanktonic life.

BIOLOGICAL CONSTRAINTS ON A PSEUDOPLANKTONIC LIFESTYLE

The biology of pseudoplankton is severely constrained by a number of ecological features unique to this mode of life. As well as an ability to attach to the float, discussed above, the great rarity of floating substrates necessitates a rapid response when such a site is encountered. Species which produce large numbers of planktonic larvae will clearly have the greatest potential for exploiting floating objects. This can be achieved by large adults producing a large number of offspring at one time or by small adults producing fewer larvae but at more frequent intervals (Jablonski and Lutz 1983). Increasing size of individuals in the former case and continuing recruitment onto the original float in both cases results in a population of large biomass which will rapidly overload the floating attachment site, possibly before the epizoans can reach sexual maturity. Even before the float becomes overloaded it may run aground and cause the premature demise of its occupants. Thus two counteracting selective pressures can be seen to operate on pseudoplanktonic species. A solution to this problem includes the rapid attainment of maturity. This may be achieved by maturation at a relatively small size or by accelerating the growth rate to reach a large size in a short time. The former can be attained relatively easily through heterochrony, in particular paedomorphosis (McNamara 1986), although such forms will be restricted by their small size of producing relatively few larvae at a time. Accelerating growth rates is, perhaps, less straightforward since it requires considerable extra expenditure of both energy and materials. Amongst the pseudoplankton only crinoids appear to have adopted this latter strategy of rapid growth to large size but this required specialized adaptations to increase feeding efficiency. In both the Devonian camerate *Melocrinites* and the early Jurassic articulates *Pentacrinites* and *Seirocrinus*, the arms branch endotomously beyond the second division, an unusual arrangement amongst crinoids generally. This is interpreted as the most efficient filtering arrangement possible for the most economical outlay of materials, comparable with the ideal arrangement of roads on a banana plantation (Cowen 1981). The early Jurassic pentacrinitids further enhanced the efficiency of their filtration fan by the suppression of syzygial articulations in the arms, resulting in the attainment of almost complete pinnulation, a feature peculiar to this group (Simms 1986).

A further strategy which increases the likelihood of colonizing rare attachment sites includes the delay of larval metamorphosis, thereby prolonging the time spent in the water column and thus the time available for encountering attachment sites. Lockley and Antia (1980) documented a probable example of delayed larval metamorphosis in *Schizocrania*, an inarticulate brachiopod attached to orthoconic nautiloids in the Ordovician. There is strong evidence to suggest that the presence of adults may also encourage larval settlement, possibly by a chemoautotrophic response (Crisp 1979; Grosberg and Quinn 1986). The ability of adults to attract larvae probably accounts for the often observed pattern of 'all-or-nothing' pseudoplanktonic colonization. Thus, once a few epizoans are established, their presence can rapidly induce large numbers of other individuals to colonize. For

example, the heavily encrusted log in text-figure 2 occurred with several other large logs which were totally devoid of epizoans. Similarly, Baird *et al.* (1989) noted all-or-nothing encrustation of orthocones.

The development of a relatively lightweight body plan and the reduction of any skeletal components is a further strategy which is likely to prolong the floating duration of attachment sites. Thus, the pseudoplanktonic bivalves of the Lower Jurassic are considerably thinner-shelled than their benthic relatives (Seilacher 1984; text-fig. 5).

Many of the biological constraints on marine wood-borers are very similar to those acting on pseudoplankton as both exploit generally rare resources. It is thus interesting that wood-boring bivalves exhibit many of the life strategies found in pseudoplanktonic species; indeed many such bivalves are also pseudoplanktonic due to the nature of their substrate! Turner (1973) noted that such bivalves tended to be 'r'-strategists.

THE CLASSIFICATION OF PSEUDOPLANKTON

It is clear from an examination of the Recent and ancient record that pseudoplanktonic species can be readily classified on the basis of the relative frequency with which they adopt this mode of life and their dependence upon it.

Obligate Pseudoplankton

This group encompasses forms which have an exclusively pseudoplanktonic adult stage. The biological constraints, discussed above, require highly specialized adaptations which may inhibit them from returning to a benthic existence. Ancient examples include two independent crinoid groups, the Melocrinidae and Pentacrinidae (Wells 1941; Simms 1986) and probably many of the thin-shelled, lanceolate bivalve genera of the Palaeozoic and Mesozoic (text-fig. 5). Certain genera of lepadomorph barnacles constitute the most important group of obligate pseudoplankton at the present day with cosmopolitan genera such as *Conchoderma* and *Coronula* occurring attached to a wide range of substrates including whales, turtles and sea snakes (Friedrich 1969). Other genera, such as *Lepas* itself, occur on driftwood (Schäfer 1972). In the past many apparently obligate pseudoplanktonic species appear to have been substrate-specific; for example in the Posidonienschiefer *Gervillia* is restricted to ammonites (Seilacher 1982a).

It is noteworthy that many obligate pseudoplankton utilize the pendent strategy which suggests that a limited attachment area is a strong selective advantage. A rather more diverse range of attachment strategies is illustrated by the obligate pseudoplankton associated with *Sargassum* (Morris and Mogelberg 1973).

Facultative Pseudoplankton

The morphology and physiology of many benthic epifaunal species are pre-adapted to enable a limited number of these forms to settle successfully on floating objects. This chance colonization, by normally benthic species, considerably confuses their ecology, particularly in the fossil record, for it misleadingly suggests tolerance of a wide range of facies. For example all the pseudoplanktonic species recorded in text-figure 2 were probably also benthic, for other specimens of these species occur in greater abundance in other Kimmeridge Clay horizons where they are not associated with driftwood. *Pseudomytiloides dubius* is frequently associated with driftwood in the Posidonienschiefer (Seilacher 1982a), but in many horizons this bivalve is too abundant for all specimens to have been derived from the relatively rare examples of driftwood (Kauffman 1981). The discovery of a colony of pseudoplanktonic species, associated with a float such as driftwood, does not indicate that all individuals of that species led such an existence.

Accidental Pseudoplankton

This category includes very rare occurrences where benthic species are unintentionally cast adrift. Examples include forams attached to blades of seagrass which become detached (Brasier 1975), the

gastropods found on turtles which are thought to have attached whilst the turtles were at rest on the sea floor (Frazier *et al.* 1984) and possibly an early Jurassic crinoid (Simms 1988*b*). Whilst such chance occurrences are highly unlikely to be preserved in the fossil record, they are of great importance in palaeobiogeography as they vastly increase the dispersal ability of a huge range of benthic species across wide oceans (Ekman 1953; Hallam 1973; Jokieli 1984).

The classification of pseudoplankton is complicated by those species which are able to survive once the floating object has sunk to the substrate. For example ammonites have been observed encrusted by oysters, nucleated in the umbilical region, which have grown over the outer whorls and across the substrate (Clausen and Wignall, 1990, plate 6*d*). In such examples initial colonization probably occurred whilst the ammonite was alive and floating in the water column, but they subsequently became 'facultative benthos' after the ammonite had died and settled to the sea floor.

The ability to distinguish between obligate and facultative pseudoplankton is of great importance both in evolutionary and ecological studies. The biological constraints, discussed above, only apply to obligate pseudoplankton. For the facultative species the evolutionary pressures are basically those experienced by the benthic population which contains the majority of individuals of that species. In palaeoecological studies the discovery of a colony of facultative pseudoplankton may be incorrectly extrapolated to assume that all populations of the species pursued this mode of life. The distinguishing features between obligate and facultative pseudoplankton are given in table 1.

TABLE 1. Criteria used to distinguish obligate from facultative pseudoplankton in the fossil record.

	Obligate	Facultative
Abundance and facies distribution	Always rare, found in a wide range of facies.	Occur in a wide range of facies but they reach a peak abundance in one facies type.
Occurrence	Nearly always associated with a floating object. Commonly found with a particular type of float (host specific)	Very rarely associated with floating objects. Found with a range of floating objects.
Morphology	Normally thin-shelled, commonly pendent.	Broad range of morphologies, e.g. cemented, adpressed.
Lifestyle	In comparison to their nearest benthic relatives, they may illustrate delayed larval metamorphosis followed by rapid growth rates.	No unusual adaptations.

EVOLUTION IN OBLIGATE PSEUDOPLANKTON

The profound ecological constraints which influence the biology and morphology of obligate pseudoplankton exert a considerable influence on the evolution of pseudoplanktonic taxa. Once the two basic problems of attachment and reproductive success have been overcome by such taxa, further evolution is likely to be restricted largely to 'fine tuning' of the original strategy. However, opportunities to investigate this hypothesis are severely limited as relatively few supraspecific taxa have a fossil record that is sufficiently good to document evolutionary lineages. This problem is compounded in obligate pseudoplankton due to the rarity of such groups, both in numbers of individuals and taxonomic diversity.

The Mesozoic crinoid family Pentacrinidae is the only group of obligate pseudoplankton for which an evolutionary lineage has been recognized and documented. The two closely related genera, *Pentacrinites* and *Seirocrinus*, were already quite distinct when first recorded in the late Triassic. Thereafter the two lineages underwent very little morphological change through time and individual species showed unusual longevity by comparison with contemporaneous benthic crinoids. They also showed apparent immunity to the benthic hypoxic event which caused a major faunal turnover in the early Toarcian (Hallam 1986; Simms 1986, 1988a), a feature perhaps to be anticipated in pseudoplanktonic taxa. *Seirocrinus subangularis*, a Carixian to Toarcian (Lower Jurassic) species, differs from the Norian (Upper Triassic) *S. klikushini* only in having slightly fewer brachials in each brachitaxis and in the development of a slightly more complex pattern of endotomous arm branching than is seen in other pentacrinids (Simms 1988a, 1990). The two earlier species of *Pentacrinites*, *P. doreckae* (Hettangian to lower Sinemurian) and *P. fossilis* (upper Sinemurian) show an almost parallel change in the number of brachials per brachitaxis (Simms 1988a). These changes relate to an increased food-gathering capability in the later species.

In the four described species of *Pentacrinites* there are several marked changes between the earlier *Pentacrinites doreckae-fossilis* part of the lineage and the succeeding *P. dichotomus-dargniesi* lineage. In the latter group the stem is very much shorter with densely-spaced cirri, while the arms have a more poorly developed pattern of endotomous branching and contain syzygial articulations at one or two points, interrupting the pinnule spacing. Furthermore, although *S. subangularis*, *P. doreckae* and *P. fossilis* are very frequently found attached to driftwood (data on this are not available for *S. klikushini*), there are no records of the *P. dichotomus-dargniesi* group having been found in association with driftwood or any other float, yet *P. dichotomus*, at least, otherwise conforms to all the criteria used to identify pseudoplankton. The obvious assumption here is that a fundamental change in life strategy occurred between *P. fossilis* and *P. dichotomus*. The morphological changes suggest that the latter group were no longer subject to the severe selection pressures which operated on the earlier, definitely pseudoplanktonic, taxa. The implication of this is that they either exploited an unusually stable floating substrate, not preserved in the fossil record, or became either truly planktonic, which seems unlikely, or benthic. The latter strategy certainly seems to apply to *P. dargniesi*, but the mode of life of *P. dichotomus* remains unclear.

Evolutionary case histories are less well documented for other pseudoplanktonic groups. *Gervillia lanceolata*, a probable obligate pseudoplanktonic bivalve from the Lower Jurassic, has a long fossil record extending from the Hettangian to the Lower Toarcian (Hallam 1976), although this is not exceptional for a bivalve. Unlike the pentacrinids, *G. lanceolata* did not survive the early Toarcian hypoxic event (Hallam 1986). The species duration for the mid-Carboniferous homeomorphs (text-fig. 5) is considerably shorter (P. B. Wignall, unpublished data). In all cases the pseudoplanktonic bivalves appear to be species derived from benthic ancestors rather than part of a pseudoplanktonic lineage, implying that this mode of life was, in many cases, an evolutionary 'dead-end'.

BLACK SHALE PSEUDOPLANKTON

The previous review of pseudoplankton in the fossil record has revealed that the majority of examples are reported from finely laminated black shale facies. This may be due to the favourable preservational conditions that occur in black shale depositional environments. The generally low sedimentation rates allow relatively large numbers of pseudoplankton to accumulate whilst the low energy conditions and lack of scavengers in such oxygen-restricted environments are further factors which increase the preservational potential of commonly fragile pseudoplanktonic species.

In the mid and late Palaeozoic the most commonly reported pseudoplankton in black shales are thin-shelled brachiopods belonging to the chonetids, plectambonitids, strophomenids and *Leiorhynchus* (Havlíček 1967; Bergstrom 1968; Thayer 1974), and praecardioid bivalves (Krebs 1979; Watkins 1978), which are inferred to have attached to algae. These groups are widespread spatially within a deep-water, fine grained facies, but they do not occur in other facies. This argues against a pseudoplanktonic lifestyle. Their distribution within the sediment is similarly suggestive

of a benthic existence for they are common on certain bedding planes and absent in the intervening strata; a distribution typical of frequent, opportunistic colonization (Wignall and Myers 1988). Floating algal communities in Recent oceans are characterized by high diversity assemblages dominated by bryozoa. However, the Palaeozoic assemblages are generally mono- or paucispecific. The combined evidence of low diversity, facies restriction and large numbers restricted to individual horizons strongly suggests that the brachiopods and praecardioids were benthic forms in black shales (Thompson and Newton 1987; Sheehan 1977). This has important implications for the depositional conditions of this facies as it indicates that benthic oxygen was available for at least short periods of time.

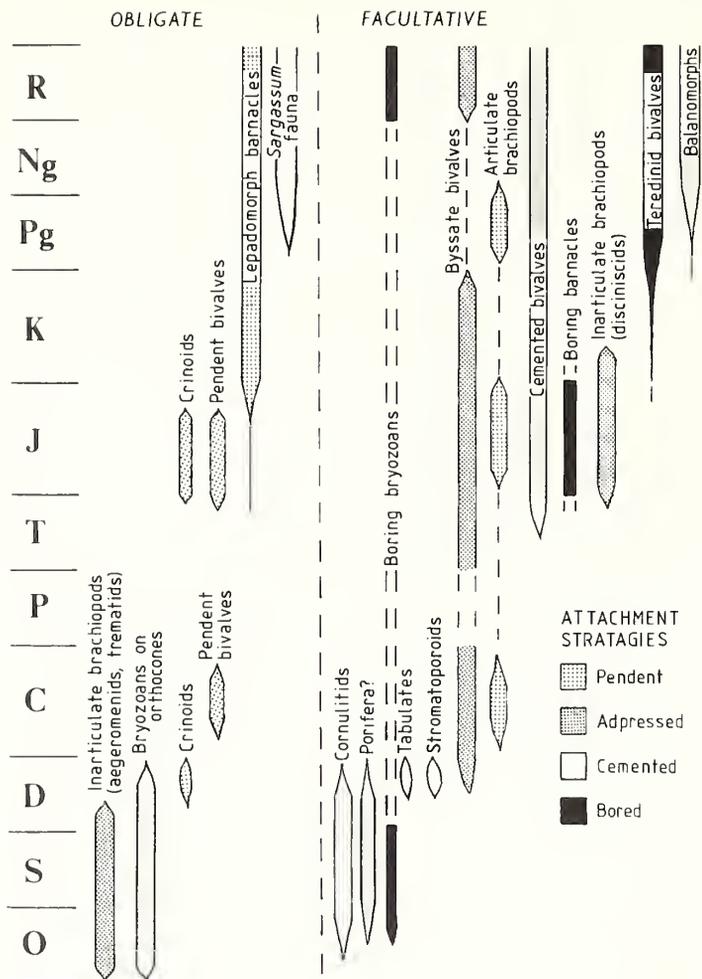
An even larger volume of literature on pseudoplankton relates to a diverse group of pterioid bivalves which occur in black shales from the Devonian to the Cretaceous (Hudson and Cotton 1943; Ichikawa 1958; Hayami 1969). The group includes the posidoniids, halobiids and some of the monotids, buchiids and inoceramids. The functional morphology of these bivalves is far from clearly understood and opinions have changed markedly over the past hundred years. Initially they were thought to be benthic, reclining forms but, with the interpretation of black shale as hostile, anoxic depositional environments, inimical to benthic life, they were reinterpreted as pseudoplankton (e.g. Paul 1939; Hudson and Cotton 1943); a view still widely held today (Hayami 1969; Krebs 1979; Rieber 1982; Campbell 1985; Schumann 1988). Jefferies and Minton (1965) proposed the interesting alternative of a free-swimming lifestyle for some posidoniids. Other recent studies of Carboniferous and Lower Jurassic black shales have concluded that pterioids were probably truly benthic (Antia and Wood 1977; Kauffman 1981; Wignall 1987) with a few, specialized, pendent exceptions (text-fig. 5). The evidence for a pseudoplanktonic existence is slightly more compelling for these pterioids than for the Palaeozoic brachiopods and praecardioids. Many pterioids occur in a greater range of facies than just black shales, although they are nearly always in fine-grained facies. Also, examples of driftwood and other floating objects colonized by such bivalves are relatively common (e.g. Paul 1939; Hauff and Hauff 1981; Tanabe 1983), but these may only be facultative occurrences. However, it is their distribution within the sediment which provides the strongest evidence of a benthic lifestyle. Like the brachiopods discussed above, the pterioids tend to be abundant in thin horizons and absent in the intervening sediment, suggesting brief benthic opportunistic colonization.

Thus, it appears that many of the reported occurrences of pseudoplankton may be more realistically interpreted as true benthos. This considerably increases the diversity of benthic life recorded from black shales whilst substantially reducing the diversity of the pseudoplanktonic record. Many of these occurrences owe their interpretation to the tacit assumption that black shale depositional environments are permanently anoxic, and thus fail to appreciate the highly dynamic nature of many such environments (Sageman *et al.* in press) where even transient improvements in benthic oxygen levels are rapidly exploited by benthic opportunists.

THE PHANEROZOIC HISTORY OF PSEUDOPLANKTON

Having re-interpreted a large number of 'pseudoplanktonic' occurrences as benthic, the remaining record is relatively sparse and weighted towards cementing forms which are the least likely to become detached from their float. The data have been divided into obligate and facultative pseudoplankton (table 1 and text-fig. 6), thus distinguishing between relatively rare, specialized forms specifically adapted to this lifestyle and the more common benthic forms which have occasionally exploited a chance encounter with a floating object.

The potential floating attachment sites in the Cambrian were pumice and possibly algae, but no organisms have been inferred to have adopted a pseudoplanktonic lifestyle during this interval. The appearance of large cephalopods, particularly the orthoconic nautiloids, in the Ordovician was exploited by bryozoans and inarticulate brachiopods (text-fig. 6). Nearly all of these appear to have been host-specific suggesting that they were commensal forms and obligate pseudoplankton (Havlíček 1972; Lockley and Antia 1980; Baird *et al.* 1989). Drifting graptolites also appeared



TEXT-FIG. 6. Changes in the composition of pseudoplankton through the Phanerozoic with obligate and facultative occurrences distinguished. Variation in attachment strategies is also illustrated. The majority of obligate forms appears to have been pendent.

at this time but are considered to be true plankton (Rickards 1975) and are thus beyond the scope of our study. Pseudoplankton diversity reached new heights in the Devonian with the first appearance of driftwood which was rapidly exploited by both crinoids (Wells 1941; McIntosh 1978) and bivalves (Nye *et al.* 1975). Curiously, the Carboniferous marked a decline in the fortunes of pseudoplankton despite the increase in driftwood in the world's oceans. However, a number of lanceolate bivalves may have attached to driftwood (text-fig. 5). The main cause of the low diversity is the rarity of cephalopod encrustation. A review by Boston *et al.* (1988) revealed that less than 2% of shells were colonized by epizoans in the Carboniferous and some of these examples may have occurred on the sea floor. This low value was attributed to the success of the cephalopods at defending themselves against unwanted infestation either by physical or chemical means. But this apparent 'success', on the part of the cephalopods, may also be due to the rarity of large forms at this time as the dominant group, the goniatites, were typically small.

Diversity of pseudoplankton appears to have declined to zero in the Permian. The thick sequence of organic-rich shales in the Upper Permian Phosphoria Formation of the United States would have provided good preservational conditions but no pseudoplanktonic forms have been recorded, despite detailed study (e.g. Yochelson 1963).

The Triassic was marked by the appearance of several groups able to exploit a pseudoplanktonic

lifestyle. These include lepadomorph barnacles, cementing bivalves, the reappearance of the lanceolate bivalve morphotype in the bakevelliid lineage, and pseudoplanktonic crinoids (text-fig. 6). Pseudoplanktonic diversity rose to an all time high in the Lower Jurassic with crinoids, inoceramids and lepadomorphs occurring on driftwood (Moore 1867; Tanabe 1983; Simms 1986). Ammonites were infested by an equally diverse range of epizoans including bryozoans, inarticulate brachiopods, oysters and a range of byssate bivalves (Seilacher 1982a). A number of Jurassic articulate brachiopod genera also may have attached to floating algae (Ager 1962, 1965; Tchoumatchenco 1972), although, as in many supposed ancient algal colonies, associated fauna such as bryozoans curiously are absent.

Towards the end of the Lower Jurassic the first wood-boring, teredinid bivalves appeared (Kelly 1988b). However these Jurassic forms appear to have been exclusively benthic colonizers because, as Kelly (1988a) noted for the Upper Jurassic, bored wood is only found in shallow marine arenaceous sediments. Driftwood from contemporary deeper water, muddier facies was not bored. Such a strong facies control upon boring could only occur if the bivalves colonized after the wood had reached the sea floor. During the Cretaceous the frequency of bored wood appears to have increased considerably in all facies, suggesting that the bivalves were able to settle on floating driftwood. This may have had serious consequences for other pseudoplanktonic species as the activity of boring bivalves greatly shortens the floating duration of driftwood.

Faunal changes amongst driftwood faunas in the Upper Jurassic may be at least partially driven by the rise of wood-borers. Obligate, pendent, pseudoplanktonic crinoids and lanceolate bivalves both occur for the last time in the late Jurassic (text-fig. 6). The pseudoplanktonic driftwood colony recorded from the Upper Jurassic in text-figure 2 contains an unusual fauna dominated by encrusting forms (serpulids and oysters) in contrast to the adpressed and pendent strategies of earlier Jurassic driftwood colonies (Hauff and Hauff 1981) and coeval colonies of Antarctica (Doyle and Whitham, in press). By the Cretaceous driftwood is rarely associated with any epizoans apart from boring bivalves (E. G. Kauffman, pers. comm.).

The Cretaceous, like the Carboniferous, marked a low point in pseudoplanktonic diversity primarily due to the virtual absence of cephalopod epizoans, except for some examples from the Maastrichtian (Dunbar 1928; Riccardi 1980). This may have been due to a widespread ability amongst all cephalopod groups to defend themselves against colonization (cf. Boston *et al.* 1988). It also testifies to the likelihood that such infestation occurred during life, for nekroplanktonic infestation would produce a more uniform record through the Phanerozoic. However, preservational factors may also have a major influence on the record. Cretaceous and Carboniferous ammonoids are commonly collected as composite moulds produced by aragonite dissolution. Hence any encrusters may remain embedded in the matrix following collection of the ammonoid.

A few examples of Lower Tertiary pseudoplankton are known (Davis and Elliot 1958; Lindqvist 1986). Associated with many logs of driftwood in the Eocene London Clay of south east England are crinoids (*Isselocrinus subbasaltiformis*) and pendent bivalves (*Pteria papyracea*) – an assemblage strongly reminiscent of Lower Jurassic pseudoplanktonic driftwood colonies, although the Eocene examples more probably colonized the wood after it sank to the sea floor (Taylor 1978). The Eocene also marks the first appearance of a genuine *Sargassum*-like fish fauna (Jerzemska and Kotlarczyk 1976), but without any associated invertebrate fauna.

The *Sargassum* fauna constitutes the most diverse pseudoplanktonic community in the modern oceans with over 70 species recorded (Fine 1970; Morris and Mogelberg 1973). The majority are small forms, a strategy to reduce weight and the possibility of overloading the brown algae to which they were attached. The bryozoan *Membranipora* is the dominant form and, along with the co-occurring annelid, *Spirorbis*, and the gastropod *Litiopa*, has a fairly high preservation potential. Thus the absence of a pre-Eocene occurrence of these faunas strongly suggests that *Sargassum* is a relatively recent innovation of the Cenozoic. Diverse pseudoplanktonic communities are also known from recent studies of *Nautilus* (Landman *et al.* 1987) and turtles (Frazier *et al.* 1984). Indeed, pseudoplankton is probably more abundant today than at any time in the past due to the large amounts of man-made flotsam found in the oceans, such as hollow plastic, glass and metal

containers. In particular, the use of expanded polymers has created flotsam of very extended floating duration thus increasing the time available for colonization. Boats and ships theoretically provide even more ideal attachment sites since, not only do they have very extended floating durations, they are able deliberately to avoid being cast ashore, thus eliminating one of the major hazards of the pseudoplanktonic lifestyle. Consequently, a wide range of organisms attach to ships (Carlton 1985), much to the chagrin of their owners. Lepadomorph barnacles appear, from personal observations, to be the main group exploiting this new diversity of attachment sites.

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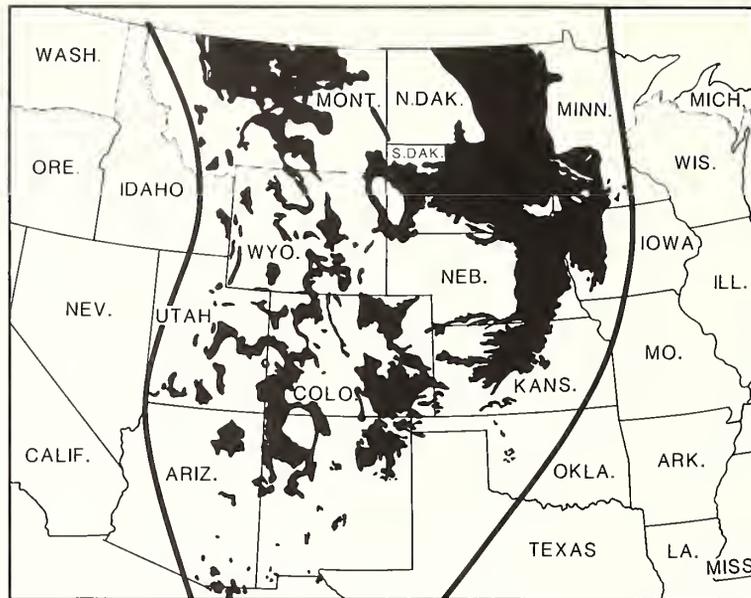
CENOMANIAN MICROMORPHIC AMMONITES FROM THE WESTERN INTERIOR OF THE USA

by W. J. KENNEDY and W. A. COBBAN

ABSTRACT – Calcareous concretions from middle and upper Cenomanian (Cretaceous) shale sequences in Montana and Wyoming yield, on rare occasions, abundant minute ammonites. Some are juveniles of large species, and give valuable evidence on early ontogeny and evolutionary affinities of these taxa. They provide evidence for the probable evolutionary origins of a series of hitherto undescribed progenic dwarf genera, adult at 4.5–16.5 mm diameter that are a remarkable feature of these assemblages. Five new genera, *Kastanoceras*, *Alzadites*, *Microsulcatoceras*, *Cryptometoicoceras* and *Buccinammonites* are introduced. 33 species are described from Montana, Wyoming, Utah, New Mexico and Texas; 16 are new, the others were previously unknown in the region or show new details of early ontogeny. New taxa are: *Moremanoceras montanaense* sp. nov.; *Cunningtoniceras* sp. juv.; *Tarrantoceras exile* sp. nov.; *Kastanoceras spiniger* gen. et sp. nov.; *Alzadites alzadensis* gen. et sp. nov.; *A. westonensis* gen. et sp. nov.; *A. incomptus* gen. et sp. nov.; *Alzadites?* sp.; *Alzadites* sp. A; *Microsulcatoceras puzosiiforme* gen. et sp. nov.; *M. crassum* gen. et sp. nov.; *M. texanum* gen. et sp. nov.; *Microsulcatoceras* sp.?.; *Cryptometoicoceras mite* gen. et sp. nov.; *Nannometoicoceras nanos* sp. nov.; *Nannometoicoceras? glaber* sp. nov.; *Buccinammonites minimus* gen. et sp. nov.; *Idiohamites pulchellus* sp. nov.; *I. bispinosus* sp. nov.; *Carthaginites aquilonius* sp. nov.; and *Scaphites (Scaphites)* sp.

OVER wide areas of the Western Interior of the United States (text-fig. 1), marine rocks of middle to late Cenomanian age are partly or wholly in a non-calcareous shale facies. Most of the fauna known from this facies comes from calcareous concretions of early diagenetic origin, although in some units, crushed moulds can be obtained by splitting shales. At many levels concretions are only sparingly fossiliferous, and even then yield only large fossils. In the present communication we describe some remarkable faunas collected over the past 60 years from concretions in the Middle to Upper Cenomanian part of the Belle Fourche Shale of the Black Hills in Wyoming and Montana. In this area we estimate that less than 1% of concretions are fossiliferous, and only six out of thousands examined preserve minute ammonites in abundance (text-fig. 2) although others preserve larger fossils, including both macro- and microconch ammonites. This preservation is all the more remarkable, since adjacent concretions at the same stratigraphic horizon at the same locality lack such assemblages. Occurrence is not simply a matter of concretions preserving a particular level of fossil concentration, the occurrences are areally limited. The palaeogeographical setting of the Black Hills area during late Cenomanian time places it far from shore, and we find it difficult to interpret these fossil occurrences as current accumulations, especially as some ammonites preserve delicate features of ornament, and occur scattered throughout the concretions rather than concentrated on a single plane. It is also difficult to accept the occurrences as faecal concentrations for the fossils are embedded in sediment matrix, and are in this respect unlike the great mass occurrences of ammonites in the Mowry Shale (Reeside and Cobban 1954, 1960), where the fossils are bound in a matrix of fish scales and debris.

The occurrences provide a unique opportunity to study elements of the late Cretaceous ammonite fauna of the Western Interior that were previously unrecognized, especially a series of micromorphs, ammonites that are adults at 4.5 to 16.5 mm diameter. Five new micromorph genera and 12 new species are described, including several additional micromorphs from areas in New Mexico, Utah and northeast Texas. Most have adult phragmocone whorls that share common features with the innermost ornamented phragmocone whorls of co-occurring 'normal' size dimorphic ammonites.



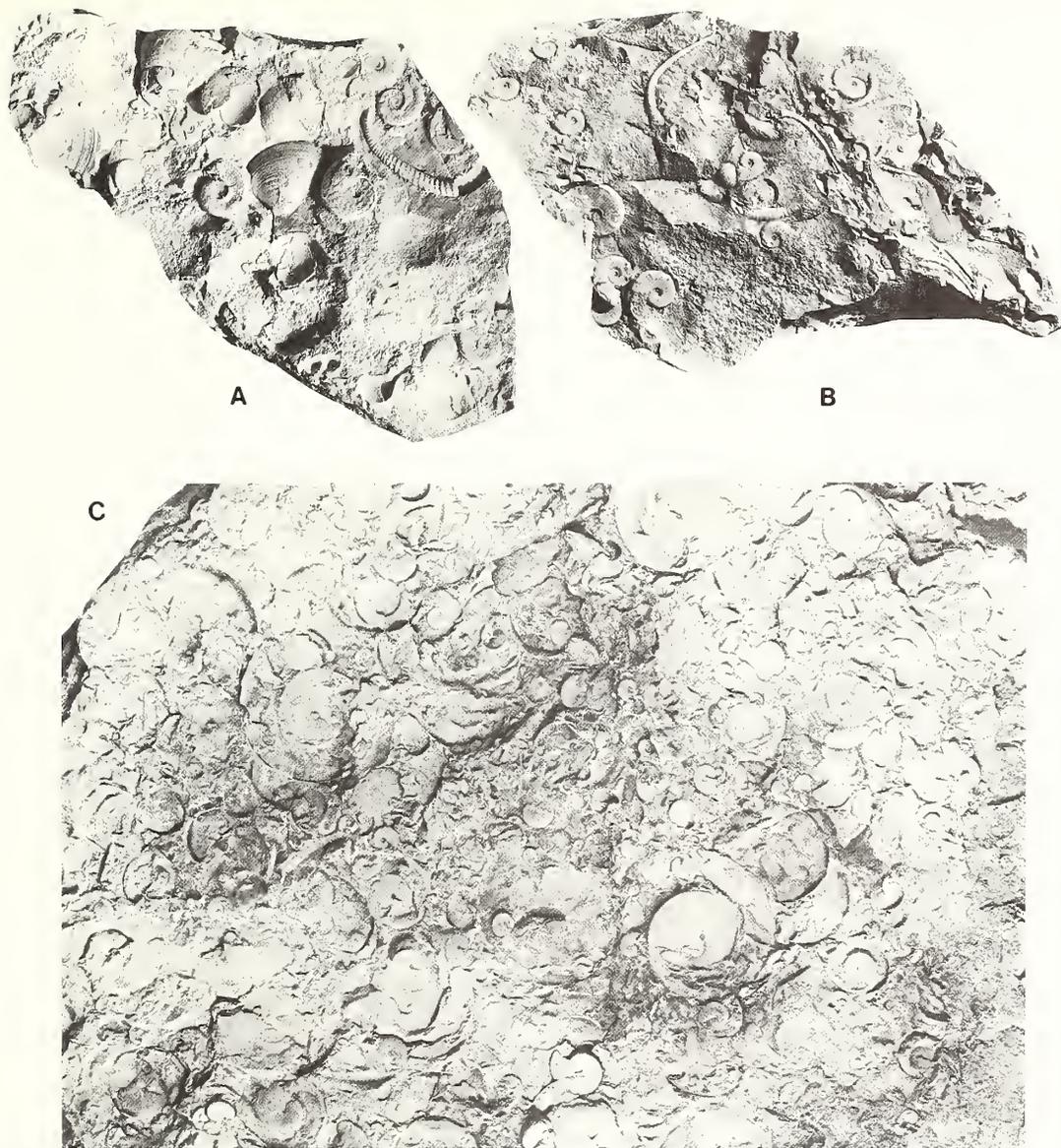
TEXT-FIG. 1. Map of outcrop areas of Cretaceous sedimentary rocks in the Western Interior of the United States. The heavy black bounding lines show the maximum known extent of the mid-Cretaceous seaway. Modified from Cobban and Reeside, 1952, fig. 1.

We interpret the new genera as progenic dwarfs that evolved through precocious sexual maturation, an evolutionary process previously invoked to explain the origin of certain other Upper Cretaceous micromorphs, notably *Protacanthoceras* Spath, 1923 from *Acanthoceras* Neumayr, 1875 (Wright and Kennedy 1980, 1987; Kennedy and Wright 1985); *Nannometoicoceras* Kennedy, 1988, from *Metoicoceras* Hyatt, 1903 (Kennedy 1988, p. 63); *Plesi-acanthoceratoides* Kennedy and Cobban, 1990, from the Western Interior acanthoceratine lineage.

These micromorphs are not, it must be stressed, juveniles of 'normal' sized taxa. They show all the features of maturity common to ammonites, including septal crowding, modification of ornament on the body chamber, and development of distinctive apertural processes. Several of the taxa are monotypic, or represented by few specimens. We justify naming them because they are so distinctive and utterly different in most cases from all previously known taxa. We also hope that their description will stimulate other workers to look carefully for such micromorphs amongst apparent juveniles in their own collections, since we consider it unlikely that the Western Interior occurrences are unique to that region.

What the life habits of these micromorphs may have been is a matter of speculation. Their concentrated occurrence suggests to us that some at least may have lived close to the bottom where they were preserved, because we cannot easily accept or see evidence for any physical or biological process that led to their concentration.

Micromorphs apart, the concretion faunas studied include abundant juvenile individuals that show for the first time the early ontogenetic development of several genera and species, clarifying their affinities and also pointing to the possible ancestors of the progenic dwarfs. Also present are a series of taxa that are either new, or not previously recorded from the area, including first records of *Sumitomoceras* in the region, and the first *Scaphites* (*Scaphites*) from the Cenomanian of the Western Interior. In all, 33 species are documented.



TEXT-FIG. 2. Mass occurrence of small ammonites in concretions. A, B, USNM 423785 and 423784 from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone, with *Borissiakoceras* and heteromorphs. C, USNM 423665, from USGS Mesozoic locality 528, Frontier Formation, Middle Cenomanian, 1.5 km (1 mile) northeast of Wilcox, Albany County, Wyoming, with *Johnsonites sulcatus* Cobban, 1961. Collected by Alpheus Hyatt and I. C. Russel in 1888.

BIOSTRATIGRAPHY

The standard ammonite zonation for the Middle and Upper Cenomanian of the Western Interior is shown in text-fig. 3, and is modified after the work of Cobban (1984, 1987a). These are assemblage zones, the bases of the zones marked by the first appearance of a variety of ammonites, including the index species, which is usually, but not invariably limited to its zone. Because of the limited

CRETACEOUS STAGE		AMMONOID ZONE	USGS MESOZOIC LOCALITY
Cenomanian (part)	upper	<i>Nigericeras scotti</i>	
		<i>Neocardioceras juddii</i>	
		<i>Vascoceras cauveni</i>	
		<i>Sciponoceras gracile</i>	← 23042, D12052
		<i>Metoicoceras mosbyense</i>	← D8314 ← 12650, 12740
		<i>Dunveganoceras pondi</i>	← D4462, D4466, D5947
	middle	<i>Plesiacanthoceras wyomingense</i>	← 22871
		<i>Acanthoceras amphibolum</i>	
		<i>Acanthoceras bellense</i>	
		<i>Acanthoceras muldoonense</i>	
		<i>Acanthoceras granerosense</i>	
<i>Conlinoceras tarrantense</i>			

TEXT-FIG. 3. Middle and Upper Cenomanian ammonite zones of the US Western Interior, with the levels of some of the more important collections indicated.

vertical and horizontal distributions of ammonites within sedimentary sequences which result from both sedimentary and biological controls, these zones are of different scales and may be recognized over quite limited areas (as in the case of the *Conlinoceras tarrantense* to *Acanthoceras bellense* zones), while others can be recognized throughout the Western Interior (e.g. the *Acanthoceras amphibolum* zone). The oldest fauna described here comes from the *Plesiacanthoceras wyomingense* zone, which is placed at the top of the Middle Cenomanian. The *Dunveganoceras pondi* zone has *Calycoceras (Proeucalyoceras) canitaurinum* Haas, 1949 as an alternative index species in the southern part of the Interior, where *D. pondi* is absent. Their contemporaneity is established by the co-occurrence of the two index species at their common type locality near Greybull, Wyoming as well as common occurrence of other species. The *Metoicoceras mosbyense* zone is represented by a great thickness of sediment in the northern Western Interior, and may represent a greater time interval than the other Upper Cenomanian zones, although not susceptible to finer division at present. *Sciponoceras gracile* is retained as a zonal index because of long and widespread usage and because it is by far the commonest ammonite at that level although it ranges up to the *Neocardioceras juddii* zone. *Metoicoceras geslinianum* (d'Orbigny, 1850), *M. whitei* Hyatt, 1903 (a synonym) and *Euomphaloceras [Kanabicerias] septemseriatum* (Cragin, 1893) have also been used as indices for this zone in recent years.

Suggestions that the *S. gracile* zone can be divided into a lower subzone of *Vascoceras diartianum* (d'Orbigny, 1850) and an upper subzone of *E. septemseriatum* (Cobban 1984, p. 81) are here abandoned; *V. diartianum* occurs below the base of the *gracile* zone in association with *Euomphaloceras euomphalum* (Sharpe, 1855), *Eucalyoceras pentagonum* (Jukes-Browne, 1896) and other ammonites in southwestern New Mexico and the Black Hills area at the top of the *M. mosbyense* zone.

Vascoceras cauveni Chudeau, 1909, was proposed as a provisional index for a distinctive and as yet undescribed fauna between the *S. gracile* and *N. juddii* zones known only from southwest New Mexico. Subsequent work shows *V. cauveni* to range down into the correlatives of the *gracile* zone in Israel (Lewy, Kennedy and Chancellor 1984), and up into the *Neocardioceras juddii* zone at Chispa Summit in Trans-Pecos Texas, and a replacement index for the zone is needed from among the, at present, undescribed Euomphaloceratinae present in the assemblage.

The *Neocardioceras juddii* zone can be recognized in Trans-Pecos Texas, New Mexico, Colorado, Arizona, Utah, Wyoming and Montana. Apart from the index species (which is the last of a lineage of *Neocardioceras* that extends down to the *D. pondi* zone), *Pseudaspidoceras pseudonodosoides* (Choffat, 1898) is locally common in Trans-Pecos Texas and New Mexico and there is also a diverse, but as yet undescribed, vascoceratid and pseudotissotid fauna in these two states. Suggestions that *Gauthiericeras* aff. *bravaisi* (d'Orbigny) of Moreman (1927, p. 96, pl. 4, fig. 2) was an *N. juddii* (Wright and Kennedy 1981, p. 50) and indicated the presence of the *juddii* zone in northeast Texas must be discounted; subsequent work shows Moreman's form to be lower Turonian *Watinoceras* (Kennedy 1988, p. 50).

The highest Cenomanian zone recognized here has *Nigericeras scotti* Cobban, 1972, as index species, the index species itself being limited to southeast Colorado and northeastern and southwestern New Mexico.

LOCALITY DETAILS

The more important localities of ammonites described below are shown on text-fig. 4 and their stratigraphic positions are shown in text-fig. 3. Where localities have yielded only limited numbers of specimens, details are given at the appropriate point in the text. Nine localities yielded large assemblages, and in the interests of brevity, full details and faunal lists are given here.

USGS Mesozoic locality 12650. Collected by W. W. Rubey and others, 1924. Sec. 7, T. 48 N., R. 65 W., 3.2 km southeast of Thornton, Weston County, Wyoming. Belle Fourche Shale, 18.3 m (60 feet) beneath highest yellow concretion. Upper Cenomanian *Metoicoceras mosbyense* zone. Ammonite fauna is: *Borissiakoceras* sp. juv., *Moremanoceras costatum* Cobban, Hook and Kennedy, 1989 (common), *Cunningtoniceras* sp. juv., *Tarrantoceras exile* sp. nov., *Metoicoceras* cf. *mosbyense* Cobban, 1953 (juveniles), *Carthaginities aquilonius* sp. nov.

USGS Mesozoic locality 12740. Collected by M. N. Bramlette and W. W. Rubey, 1924. E $\frac{1}{2}$ sec. 6, T. 9 S., R. 59 E., Carter County, Montana. Belle Fourche Shale. Upper Cenomanian *Metoicoceras mosbyense* zone. Ammonite fauna is: *Moremanoceras costatum* (common), *Neocardioceras* sp. nov., *Nannometoicoceras nanos* gen. et sp. nov., *Metoicoceras* cf. *mosbyense* (juveniles).

USGS Mesozoic locality 23062. Collected by J. B. Reeside Jr., W. A. Cobban and H. R. Christner. 0.8 km east of Five Mile Creek, in the SE $\frac{1}{4}$ Sec. 25, T. 9 S., R. 60 E., Carter County, Montana. Greenhorn Formation. Upper Cenomanian *Sciponoceras gracile* zone. The ammonite fauna is: *Borissiakoceras* sp., *Sunitomoceras* sp. juv., *Kanabicerias septemseriatum* (Cragin, 1893), *Buccinammonites minutus* gen. et sp. nov., *Microsulcatoceras puzosiforme* gen. et sp. nov., *Metoicoceras geslinianum* (d'Orbigny, 1850), *Cryptometoicoceras mite* gen. et sp. nov., *Allocioceras annulatum* (Shumard, 1860), *Sciponoceras gracile* (Shumard, 1860) (common), *Yezoites delicatulus* (Warren, 1930).

USGS Mesozoic locality 22871. Collected by W. A. Cobban, 1947. 9.7 km northwest of Alzada in SE $\frac{1}{4}$ Sec. 6, T. 9 S., R. 59 E., Carter County, Montana. Middle Cenomanian *Plesiacanthoceras wyomingense* zone. *Borissiakoceras orbiculatum* Stephenson, 1955 (common), *Moremanoceras straini* Kennedy, Cobban and Hook, 1988, *M. montanense* sp. nov., *Plesiacanthoceratoides alzadense* (Cobban, 1987b), *Plesiacanthoceras wyomingense* (Reagan, 1924), *Tarrantoceras cuspidum* Stephenson, 1953, *Tarrantoceras* sp., *Kastanoceras spiniger* gen. et sp. nov., *Alzadites alzadensis* gen. et sp. nov., acanthoceratinae indet., *Hamites cimarronensis* (Kaufmann and Powell, 1977) (common), *Idiohamites pulchellus* sp. nov., *I. bispinosus* sp. nov., *Anaptychus* sp.

USGS Mesozoic locality D4462. Collected by W. A. Cobban, 1964. NW $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ Sec. 24, T. 47 N., R. 65 W., Weston County, Wyoming. Belle Fourche Shale. Upper Cenomanian *Dunveganoceras pondi* zone. Ammonite fauna is: *Borissiakoceras orbiculatum*, *Metoicoceras* aff. *praecox* Haas, 1949, *Cryptometoicoceras mite* gen. et sp. nov., *Hamites cimarronensis*, *Idiohamites bispinosus*.

USGS Mesozoic locality D4466. Collected by W. A. Cobban, 1964. 4.8 km NW of Alzada in NE $\frac{1}{4}$ NW $\frac{1}{4}$ Sec. 14, T. 9 S., R. 59 E., Carter County, Montana. Belle Fourche Shale, near bentonite G of Knechtel and Patterson (1962). Upper Cenomanian, *Dunveganoceras pondi* zone. Ammonite fauna is: *Borissiakoceras* sp.,



TEXT-FIG. 4. Locality map for some of the more important localities mentioned in the text.

Moremanoceras costatum, *Tarrantoceras cuspidum*, *Tarrantoceras* sp., *Dunveganoceras pondi* Haas, 1949, *Hamites cimarronensis*, *Idiohamites bispinosus* sp. nov.

USGS Mesozoic locality D5947. Collected by W. A. Cobban, 1961. 4.8 km south of Upton in NW $\frac{1}{4}$ sec. 14, T. 47 N., R. 65 W., Weston County, Wyoming. Belle Fourche Shale, 19.8 m (65 feet) above 0.6 m (2 feet) bentonite. Upper Cenomanian, *Dunveganoceras pondi* zone. Ammonite fauna is: *Borissiakoceras* cf. *orbiculatum*, *Moremanoceras costatum*, *Tarrantoceras* sp., *Neocardioceras* sp. nov., *Plesiacanthoceras* cf. *bellsanum* (Stephenson, 1953), *P.* cf. *wyomingense*, *Alzadites westonense* gen. et sp. nov., *Alzadites?* sp., *Metoicoceras* sp. A; *Hamites cimarronensis*, *Idiohamites bispinosus* sp. nov.

USGS Mesozoic locality D8314. Collected by E. A. Merewether, 1971. SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 33, T. 50 N., R. 66 W., Crook County, Wyoming. Belle Fourche Shale, from ferruginous concretions 7.6–10.7 m (25–35 feet) below top. Upper Cenomanian, *Metoicoceras mosbyense* zone. Ammonite fauna is: *Borissiakoceras* sp. juv., *Moremanoceras scotti*, *Euomphaloceras merewetheri* Cobban, Hook and Kennedy, 1989, *Hamites salebrosus* Cobban, Hook and Kennedy, 1989, *Metapyhoceras* sp.

USGS Mesozoic locality D12052. Collected by S. C. Hook, O. J. Anderson and W. A. Cobban, 1982. Near mouth of Yellowrock Canyon in NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 17, T. 7 N., R. 20 W., Cibola County, New Mexico. Rio Salado Tongue of Mancos Shale, from white concretions 4.6 m (15 feet) above base. Upper Cenomanian *Sciponoceras gracile* zone. Ammonite fauna is: *Pseudocalycoceras angolaense* (Spath, 1931), *Euomphaloceras septemseriatum*, *Sumitomoceras* sp. juv., *Metoicoceras geslinianum*, *Nannometoicoceras? glabrum* gen. et sp. nov., *Allocrioceras annulatum* (Shumard, 1860), *Sciponoceras gracile*, *Worthoceras vermiculus* (Shumard, 1860).

REPOSITORIES OF SPECIMENS

The following abbreviations are used to indicate the repositories of collections: TMM: University of Texas Memorial Museum, Austin, Texas. USNM: National Museum of Natural History, Washington, DC. AMNH: American Museum of Natural History, New York.

CONVENTIONS

All diameters are given in millimetres; D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; ic = intercostal dimension; c = costal dimension. Figures in parentheses are dimensions as a percentage of the diameter. The term rib index as applied to heteromorphs is the number of ribs in a distance equal to the whorl height at the mid-point of the interval where the count was taken. The suture terminology of Wedekend (1916) as propounded by Kullmann and Wiedmann (1970) is used here with E = external lobe, L = lateral lobe, U = umbilical lobe and I = internal lobe.

SYSTEMATIC PALAEOLOGY

Order AMMONOIDEA Zittel, 1884, pp. 355, 392

Suborder AMMONITINA Hyatt, 1889, p. 7

Superfamily HAPLOCERATACEAE Zittel, 1884, p. 463

Family BINNEYITIDAE Reeside, 1928, p. 4

Genus BORISSIAKOCERAS Arkhanguelsky, 1916, p. 55

Type species. By original designation: *Borissiakoceras mirabilis* Arkhanguelsky, 1916, p. 55, pl. 8, figs. 2, 3.

Borissiakoceras orbiculatum Stephenson, 1955

Plate 1, figs. 1–39; Plate 4, figs. 78–83

1955 *Borissiakoceras orbiculatum* Stephenson, p. 64, pl. 6, figs. 1–4.

1961 *Borissiakoceras orbiculatum* Stephenson; Cobban, p. 750, pl. 88, figs. 15–41; text-figs. 5a–f (with synonymy).

1988 *Borissiakoceras orbiculatum* Stephenson; Kennedy, p. 18, pl. 1, figs. 23–26 (with synonymy).

1990 *Borissiakoceras orbiculatum* Stephenson, 1955; Kennedy and Cobban, p. 85, pl. 1, figs. 1–14.

Holotype. USNM 108832 from the basal Eagle Ford Group on Walnut Creek, 7.6 km (4.75 miles) northeast of Mansfield, Texas. Middle Cenomanian, *Acanthoceras amphibolum* zone.

Material. More than 100 specimens, including USNM 423646–423665, from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Discussion. Cobban (1961) described this species in some detail and indicated how it differed from others referred to the genus. The present collection contains 50 specimens that were suitable for

measurement. Of these, 35 were microconchs and 13 macroconchs, two being unassigned. Microconchs (Pl. 1, figs. 1–8, 26–38) are adult at 5–11 mm diameter and have umbilical ratios of 0·21–0·32. Macroconchs (Pl. 1, figs. 9–25, 39) are adult at 9·7–27·3 mm and have umbilical ratios of 0·13–0·19.

Occurrence. *Acanthoceras amphibolum* zone of Wyoming, Colorado, Kansas and Texas; *Plesiacanthoceras wyomingense* zone of Montana; *Sciponoceras gracile* zone of Texas.

Superfamily DESMOCERATAEAE Zittel, 1895, p. 426

(*nom.trans.* Wright and Wright, 1951, p. 18;

ex Desmoceratidae Zittel, 1895)

Family DESMOCERATIDAE Zittel, 1895, p. 426

Subfamily DESMOCERATINAE Zittel, 1895, p. 426

Genus MOREMANOCERAS Cobban, 1972, p. 465

Type species. *Tragodesmoceras scotti* Moreman, 1942, p. 208, pl. 33, fig. 8, text-fig. 2D; by original designation.

Moremanoceras straini Kennedy, Cobban and Hook, 1988

Plate 1, figs. 40–45, 55, 56, 60–72

1955 *Desmoceras?* sp. Stephenson, p. 58, pl. 4, figs. 12, 13.

1977a *Desmoceras (Pseudoulligella)* aff. *D. japonicum* Yabe; Cobban, p. 22, pl. 11, figs. 1–6, 9, 10.

1977b *Desmoceras (Pseudoulligella)* aff. *japonicum* Yabe; Cobban, fig. 4a–e.

1988 *Moremanoceras straini* Kennedy, Cobban and Hook, p. 36, fig. 1a–g, i–t.

Types. Holotype is USNM 416051 by original designation; paratypes USNM 416052–416060, from the base of the Boquillas Formation, Cerro de Cristo Rey, New Mexico, *Acanthoceras amphibolum* zone.

Material. More than 60 specimens, including USNM 423667–423673, from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Discussion. Many of the present specimens retain original shell; specimens studied range from 2·5 to 67 mm diameter. The diagnostic features of the species are the compressed to slightly depressed

EXPLANATION OF PLATE 1

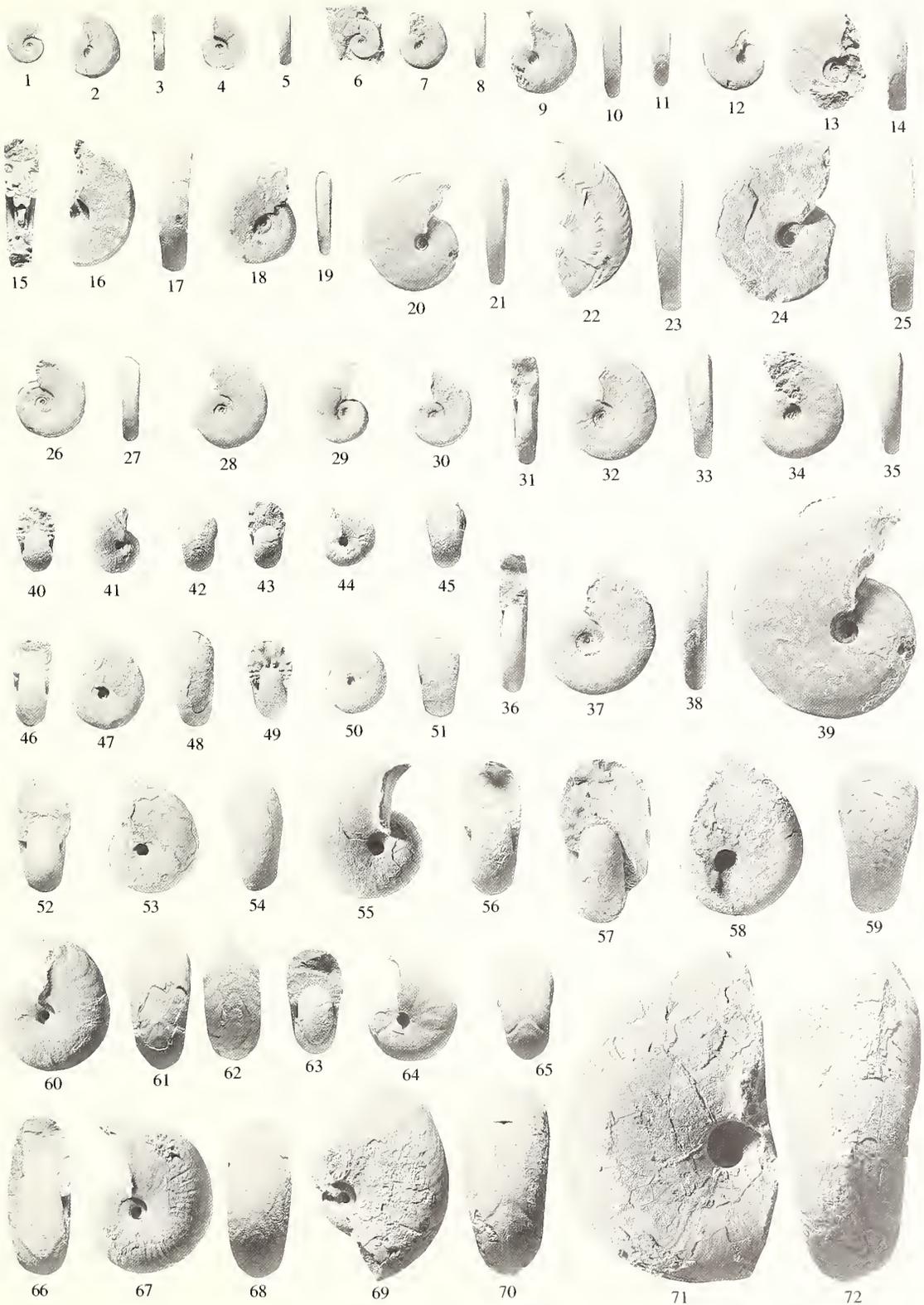
Figs. 1–39. *Borissiakoceras orbiculatum* Stephenson, 1955. 1, USNM 423646; 2, USNM 423647; 3–5, USNM 423648; 6, 30, USNM 423649; 7, 8, 34, 35, USNM 423656; 9–11, USNM 423650; 12, USNM 423651; 13, 14, USNM 423652; 15–17, USNM 423653; 18, 19, USNM 423654; 20, 21, 39, USNM 423655; 22, 23, USNM 423657; 24, 25, USNM 423658; 26, 27, USNM 423659; 28, USNM 423660; 29, USNM 423661; 31–33, USNM 423662; 36–38, USNM 423666, all from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Figs. 40–45, 55, 56, 60–72. *Moremanoceras straini* Kennedy, Cobban and Hook, 1988. 40–42, USNM 423667; 43–45, USNM 423668; 55, 56, 60–62, USNM 423669; 63–65, USNM 423670; 66–68, USNM 423671; 69, 70, USNM 423672; 71, 72, USNM 423673, all from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Figs. 46–48, 52–54. *Moremanoceras costatum* Cobban, Hook and Kennedy, 1989. 46–48, USNM 423676; 52–54, USNM 423690, from USGS Mesozoic locality D4466, *Dumveganoceras pondi* zone.

Figs. 49–51, 57–59. *Moremanoceras scotti* (Moreman, 1942). 49–51, USNM 423674; 57–59, USNM 423675, from USGS Mesozoic locality D8314, *Metoicoceras mosbyense* zone.

Figs. 15–17, 26–35, 39 are $\times 2$; Figs. 18, 19, 36–38 are $\times 3$; the remainder $\times 1$.



whorls, biconcave growth lines on the shell surface (Pl. 1, figs. 60, 64, 67) and periodic constrictions on the mould, both of which form an acute chevron on the venter (Pl. 1, figs. 61, 65, 70). The venter is initially evenly rounded (Pl. 1, figs. 40–45) but a blunt, rounded keel develops at maturity (Pl. 1, figs. 69–72) as do blunt adapical collars to the constrictions. *Moremanoceras elgini* (Young, 1958) (p. 292, pl. 39, figs. 4–20, 24, 25, 30, 31; text-fig. 1a–e) is more compressed when young, develops thickened collar-ribs to the constrictions from 15 mm diameter, has strong ventrolateral flank ribs when mature and never has a siphonal keel or ridge.

M. costatum Cobban, Hook and Kennedy (1989) has a sharp keel that is present from a much earlier stage and strong concave ribs on the ventrolateral shoulder. *M. montanaense* sp. nov., described below, is a large, stout species that has ribs that are straight on the flanks rather than biconcave, and lacks the pronounced ventral chevron and keel of *M. straini*. *M. scotti* (Moreman, 1942) (p. 208, pl. 33, fig. 8; text-fig. 20; see Cobban, 1972, p. 6, pl. 2, figs. 1–23; text-figs. 3–5) has distant, flared collar ribs that are transverse over the venter, and never develops a keel (Pl. 1, figs. 49–51; 57–59).

Occurrence. *A. amphibolum* zone of central and Trans-Pecos Texas; *Plesianthoceras wyomingense* zone of Montana.

Moremanoceras costatum Cobban, Hook and Kennedy, 1989

Plate 1, figs. 46–48, 52–54; Plate 2, figs. 1–35; Plate 4, figs. 76 and 77

1989 *Moremanoceras costatum* Cobban, Hook and Kennedy, p. 19, figs. 19, 64a–k, 65a–d, g, h (with full synonymy).

Types. Holotype is USNM 425133, paratypes USNM 425134–425142, from the *Metoicoceras mosbyense* zone of USGS Mesozoic locality D10186 in Luna County, New Mexico.

Material. USNM 423677 to 423683 from USGS Mesozoic locality 12740, all *M. mosbyense* zone. USNM 423684 to 423687 and 423738 from USGS Mesozoic locality D5947; USNM 423676, 423688 and 423690, from USGS Mesozoic locality D4466, are from the *Dunveganoceras pondi* zone.

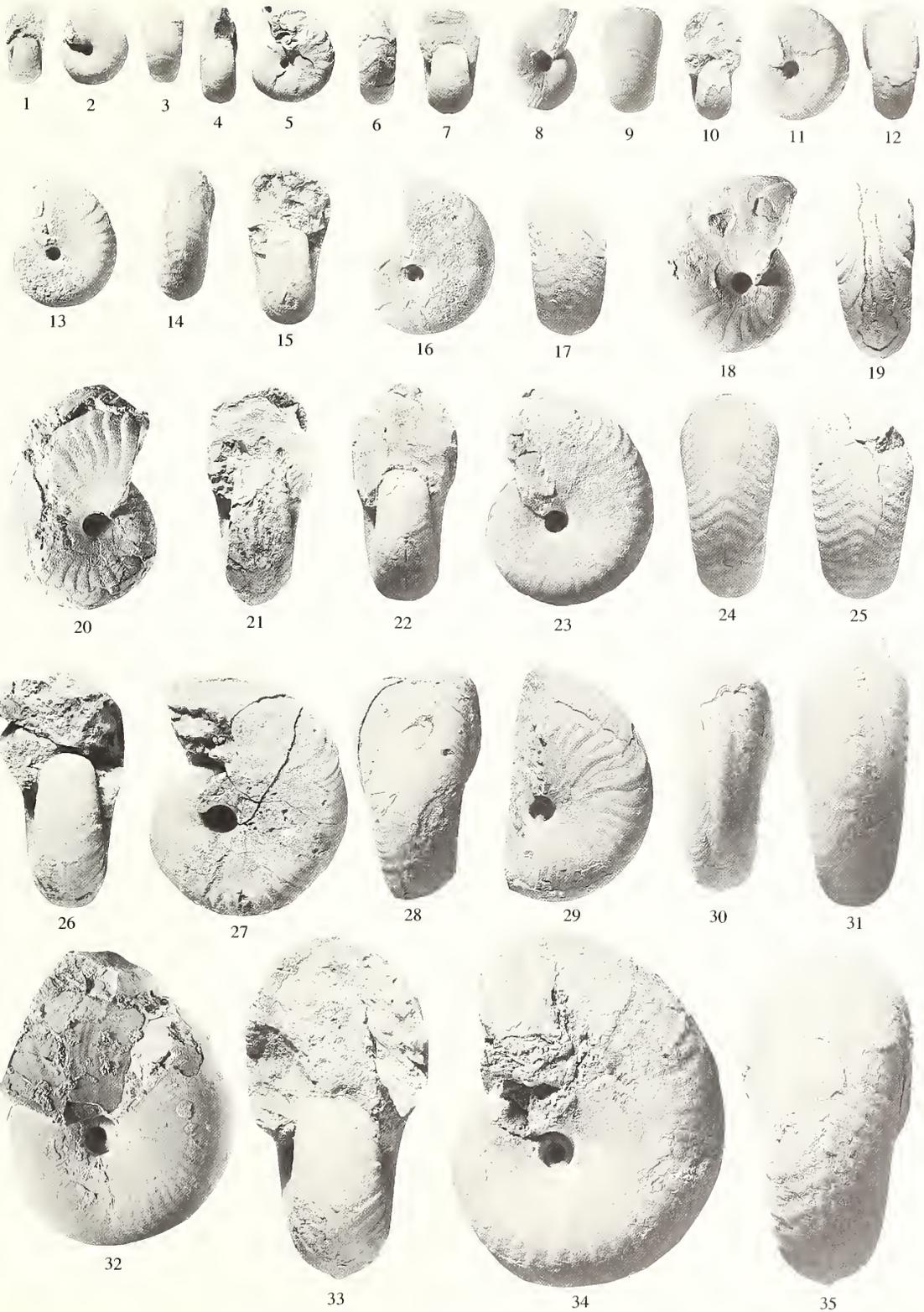
Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
423677	19.5 (100)	6.8 (34.9)	7.2 (36.9)	0.94	0.7 (3.6)
423678	18.2 (100)	9.0 (49.4)	10.5 (57.6)	0.86	1.2 (6.6)
423679	22.2 (100)	12.2 (55.4)	—	—	1.2 (5.4)
423680	25.0 (100)	13.0 (52.0)	13.9 (55.6)	0.94	2.1 (8.4)
423681	33.0 (100)	16.6 (50.3)	18.5 (56.1)	0.90	2.4 (7.3)
423682	36.7 (100)	19.5 (53.1)	20.3 (55.3)	0.96	3.3 (9.0)
423683	57.8 (100)	30.0 (51.9)	33.6 (58.1)	0.89	6.2 (10.7)

Discussion. The present material is much better preserved than the types. Very young specimens with shell preserved (Pl. 2, figs. 1–12) show distant feebly flexuous ribs, and moulds bear constrictions that cross the venter in a narrow chevron with an adapical collar-rib. Both ribs and

EXPLANATION OF PLATE 2

Figs. 1–35. *Moremanoceras costatum* Cobban, Hook and Kennedy, 1989. 1–3, USNM 423677; 4–6, USNM 423684; 7–9, USNM 423685; 10–12, USNM 423678; 13, 14, USNM 423679; 15–17, USNM 423680; 18, 19, USNM 423686; 20, 21, USNM 423687; 22–25, USNM 423681; 26–28, USNM 423682; 29–30, USNM 423688; 31, 32, USNM 423689; 33–35, USNM 423683. 1–3, 10–17, 22–28, 33–35 are from USGS Mesozoic locality 12740, *Metoicoceras mosbyense* zone. 4–9, 18–21 are from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone. 29–30 are from USGS Mesozoic locality D4466, *Dunveganoceras pondi* zone. 31, 32 are from USGS Mesozoic locality 12621, *Dunveganoceras pondi* zone. Figs. 7–9 are $\times 2$; the remainder are $\times 1$.



constrictions strengthen as size increases (Pl. 2, figs. 13–35), while a pronounced siphonal ridge is present on the shell from a diameter as small as 20 mm (Pl. 2, figs. 18 and 19). This ridge may be markedly crenulate where crossed by the ribs. Both ribs and keel are present, if less prominent, on large moulds. The presence of pronounced falcoid ribs, especially well-developed on the outer flanks and venter plus the siphonal keel at the apex to a narrow ventral chevron distinguish this species from all others, as is apparent from the discussion under *M. straini* above.

Occurrence. *Calycoceras canitaurinum* zone in New Mexico, Trans-Pecos Texas, western Oklahoma, central Kansas and north-central Colorado, and in the correlative *Dunveganoceras pondi* zone in Wyoming and Montana. *Metoicoceras mosbyense* zone in Wyoming and New Mexico.

Moremanoceras montanaense sp. nov.

Plate 3, figs. 62–64

Types. Holotype is USNM 423691 from USGS Mesozoic locality D12890, in the lower part of the Greenhorn Formation in sec. 5, T. 9 S., R. 59 E., Carter County, Montana. Paratype USNM 423692 is from USGS Mesozoic locality D10201, Colorado Formation, 3 m (10 feet) to 4.6 m (15 feet) above base, NE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 20, T. 18 S., R. 20 W., Hidalgo County, New Mexico. *M. mosbyense* zone.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
Holotype					
USNM 423691	60.5 (100)	31.3 (51.7)	36.0 (59.7)	0.86	3.7 (6.1)
at	45.0 (100)	23.0 (51.1)	24.8 (55.1)	0.93	5.6 (12.4)

Description. Holotype is a phragmocone 62 mm in diameter, retaining recrystallized shell, and slightly crushed, making accurate measurements impossible. Coiling is very involute, with a tiny, deep umbilicus with a flattened subvertical wall and narrowly rounded umbilical shoulder. Whorl section compressed, with flattened subparallel flanks and broadly rounded venter. Ornament is not visible on the innermost flank, but the mid to outer flanks and venter bear crowded ribs of variable strength and spacing. They arise as mere striae, are feebly convex at mid flank, concave over the outer flank and ventrolateral shoulder and cross the venter in a broad convexity. Periodic interspaces are deepened and presumably correspond to constrictions on the mould. Sutures not seen.

Discussion. Large size and density of ribbing, course of ribs and lack of a siphonal ridge immediately separate *M. montanaense* from *M. elgini*, *M. straini* and *M. costatum*. The closest similarities are to *M. scotti* (Moreman, 1942) (p. 208, pl. 33, fig. 8; text-fig. 28; see Cobban, 1972, p. 6, pl. 2, figs. 1–23; text-figs 3–5), but this *Sciponoceras gracile* zone species has very widely separated flared ribs that extend down to the umbilical shoulder, and are separated by very fine riblets and growth striae only in middle and later growth. *M. montanaense* sp. nov. probably arose from *M. costatum* by retention of the ribbed, non-carinate morphology of the juvenile stages of the latter to a large size, plus modification in rib style and elimination of the marked ventral chevron of the later stages of *M. costatum*, leaving the broad ventral curvature of the juvenile (Pl. 2, figs. 1–10). *M. montanaense* sp. nov. in turn probably gave rise to *M. scotti* by differentiation of ribbing during later growth.

Occurrence. As for types.

Superfamily ACANTHOCERATAEAE de Grossouvre, 1894, p. 22

(*nom. correct.* Wright and Wright, 1951, p. 24, *pro.* Acanthoceratida Hyatt, 1900, p. 585; *nom. transl. ex* Acanthoceratidae Hyatt, 1900, p. 585; *nom. correct. ex* Acanthoceratidés de Grossouvre, 1894).

Family ACANTHOCERATIDAE de Grossouvre, 1894, p. 22

(*nom. correct.* Hyatt, 1900, p. 585; *ex* Acanthoceratidés de Grossouvre, 1894, p. 22).

Subfamily ACANTHOCERATINAE de Grossouvre, 1894, p. 22

(*nom. correct.* Hyatt, 1900, p. 585; *ex* Acanthoceratidés de Grossouvre, 1894; *nom. transl.* Wright and Wright, 1951, p. 28, *ex* Acanthoceratidés de Grossouvre).

Genus CUNNINGTONICERAS Collignon, 1937, p. 64 (40)

(? = *Guerangericeras* Thomel, 1972, p. 119)

Type species. *Ammonites cunningtoni* Sharpe, 1855, p. 35, pl. 15, fig. 2.

Cunningtoniceras sp. juv.

Plate 3, figs. 1–7

Material. Five specimens, including USNM 423693–423695, from USGS Mesozoic Locality 12650, *Metoicoceras mosbyense* zone.

Description. Specimens range from 7 to 12.5 mm in diameter. In the smaller specimens coiling is very involute with a small, deep umbilicus comprising approximately 19% of the diameter. The whorl section is depressed, reniform in intercostal section and polygonal in costal section, with the greatest breadth at the outer ventrolateral tubercles. There are 6–7 strong umbilical bullae per whorl that give rise to broad, blunt primary ribs. The latter weaken at mid-flank and alternate regularly with single secondary ribs that arise at mid-flank. All bear a strong conical inner ventrolateral tubercle that appears to have been the base for a long spine. These ribs broaden and sweep forwards to a strong conical outer ventrolateral tubercle on the mould of the phragmocone; USNM 423693 shows these tubercles to have been the bases of long septate spines (Pl. 3, figs. 1–3). A broad rib passes straight across the venter, and bears a weak siphonal clavus. Shorter, intercalated ribs are also present; some bear only outer ventrolateral and siphonal tubercles, others bear only the siphonal row; there are as many as 18 ventral ribs per whorl.

Discussion. Preservation of septate spines on USNM 423693 gives this specimen a quite remarkable appearance (Pl. 3, figs. 1–3). The variable nature of the intercalated ventral ribs shows these tiny specimens to be *Cunningtoniceras* beyond any doubt; see Wright and Kennedy (1987) for a recent review of the genus. The specimens are so tiny that they cannot be usefully compared with any previously described species, although we have seen comparable tiny limonitic nuclei of *Cunningtoniceras* from Upper Cenomanian pelagic clay facies in Tunisia. *Cunningtoniceras* is widespread in the US Western Interior and Gulf Coast regions, with, for instance, *C. inerme* (Pervinquier, 1907) in the *Conlinoceras tarrantense* zone, *C. lonsdalei* (Adkins, 1928) in the *Acanthoceras bellense* zone and *C. johnsonanum* (Stephenson, 1955) in the *Acanthoceras amphibolum* zone of Texas (Kennedy and Cobban, 1990). A range of species in the upper Cenomanian of New Mexico and Arizona includes *C. arizonense* Kirkland and Cobban, 1986 (p. 2, pls. 1–8), of which the present specimens might conceivably be nuclei.

Occurrence. As under *Material*.

Genus TARRANTOCERAS Stephenson, 1955, p. 59

Type species. *Tarrantoceras rotatile* Stephenson, 1955, p. 59, pl. 5, figs. 1–10; by original designation = *Mantelliceras sellardsi* Adkins, 1928, p. 239, pl. 25, fig. 1; pl. 26, fig. 1.

Tarrantoceras cuspidum (Stephenson, 1953)

Plate 3, figs. 8–12

1953 *Acanthoceras cuspidum* Stephenson, p. 202, pl. 50, figs. 1–4.1990 *Tarrantoceras cuspidum* (Stephenson, 1953); Kennedy and Cobban, p. 134, pl. 14, figs. 21–24, 26–28.

Types. Holotype is USNM 105974, by original designation; paratype is USNM 105975, both from gullies south of the old Sherman road, 4.5 km east of Whitesboro, Grayson County, Texas. An unfigured paratype is from USGS Mesozoic locality 14092, a bluff 1.6 km north and 2.9 km east of Sadler, Grayson County, Texas. All are from the Templeton Member of the Woodbine Formation, *Plesiacanthoceras wyomingense* zone.

Material. USNM 423697 as well as other specimens from USGS Mesozoic locality 22871, *P. wyomingense* zone. USNM 423696 and other specimens from USGS Mesozoic locality D4466, Upper Cenomanian *Dunveganoceras pondi* zone.

Discussion. USNM 423697 is 22 mm in diameter (Pl. 3, figs. 10–12) and differs in no significant respects from the types. USNM 423696 is larger than the types, and shows the same strong ornament persisting to a whorl height of 13 mm (Pl. 3, figs. 8 and 9). The innermost whorls of USNM 423697 are well-exposed. They show feeble umbilical bullae giving rise to low, broad prorsiradiate ribs that terminate in massive inner ventrolateral spines that are housed in notches in the umbilical wall of preceding whorl, as in the types. *I. cuspidum* has not been previously recognized outside Texas, and the present occurrence is of some importance in providing a probable date for the Templeton Member.

Occurrence. *Plesiacanthoceras wyomingense* zone of Texas and Montana; *Dunveganoceras pondi* zone of Montana.

EXPLANATION OF PLATE 3

Figs. 1–7. *Cunningtoniceras* sp. juv. 1–3, USNM 423693; 4, 5, USNM 423694; 6, 7, USNM 423695, from USGS Mesozoic locality 12650, *Metoicoceras mosbyense* zone.

Figs. 8–12. *Tarrantoceras cuspidum* (Stephenson, 1953). 8, 9, USNM 423696; 10–12, USNM 423697, from USGS Mesozoic localities D4466 and 22871, *Dunveganoceras pondi* and *Plesiacanthoceras wyomingense* zones.

Figs. 13–21, 26–31, 35–44. *Kastanoceras spiniger* gen. et sp. nov. 13–15, holotype, USNM 423699; 16–18, paratype USNM 423700; 19–21, paratype USNM 423701; 26–28, paratype USNM 423702; 29–31, paratype USNM 423703; 35–40, paratype USNM 423704; 41–44, paratype USNM 423705, all from USGS Mesozoic locality 22871, *P. wyomingense* zone.

Figs. 22–25. *Tarrantoceras exile* sp. nov. Holotype, USNM 423698, from USGS Mesozoic locality 12650, *Metoicoceras mosbyense* zone.

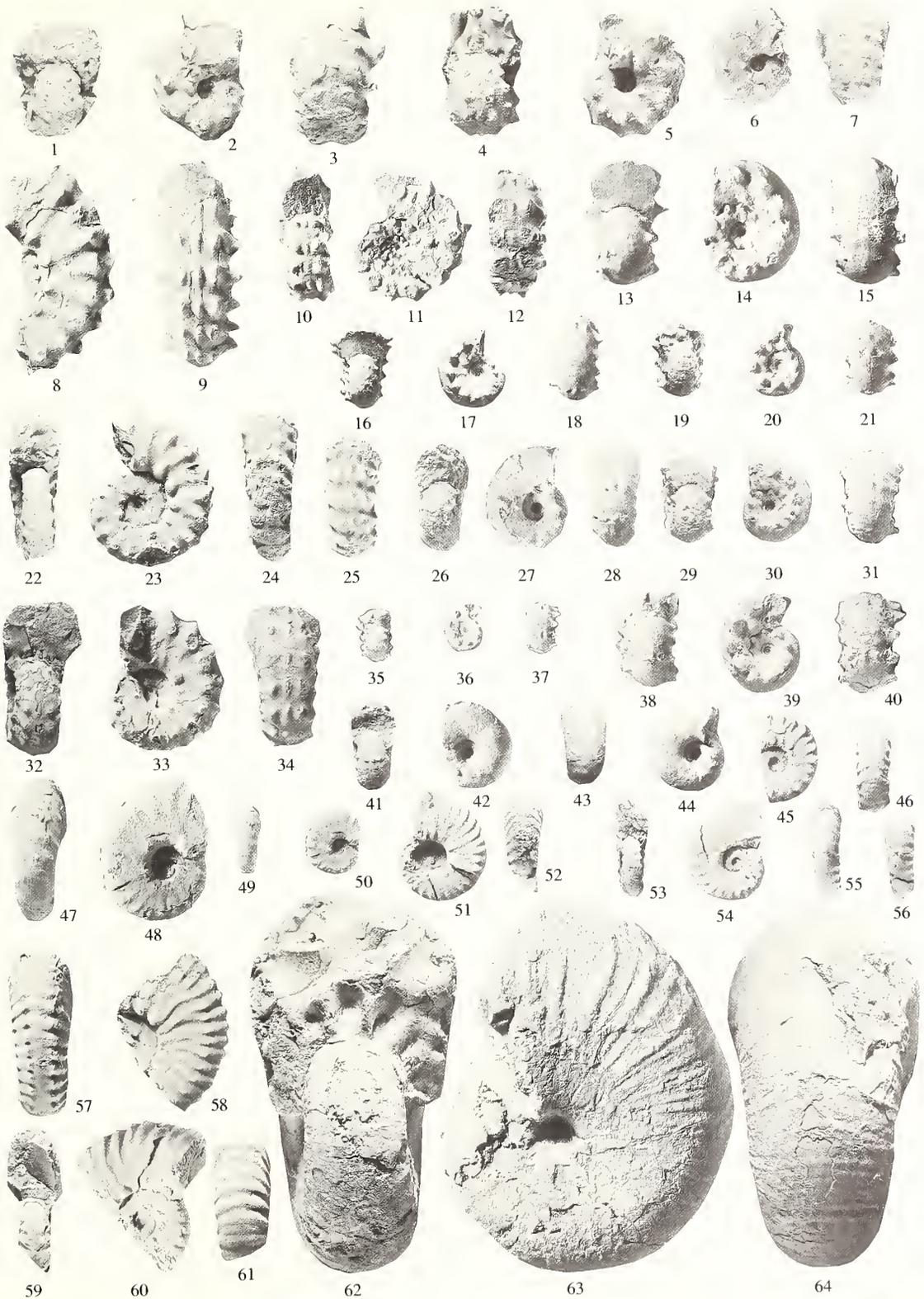
Figs. 32–34. *Tarrantoceras sellardsi* (Adkins, 1928). USNM 400767, from USGS Mesozoic locality D12626, *Acanthoceras amphibolium* zone.

Figs. 45, 46, 51–56. *Sunitomoceras* spp. juv. 45, 46, USNM 423706; 51, 52, USNM 423707, both from USGS Mesozoic locality 23062, *Sciponoceras gracile* zone. 53–56, USNM 423708, from Mesozoic locality D4628, *S. gracile* zone.

Figs. 47–50, 57–61. *Sunitomoceras conlini* (Wright and Kennedy, 1981). 47–50, USNM 400804, from USGS Mesozoic locality D11529; 57, 58, USNM 400807, from USGS Mesozoic locality D10196; 59–61, USNM 400805, from USGS Mesozoic locality D11529, all *S. gracile* zone.

Figs. 62–64. *Moremanoceras montanaense* sp. nov. Holotype, USNM 423691, from USGS Mesozoic locality D12890, *M. mosbyense* zone.

Figs. 1–3, 6, 7, 13–34, 38–48 are $\times 2$; figs. 4, 5 are $\times 3$; the remainder are $\times 1$.



Tarrantoceras exile sp. nov.

Plate 3, figs. 22–25

Derivation of name. *Exilis* (Latin): slender, thin, pertaining to the whorl section of the species.

Holotype. USNM 423698 from USGS Mesozoic locality 12650, *Metoicoceras mosbyense* zone.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
USNM 423698	12.61 (100)	4.3 (34.1)	5.1 (40.5)	0.84	4.3 (34.1)

Description. Coiling evolute, with broad shallow umbilicus comprising 34% of diameter with low, rounded wall that is indented to accommodate the inner ventrolateral tubercles of the preceding whorl (Pl. 3, fig. 23). Whorl section of this specimen is that of a *Tarrantoceras*, as can be seen by comparison with specimens of *T. sellardsi* illustrated for comparison (Pl. 3, figs. 32–34). Coarseness of ornament yet lack of massive inner and outer ventrolateral tubercles immediately distinguish it from *T. cuspidum* (Pl. 3, figs. 8–12) whereas the combination of evolute slender whorls and coarse ornament gives the shell a quite different appearance than any *T. sellardsi* we have seen. It represents the youngest member of the *Tarrantoceras* lineage.

Occurrence. As for types.

Genus KASTANOCERAS NOV.

Derivation of name. *Kastanos* (Greek); chestnut, from the common spinosity of the new genus and the seed cases of that tree.

Type species. *Kastanoceras spiniger* gen. et sp. nov., *Plesiacanthoceras wyomingense* zone of Montana.

Diagnosis. Dwarf, presumed microconch adult at 8 mm, largest (incomplete) macroconch is 10 mm in diameter. Coiling evolute, coronate, intercostal section depressed reniform, costal section with flattened sides that converge to an umbilical wall notched to accommodate outer ventrolateral spines of preceding whorl. Flank ribs feeble, prorsiradiate, terminating in large inner ventrolateral spines. Venter with feeble outer ventrolateral and siphonal clavi that decline at smallest diameters visible. Ornament declines markedly on adult body chamber. Suture with broad, little-incised, asymmetrically bifid E/L, narrower L and simple bifid L/U₂.

Discussion. Inner whorls are inseparable from those of *T. cuspidum*, with which *K. spiniger* gen. et sp. nov., occurs (Pl. 3, figs. 13–21). But whereas *T. cuspidum* grows to a diameter of at least 35 mm and has outer whorls with very strong, close-spaced clavi and strong flank ornament at this size, the present specimens show approximation of sutures and decline of body chamber ornament that indicates them to be adult at phragmocone diameters of as little as 7.5 mm in the microconch holotype. *Kastanoceras* is thus a progenic dwarf derivative of *Tarrantoceras* just as *Protacanthoceras* Spath, 1923 is a similarly derived dwarf offshoot of *Acanthoceras* Neumayr, 1875 (Wright and Kennedy, 1980, 1987; Kennedy and Wright, 1985).

Occurrence. *P. wyomingense* zone, Montana.

Kastanoceras spiniger gen. et sp. nov.

Plate 3, figs. 13–21, 26–31, 35–44

Types. Holotype is USNM 423699, paratypes USNM 423700–423705 from USGS Mesozoic locality 22871, *P. wyomingense* zone.

Diagnosis. With the characters of the genus.

Description. Small, presumed microconch 8 mm diameter, largest, incomplete macroconch has phragmocone diameter of 7.5 mm and total diameter of 10 mm with only 120° of body chamber preserved. Coiling is evolute with the umbilicus comprising 39% of the diameter, deep, with a very low, rounded wall that is notched to accommodate the inner ventrolateral spines of the preceding whorl. Whorl section depressed reniform in intercostal section. In costal section the flanks are concave and diverge outwards, with the greatest breadth at the inner ventrolateral spine; the venter is broadly arched. There are 9–11 feeble umbilical bullae that connect by low, broad prorsiradiate ribs to prominent inner ventrolateral spines that are directed outwards and normal to the median plane of the shell. Feeble outer ventrolateral and siphonal clavi are barely visible at the smallest diameter seen, but they strengthen towards the beginning of the adult body chamber and may be linked by low spiral ridges. Ventral ribbing is feeble or absent; interspaces between rows of ventral tubercles may be deepened and constriction-like. On the adult body chamber all ornament weakens markedly.

Discussion. Differences from *T. cuspidum*, from which the species arose pedomorphically, are discussed under the genus.

Occurrence. As for types.

Genus SUMITOMOCERAS Matsumoto, 1969, p. 280.

Type species. *Sumitomoceras faustum* Matsumoto and Muramoto, 1969, p. 283, pl. 283, pl. 38, figs. 1–4; text-fig. 8, by original designation.

Sumitomoceras spp. juv.

Plate 3, figs. 45, 46, 51–56; Plate 4, figs. 57, 58; Plate 6, figs. 32–35

Material. USNM 423706 and 423707 from USGS Mesozoic locality 23062; USNM 423708 from USGS Mesozoic locality D4628; USNM 423731 from USGS Mesozoic locality D5780; USNM 423747, from USGS Mesozoic locality D12052; all Upper Cenomanian *Sciponoceras gracile* zone.

Description. USNM 423706 is only 7.5 mm in diameter. Coiling is evolute, with $U = 27\%$ of diameter, with a low, subvertical wall and narrowly rounded umbilical shoulder. The whorl section is compressed with subparallel flanks, broadly rounded ventrolateral shoulders and an arched venter in intercostal section, the costal section is polygonal. Primary ribs arise from feeble bullae perched on the umbilical shoulder. They are narrow and prorsiradiate and separated by 1 or 2 shorter intercalated ribs. All ribs bear small conical inner ventrolateral tubercles. A strong rib sweeps forward across the ventrolateral shoulder to an outer ventrolateral clavus. Scarcely visible at the smallest diameter visible, this rib becomes more prominent as size increases. USNM 423707 shows similar ornament at the smallest diameter visible, but is 18 mm in diameter (Pl. 3, figs. 51, 52), and shows both inner and outer ventrolateral tubercles declining. In USNM 423706 some of the interspaces are distinctly deepened and constriction-like. USNM 423708 is 15.7 mm in diameter, has weak or no umbilical bullae, very weak ornament on the inner flanks, but prominent inner ventrolateral tubercles throughout, and no, or incipient outer ventrolaterals. USNM 423747 (Pl. 6, figs. 32–35) has a maximum preserved diameter of 22.5 mm. Coiling is very evolute, with a broad shallow umbilicus comprising 23% of diameter. Whorl section is compressed, with flattened subparallel flanks and broadly rounded venter. Flank ornament consists of low, crowded ribs, 18 per half whorl, of which eight arise at incipient umbilical bullae, the remainder intercalating. Ribs are flexuous and prorsiradiate, convex across the inner mid-flank, thereafter concave and strengthening, crossing the venter in a shallow convexity. There are feeble rounded inner ventrolateral and clavate outer ventrolateral and siphonal tubercles at the smallest diameter visible. The inner ventrolateral tubercles efface as size increases but feeble outer ventrolateral and siphonal tubercles persist to the largest diameter seen. Suture with broad, symmetrically bifid E/L, smaller bifid L, little incised L/U₂ and small U.

Discussion. The identity of these specimens is demonstrated by comparison with an ontogenetic series of *S. conlini* (Wright and Kennedy, 1981) from the *S. gracile* zone in New Mexico (Pl. 3, figs. 47–50, 57–61). The smallest, USNM 400804, can be linked to USNM 400805 which shows very early loss of all tuberculation and is presumed to be a microconch (Pl. 3, figs. 59–61); in others, the tubercles persist to a much greater size (USNM 400807: Pl. 3, figs. 57 and 58).

Occurrence. As for material.

Genus ALZADITES nov.

Derivation of name. From the town of Alzada, Carter County, Montana, 9.7 km southeast of the type locality.

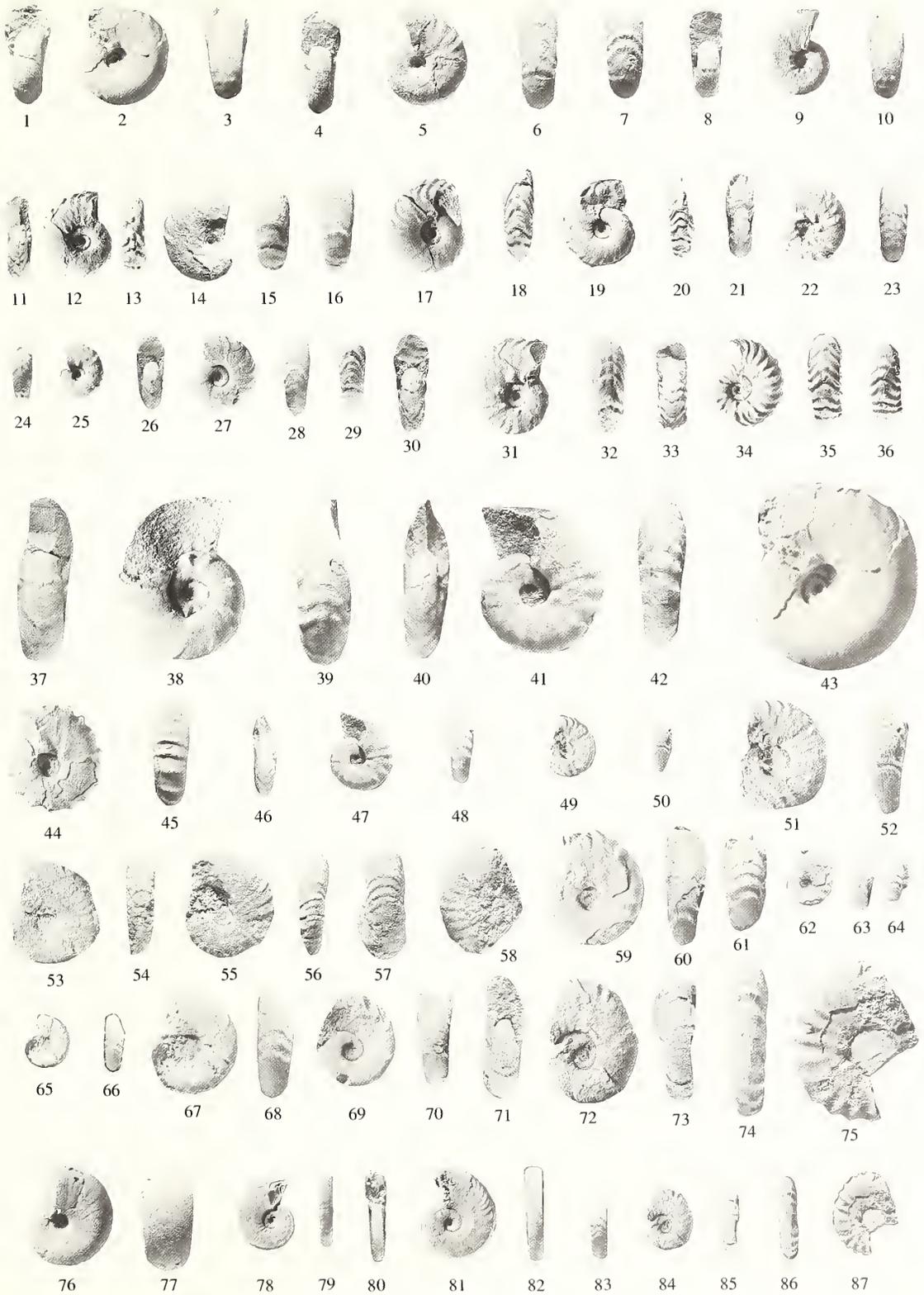
Type species. *Alzadites alzadensis* gen. et sp. nov., *Plesiacanthoceras wyomingense* zone, Montana.

Diagnosis. Small, adult at 16.5 mm or less in diameter. Involute with small umbilicus, whorl section compressed with flattened subparallel flanks and rounded venter. Phragmocone with tiny, distant umbilical bullae, distant prorsiradiate ribs and feeble to strong inner ventrolateral tubercles plus outer ventrolateral and siphonal clavi. Ventral ribbing strengthens on adult body chamber and tubercles decline, leaving strong, coarse, prorsiradiate, concave ribs on outer flank that cross venter in a broad convexity, or a chevron, separated by broad interspaces. Constrictions may develop on internal moulds of phragmocone and body chamber. Suture with simple, little-incised elements; E/L broad, and symmetrically bifid, L narrow, shallow, bifid, saddles on umbilical lobe simple, bifid.

Discussion. *Alzadites* most closely resembles certain *Protacanthoceras* Spath, 1923, and the type species is homeomorphic with *P. asgeirri* Wright and Kennedy, 1980 (p. 90, figs. 20–21, 47). This is scarcely surprising inasmuch as both are interpreted as progenic dwarfs and as a result share certain features that are common to most acanthoceratine nuclei. *Protacanthoceras* derives from *Acanthoceras* Neumayr, 1875, and the type species, *Ammonites bunburianus* Sharpe, 1853 (p. 25, pl. 9, fig. 3; see Wright and Kennedy, 1980, p. 91, figs. 29–33, 41–43, 48; 1987, p. 215, pl. 55, figs. 10–16; text-figs. 83B, C) and many of the other early *Protacanthoceras* species are easily differentiated from

EXPLANATION OF PLATE 4

- Figs. 1–10, 14–16, 43. *Alzadites alzadensis* gen. et sp. nov. 1–3, 43, paratype USNM 423710; 4–7, holotype USNM 423709; 8–10, paratype USNM 423712; 14–16, paratype USNM 423711, all from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.
- Figs. 11–13, 17–39. *Alzadites westonensis* gen. et sp. nov. 11–13, paratype USNM 423715; 17, 18, paratype USNM 423716; 19, 20, paratype USNM 423717; 21–23, paratype USNM 423718; 24, 25, paratype USNM 423719; 26–29, paratype USNM 423720; 30–32, paratype USNM 423721; 33–36, holotype USNM 423714; 37–39, paratype USNM 423722, all from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone.
- Figs. 40–42, 46–48. *Alzadites incomptus* gen. et sp. nov. Paratype USNM 423728, from USGS Mesozoic locality D5249, *Sciponoceras gracile* zone.
- Figs. 44, 45. *Alzadites?* sp. USNM 423730, from USGS Mesozoic locality D5947, *D. pondi* zone.
- Figs. 49–52, 65–70. *Microsulcatoceras puzosiiforme* gen. et sp. nov. 49–52, holotype, USNM 423734; 65–68, paratype USNM 423735; 69, 70, paratype USNM 423736, all from USGS Mesozoic locality 23062, *S. gracile* zone.
- Figs. 53–56. *Alzadites* sp. A. 53–54, USNM 423732; 55–56, USNM 423733; from USGS Mesozoic locality D5780, *S. gracile* zone.
- Figs. 57, 58. *Sumitomoceras* sp. juv. USNM 423731, from USGS Mesozoic locality D5780.
- Figs. 59–64. *Microsulcatoceras texanum* gen. et sp. nov. Holotype USNM 423739 from stream bank 2.4 to 2.9 km southwest of Britton, on and east of Rogers Farm, Ellis County, Texas. Britton Formation, *S. gracile* zone.
- Figs. 71–73, 84, 85. *Microsulcatoceras?* sp. USNM 423740, from USGS Mesozoic locality D11514, *Neocardioceras juddii* zone.
- Figs. 74, 75, 86, 87. *Microsulcatoceras crassum* gen. et sp. nov. Holotype, USNM 423737, from USGS Mesozoic locality D4682, *S. gracile* zone. Figs. 76, 77. *Morenanoceras costatum* Cobban, Hook and Kennedy, 1989. USNM 423738, from USGS Mesozoic locality D5947, *D. pondi* zone.
- Figs. 78–83. *Borissiakoceras orbiculatum* Stephenson, 1955. 78, 79 are USNM 423663, from USGS Mesozoic locality D5947; 80–83 are USNM 423664 from USGS Mesozoic locality D4462, all from *D. pondi* zone.
- Figs. 37–45, 51, 52, 59–61, 67–77 are $\times 2$; the remainder are $\times 1$.



Alzadites by their polygonal costal whorl section, coarse ribbing and tuberculation which persists to the body chamber. Only the later *Protacanthoceras* species that are progenitically derived from other, already diminutive species of the genus come to resemble *Alzadites*.

The evolutionary origin of *Alzadites* lies in some upper Cenomanian acanthoceratine of the US Western Interior lineages, rather than in Old World *Acanthoceras*. There is a marked similarity between the smooth, distantly and feebly ribbed and tuberculate phragmocones of *Alzadites* and the early whorls of certain *Tarrantoceras* Stephenson, 1955 (e.g. Pl. 4, figs. 32 and 33) although these generally have stronger inner ventrolateral tubercles than in the type species of *Alzadites* (Pl. 4, figs. 1–10, 14, 15, 17, 43), more closely resembling the inner whorls of *A. westonensis* gen. et sp. nov. (Pl. 4, figs. 8–39).

Occurrence. *Plesiacanthoceras wyomingense* zone of Montana and Wyoming. Upper Cenomanian *Sciponoceras gracile* zone of Utah.

Alzadites alzadensis gen. et sp. nov.

Plate 4, figs. 1–10, 14–16, 43

Types. Holotype is USNM 423709, paratypes USNM 423710 to 423712; three unfigured paratypes USNM 423713, all from USGS Mesozoic locality 22871, *P. wyomingense* zone.

Dimensions.

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
USNM 423710	16.0 (100)	5.6 (35.0)	7.4 (46.3)	0.76	2.9 (18.1)
USNM 423709	16.6 (100)	6.5 (39.2)	9.5 (57.2)	0.68	2.4 (14.5)
at	14.2 (100)	5.7 (40.1)	7.2 (50.7)	0.79	1.7 (12.0)
USNM 423711	15.6 (100)	6.4 (41.0)	8.3 (53.2)	0.77	2.1 (13.5)
USNM 423712	13.4 (100)	5.7 (42.5)	6.7 (50.0)	0.85	1.7 (12.7)

Diagnosis. *Alzadites* with coarse, blunt ribs on body chamber, where tubercles decline and ultimately disappear.

Description. Coiling involute with small, shallow umbilicus. Umbilical wall low, umbilical shoulder narrowly rounded. Whorl section compressed, with flattened, subparallel flanks, ventrolateral shoulders and venter broadly and evenly rounded. Phragmocone very feebly ornamented. In the best preserved specimen, up to 11 feeble umbilical bullae give rise to low, narrow, prorsiradiate, distant ribs that efface at mid-flank (Pl. 4, figs. 8–10); feeble intercalated ribs are also present. Most if not all ribs bear a feeble inner ventrolateral tubercle. The ribs efface over the venter, where there are outer ventrolateral and siphonal clavi (Pl. 4, figs. 8 and 10). On the adult body chamber, outer flank and ventral ribbing strengthens and coarsens markedly; the ribs are concave on the outer flank and cross the venter in a broad convexity. The ribs bear outer ventrolateral and siphonal clavi at the beginning of the body chamber, but these progressively efface and disappear. The interspaces between ribs are broad and some are deepened into constrictions. There is a great variation in the strength and visibility of ornament, especially on phragmocones.

Suture simple, as for genus.

Discussion. *A. alzadensis* gen. et sp. nov., differs from *A. westonensis* gen. et sp. nov., in the following respects: it is larger, the inner ventrolateral tubercles are much weaker, the body chamber ribbing blunt and restricted to the outer flank whereas that of *A. westonensis* extends to the umbilical seam, is markedly flexuous and sharper, with a pronounced acute ventral chevron and persistent tubercles.

Occurrence. As for types.

Alzadites westonensis sp. nov.

Plate 4, figs. 11–13, 17–39

Derivation of name. From Weston County, Wyoming, where the types were found.

Types. Holotype is USNM 423714, paratypes are USNM 423715 to 423723, 12 unfigured paratypes are USNM 423724, all from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone.

Diagnosis. *Alzadites* with variable, generally strong ribs that arise singly or in pairs from umbilical bullae or intercalate. The ribs are flexuous, with persistent inner ventrolateral tubercles. Outer ventrolateral and siphonal clavi are borne on chevron ribs that persist to the adult body chamber.

Description. Small, adults 15 mm or less in diameter. Coiling involute with small shallow umbilicus, umbilical wall low, rounded, umbilical shoulder narrowly rounded. Whorl section compressed with subparallel flanks and rounded venter in intercostal section; costal section polygonal with greatest breadth at inner ventrolateral tubercle; venter fastigiate. Phragmocone ornament varies from weak to strong. There are thus weak to strong umbilical bullae that give rise to pairs of weak to strong ribs, either singly or in pairs, with occasional intercalated ribs to give a total rib density of around 11 ribs per half whorl in robustly ornamented individuals. The ribs are prorsiradiate and flexuous, and bear weak to strong, conical, inner ventrolateral tubercles that are housed in notches in the umbilical wall of the succeeding whorl (Pl. 4, fig. 38). The ribs sweep forward over the ventrolateral shoulders to clavate inner ventrolateral clavi, linked to turn to strong siphonal clavi at the apex of an acute chevron. This ornament persists onto the adult body chamber. Towards the mature aperture umbilical and ventrolateral tubercles decline first. The adult aperture is preceded by a few crowded ribs that are restricted to the outer flank and venter and lack tubercles. There is a pronounced ventral lappet (Pl. 4, fig. 34).

Suture simple, as for genus.

Discussion. Differences from *A. alzadensis* gen. et sp. nov., are discussed under that species.

Occurrence. As for types.

Alzadites incomptus gen. et sp. nov.

Plate 4, figs. 40–42, 46–48; Plate 6, figs. 1–22

Derivation of name. *Incomptus* (Latin): unadorned.

Types. Holotype is USNM 423725, from USGS Mesozoic locality D12052 as are figured paratypes USNM 423726 and 423727; paratype USNM 423728 is from USGS Mesozoic locality D5249, SE $\frac{1}{4}$ sec. 12, T. 43 S., R. 2 E., Kane County, Utah, Tropic Shale, 9.1–10.7 m (30–35 feet) above base; unfigured paratype USNM 423729 is from USGS Mesozoic locality D5255, NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 32, T. 41, S., R. 7 E., Kane County, Utah, Tropic Shale 4.6–9.2 m (15–30 feet) above base. All *Sciponoceras gracile* zone.

Diagnosis. Small, adult at 12 mm diameter. Phragmocone smooth to feebly to strongly ribbed with blunt umbilical bullae and feeble inner and outer ventrolateral tubercles, interspaces sometimes deepened into constrictions. Tubercles decline on adult body chamber, which is ornamented by delicate prorsiradiate ribs and may be constricted.

Description. The type specimens are rather variable (Pl. 6, figs. 1–22). Coiling is involute, with a small umbilicus, comprising 21–24% of diameter in adults, shallow, with a low, flattened wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with flattened subparallel sides and a rounded venter. Phragmocones vary from smooth (Pl. 6, figs. 10–12) to those with weak umbilical bullae, up to nine per whorl. These give rise to low, blunt, prorsiradiate ribs, singly or in pairs, while shorter, intercalated ribs arise around mid-flank. The ribs are feebly flexed, and strengthen across the flank, crossing the venter in a broad convexity. Interspaces are sometimes deepened into constrictions. Tuberculation is poorly developed, but the most coarsely ribbed individuals develop indications of inner and outer ventrolateral and siphonal tubercles on some ribs. This general style of ornament persists on to the beginning of the adult body chamber, the last part of which is characterized by delicate, flexuous flank ribs that strengthen over the ventrolateral shoulder and venter, are concave on the former and cross the latter in a broad convexity.

Suture with little-divided elements; E narrow, E/L broad and bifid, L shallow and bifid.

Discussion. Weakness of ornament, notably tubercles, plus pattern of ribbing immediately distinguish this species from *A. westonensis* gen. et sp. nov., described above. *A. alzadensis* gen. et sp. nov., is more similar, but has a broader, larger shell with coarser ribbing on the adult body chamber.

Occurrence. As for types.

Alzadites? sp.

Plate 4, figs. 44, 45

Material. USNM 423730 from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone.

Description. Specimen is a phragmocone retaining traces of the original aragonitic shell and is 8.2 mm in diameter. Coiling is involute with $U = 22\%$ of diameter, the umbilical wall low, the umbilical shoulder narrowly rounded. The whorl section is compressed, with flattened subparallel flanks and a rounded venter in intercostal section. Ribs, which number eight per half whorl, are weak and prorsiradiate on the flank but strengthen markedly on the venter where they are high and flared with flattened tops. Occasional unflared intercalated ribs are present. Sutures not seen.

Discussion. We believe this specimen to be pathological. It is slightly asymmetrical in ventral view (Pl. 4, fig. 45), and resembles symmetrical malformed specimens such as *Ammonites salteri* of Sharpe, 1857 (pl. 23, figs. 3 and 5).

Of species present in the same concretion the general shell morphology most closely resembles that of *A. westonense* gen. et sp. nov.

Occurrence. As for material.

Alzadites sp. A.

Plate 4, figs. 53–56

Material. USNM 423732 and 423733 from USGS Mesozoic locality D5780, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 8, T. 5 S., R. 2 E., Socorro County, New Mexico. Lower part of Mancos Shale, Bridge Creek Limestone Beds, second limestone from base. *Sciponoceras gracile* zone.

Description. The largest complete specimen is 18 mm in diameter. All are crushed, with consequent effacement of ornament. In USNM 423732 (Pl. 4, figs. 53–56) the phragmocone is smooth, in USNM 423733 (Pl. 4, figs. 53 and 54) feeble bullae give rise to prorsiradiate primary ribs with shorter intercalated secondaries between, all ribs strengthening over the venter. All specimens show persistent ribbing on the body chamber, with some interspaces deepened and constriction-like.

Discussion. Such of the ornament as is visible recalls that of *A. incomptus* gen. et sp. nov., but poor preservation precludes positive determination.

Occurrence. As for material.

Genus MICROSULCATOCERAS nov.

Derivation of name. Mikros (Greek), small; sulcus (Latin), groove, pertaining to the size and ornament of the shell.

Type species. *Microsulcatoceras puzosiiforme* gen. et sp. nov., *Sciponoceras gracile* zone of Montana.

Diagnosis. Small, adult at 10 mm or less. Compressed, with flattened subparallel sides and rounded venter. On phragmocone distant umbilical bullae give rise to prorsiradiate, straight, primary ribs that terminate in conical inner ventrolateral tubercles. These tubercles link over the venter via a low,

convex rib, followed by a broad, shallow constriction. Tubercles decline on adult body chamber where constrictions strengthen and are flanked by flexuous, prorsiradiate, collar ribs. Sutures unknown.

Discussion. This diminutive genus is quite unlike any other described micromorph. At first sight the presence of flexuous constrictions is suggestive of the superfamily Desmocerataceae Zittel, 1895, notably certain Puzosiinae. The presence of tubercles at such a small size is not, however, a feature of this group (although they may develop at maturity). Instead, we believe the affinities of *Microsulcatoceras* may lie in certain Acanthoceratinae. There is a marked resemblance of the innermost whorls of the *Sumitomoceras* from the *gracile* zone described above to the inner whorls of the new genus (compare Pl. 3, figs. 43–56 and Pl. 4, figs. 59–75): both have prominent umbilical and inner ventrolateral tubercles, but *Microsulcatoceras* lacks the outer, having instead a ventral rib that, although accentuated at the outer ventrolateral position, does not differentiate into a distinct tubercle. Both lack a siphonal tubercle, while certain adult *Sumitomoceras*, including the type, develop deepened, constricted interspaces between the ribs. On the balance of the evidence, we are inclined to regard *Microsulcatoceras* as a progenic dwarf derivative of *Sumitomoceras*.

Occurrence. *Sciponoceras gracile* zone of Montana, Texas, and possibly New Mexico.

Microsulcatoceras puzosiiforme gen. et sp. nov.

Plate 4, figs. 49–52, 65–70

Derivation of name. Puzosiiforme – *Puzosia*-like, from the superficial resemblance to certain *Puzosia* Bayle, 1878.

Types. Holotype is USNM 423734, paratypes USNM 423735 and 423736, from USGS locality 23062, *S. gracile* zone.

Diagnosis. *Microsulcatoceras* with delicately ribbed and constricted body chamber.

Description. Small, adult at 9.5 mm. Coiling evolute with small, shallow umbilicus; umbilical wall low, flattened, umbilical shoulder narrowly rounded. Whorl section compressed with flattened, subparallel flanks and broadly rounded venter. Phragmocone has tiny distant umbilical bullae, 8 per whorl, that give rise to low, prorsiradiate ribs that terminate in blunt inner ventrolateral tubercles linked over the venter by a broad, convex rib. Intercalated ribs with feeble to obsolete inner ventrolateral tubercles are occasionally present. The ribs are succeeded by broad, shallow constrictions, most obvious on the outer flank and over the venter. Tubercles decline on the adult body chamber and constrictions strengthen, extending down to the umbilical wall. The constrictions are prorsiradiate, markedly concave on the outer flank, and slightly flexuous; they are bordered by collar ribs and cross the venter in a broad convexity. Interspaces bear shorter intercalated ribs, most prominent just before the adult aperture.

Sutures not seen.

Discussion. *M. puzosiiforme* gen. et sp. nov., is easily differentiated from *M. crassum* and *M. texanum* gen. et spp. nov., by its delicate body chamber ornament and clearly differentiated constrictions, rather than the coarse decoration of the latter, where constrictions are less well differentiated and umbilical bullae persist.

Occurrence. As for types.

Microsulcatoceras crassum gen. et sp. nov.

Plate 4, figs. 74, 75, 86, 87

Derivation of name. *Crassus* (Latin): thick, referring to the body chamber ornament.

Types. Holotype is USNM 423737, from USGS Mesozoic locality D4628, NW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 11, T. 43. S., R. 2 E., Kane County, Utah, Tropic Shale, from concretions 3 m (10 feet) above base. *Sciponoceras gracile* zone.

Diagnosis. *Microsulcatoceras* with coarse body chamber ornament and persistent umbilical bullae.

Description. Holotype and only known specimen is 13 mm in diameter. Umbilicus small, 33 % of diameter. Whorl section compressed with flattened subparallel flanks and rounded venter. Blunt umbilical bullae give rise to pairs of flexuous prorsiradiate coarse ribs, with occasional shorter, intercalated ribs. All ribs are concave and strengthen markedly on the outer flanks and venter which they cross in a broad convexity. Inner flank ribs decline in strength on the last part of the specimen and ventral ribbing crowds, suggesting it to be adult. Some interspaces are slightly deepened.

Discussion. Coarseness of ornament and persistence of bullae onto the body chamber immediately distinguish this species from *M. puzosiforme*.

Occurrence. As for type.

Microsulcatoceras texanum gen. et sp. nov.

Plate 4, figs. 59–64

Type. USNM 423739 from stream bank 2.4 to 2.9 km southwest of Britton, on and east of the Rogers Farm, Ellis County, Texas, Eagle Ford Group, Britton Formation, *Sciponoceras gracile* zone, ex J. P. Conlin collection.

Diagnosis. Small, adult at 9.5 mm diameter. Phragmocone and early body chamber with distant, feebly bullate primary ribs with strong ventrolateral tubercles linked over the venter by a strong convex rib, and occasional prominent constrictions. Last part of body chamber loses tubercles and develops strong, crowded ventrolateral and ventral ribs.

Discussion. The phragmocone ribbing and tuberculation are much stronger than in *M. puzosiforme*, and persist onto the body chamber; the coarsely ribbed venter immediately preceding the adult aperture is equally distinctive. These features of the body chamber also distinguish the species from *M. crassum* gen. et sp. nov.

Occurrence. As for type.

Microsulcatoceras sp. ?

Plate 4, figs. 71, 72, 73, 84, 85

Material. USNM 423740 from USGS Mesozoic locality D11514, Slate Creek in the NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 36, T. 17 S., R. 18 W., Grant County, New Mexico. Colorado Formation, 9–12 m above flaggy member, *Neocardioceras juddii* zone.

Discussion. This badly preserved specimen is 9.5 mm in diameter. Features suggesting it might possibly be a late species of *Microsulcatoceras* are the presence of periodic constrictions and associated collar ribs on a compressed, flat sided shell, although the ventrolateral tubercles typical of juvenile *Microsulcatoceras* are lacking. It might also possibly be a poorly preserved *Sumitomoceras* or *Pseudocalyoceras*.

Occurrence. As for material.

Genus PLESIACANTHOCERAS Haas, 1964

(= *Paracanthoceras* Haas, 1963, p. 2; non Furon, 1935, p. 59)

Type species. By original designation: *Metoicoceras wyomingense* Reagan, 1924, p. 181, pl. 19, figs. 1 and 2.

Plesiacanthoceras cf. *bellsanum* (Stephenson, 1953)

Plate 6, figs. 26–28

- 1953 *Mammites bellsanus* Stephenson, p. 204 (*pars.*), pl. 49, fig. 3; pl. 51, figs. 8–11.
 1971 *Mammites? bellsanus* Stephenson; Kennedy, p. 122.
 1990 *Plesiacanthoceras bellsanum* (Stephenson, 1953); Kennedy and Cobban, p. 135, pl. 2, figs. 5–8; pl. 12, fig. 9; test-fig. 23c.

Types. The holotype is USNM 105983, paratypes are USNM 105984–6, from the Templeton Member of the Woodbine Formation on a branch of Cornelius Creek, 4.3 km north 50° east of Bells, Grayson County, Texas. One of the syntypes, USNM 105986, is a *Metoicoceras latoventer* Stephenson, 1953. *Plesiacanthoceras wyomingense* zone.

Material. USNM 423741 from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone.

Discussion. *Mammites? bellsanus* is a *Plesiacanthoceras* as discussed by Cobban (1987b) and Kennedy and Cobban (1990). One of the syntypes (Stephenson 1953, pl. 51, fig. 11) has smooth, non-tuberculate innermost whorls. A specimen from USGS Mesozoic locality D5974 also has a smooth nucleus, preceding a strongly ribbed and tuberculate stage that confirm this distinctive ontogenetic development. USNM 423741 has only the faintest traces of ornament to a whorl height of 6 mm. Coiling is very involute with a tiny, deep, conical umbilicus. The whorl section is depressed with flattened, subparallel flanks and a broadly rounded venter; the only decoration is prorsiradiate growth lines. Ornament appears abruptly after this smooth stage. Small umbilical bullae give rise to narrow, straight, prorsiradiate ribs, singly or in pairs, with shorter intercalated ribs. All ribs bear well-developed, conical, inner ventrolateral tubercles, linked by a broad, blunt, prorsiradiate rib to prominent outer ventrolateral clavi. A low, broad, transverse rib links these to a very weak siphonal clavus. When compared to *P. wyomingense* of comparable size (Pl. 6, figs. 36 and 37) the only significant difference is the presence of tubercles in *P. wyomingense* at a stage where *P. bellsanum* is still smooth (compare Pl. 6, figs. 52–54 and Pl. 6, figs. 26–28).

Occurrence. *Plesiacanthoceras wyomingense* zone of north-central Texas and, possibly, *Dunveganoceras pondi* zone of Wyoming.

Genus DUNVEGANOCERAS Warren and Stelck, 1940

Type species. *Acanthoceras albertense* Warren, 1930, p. 21, pl. 1, figs. 1, 2; by original designation.

Dunveganoceras pondi Haas, 1949

Plate 5, figs. 1–5; Plate 6, figs. 43–51

- 1949 *Dunveganoceras pondi* Haas, p. 22, pl. 8, figs. 1–5, 8; pl. 9, figs. 1, 3, 4; pls. 10–14; text-figs. 11–13, 16, 17.
 1979 *Dunveganoceras pondi* Haas; Merewether, Cobban and Cavanaugh, pl. 4.
 1983 *Dunveganoceras pondi* Haas; Cobban, p. 12, pl. 15, fig. 1.

Types. Holotype is AMNH 26416, the original of Haas 1949, pl. 8, fig. 1, pl. 9 figs. 1, 4; Haas mentions 28 specimens that are presumed to be paratypes, all from the basal part of the Cody Shale near Greybull, Wyoming, *Dunveganoceras pondi* zone.

Material. USNM 423742 to 423746 from USGS Mesozoic locality D4466, *Dunveganoceras pondi* zone.

Description. *D. pondi* is a very large species reaching a diameter in excess of 400 mm. It differs from other species of the genus when adult by virtue of having ribs that are depressed over the mid-line of the venter on the mature body chamber. The early whorls are rather poorly known from Haas' original work, but the present series of specimens reveals previously unknown details. The smallest specimen referred to the species is USNM

423744 (Pl. 6, figs. 43–45), only 5 mm in diameter. The shell is globose and highly involute with a depressed, reniform whorl section. The only ornament is distant radial flank ribs, 4 per half whorl, terminating in strong conical inner ventrolateral tubercles. There is no ventral ornament at this small diameter. USNM 423745 is 15 mm in diameter (Pl. 6, figs. 46–48). Coiling is very involute, with a tiny, deep umbilicus and a depressed reniform intercostal whorl section. At the smallest diameter seen the ornament is weak, but strengthens rapidly to give a depressed polygonal costal section. There are 9–10 prorsiradiate primary ribs per whorl that may or may not arise at feeble umbilical bullae and alternate irregularly with shorter intercalated ribs to give a total of 9–10 ribs per half whorl. All ribs bear strong, conical, inner ventrolateral tubercles. A broad blunt rib projects slightly forward to strong, clavate, outer ventrolateral tubercles, linked across the venter by a low, broad, transverse rib. At the smallest diameter visible there is a low siphonal ridge, beyond there is only a faint trace of siphonal clavi. USNM 423746 (Pl. 6, figs. 49–51) is 22 mm in diameter, the coastal whorl section polygonal and depressed, with a whorl breadth to height ratio of 0.86. There are approximately 14–15 coarse ribs on the outer whorl, with umbilical, inner, and outer ventrolateral tubercles as already described; feeble siphonal tubercles are present throughout. USNM 423742 (Pl. 5, figs. 1–3) is 47 mm in diameter, with the following proportions: Wb: 43.6; Wh: 53.4; Wb:Wh: 0.82; U:14.2. There are 17 ribs on the outer whorl corresponding to 8 umbilical bullae that decline markedly as size increases and from which the ribs arise singly or in pairs, with occasional intercalated ribs. Conical inner and clavate outer ventrolateral tubercles are present, but there is no trace of a siphonal row. USNM 423743 (Pl. 5, figs. 4, 5), a fragment with a maximum preserved whorl height of 30 mm, shows a change to clavate inner ventrolateral tubercles and has a pronounced siphonal ridge, accentuated between the outer ventrolateral clavi.

Discussion. The style of ribbing and tuberculation, asymmetry of outer ventrolateral clavi, siphonal ridge and transient siphonal tubercles are all features shared by *Dunveganoceras pondi* and *Plesiacanthoceras wyomingense* of similar size (compare Pl. 6, figs. 36–51 and Pl. 6, figs. 52–54), and there can be little doubt that the former genus gave rise to the latter.

Occurrence. *D. pondi* zone of Wyoming, Montana, Iowa and, possibly, South Dakota, Kansas and Colorado.

Subfamily MAMMITINAE Hyatt, 1900, p. 588
(= Buchiceratinae Hyatt, 1903, p. 26; Metoicoceratidae Hyatt, 1903,
p. 115; Fallotitinae Wiedmann, 1960, p. 741)
Genus METOICOCERAS Hyatt, 1903, p. 115

Type species. By subsequent designation by Shimer and Shrock, 1944, p. 591: *Ammonites swallowi* Shumard, 1860, p. 591.

Metoicoceras sp. A

Plate 5, figs. 10–12, 17–22

Types. Figured specimens USNM 423748–423752, from the Belle Fourche Shale at USGS Mesozoic locality D5947 in Weston County, Wyoming.

EXPLANATION OF PLATE 5

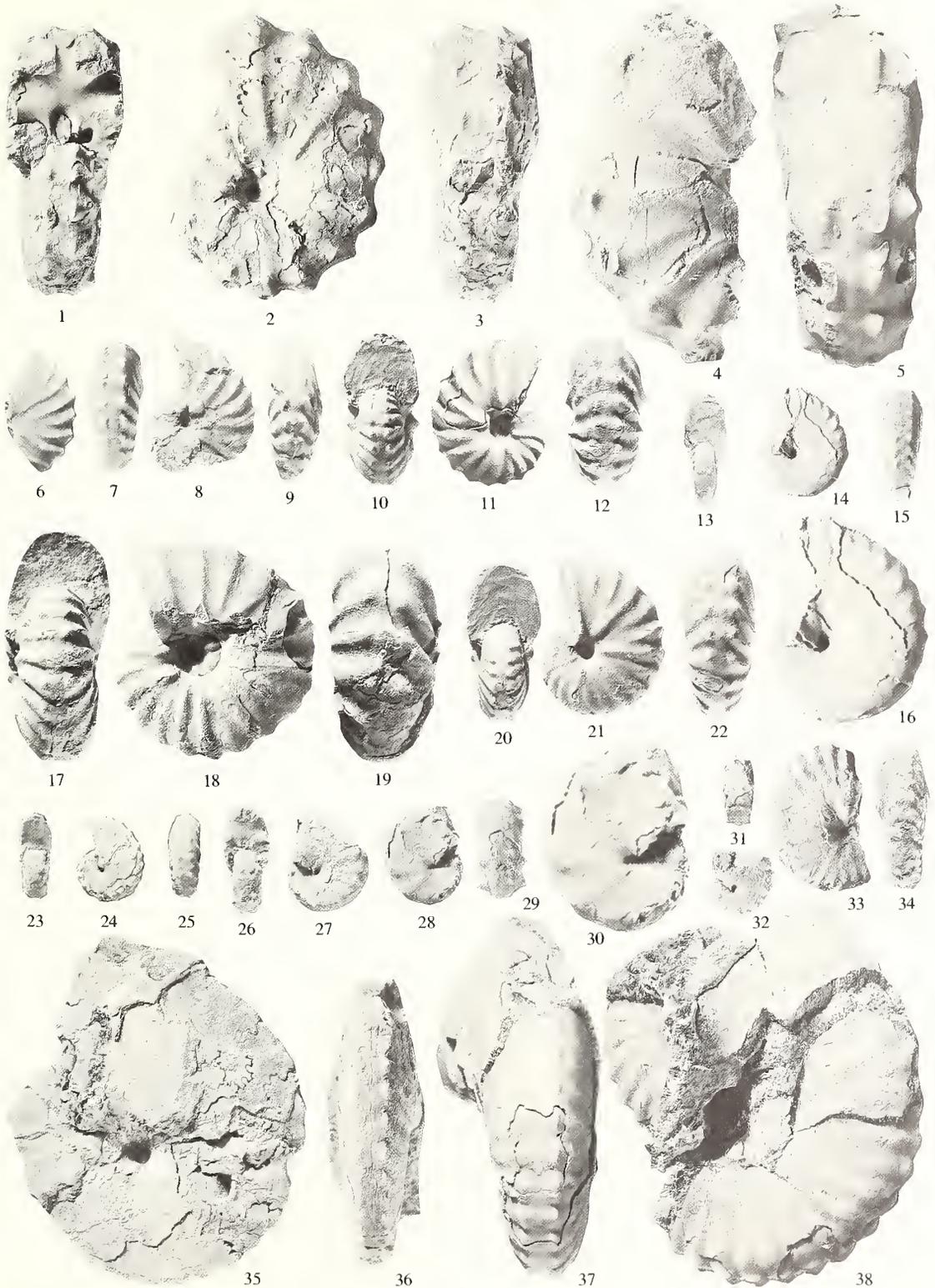
Figs. 1–5. *Dunveganoceras pondi* Haas, 1949. 1–3, USNM 423742; 4, 5, USNM 423743, from USGS Mesozoic locality D4466, *D. pondi* zone.

Figs. 6–9. *Metoicoceras* aff. *praecox* Haas, 1949. 6, 7, USNM 423753; 8, 9, USNM 423754, from USGS Mesozoic locality D4462, *D. pondi* zone.

Figs. 10–12, 17–22. *Metoicoceras* sp. A. 10–12, USNM 423748; 17–19, USNM 423749; 20–22, USNM 423750, all from USGS Mesozoic locality D5947, *D. pondi* zone.

Figs. 13–16, 23–38. *Metoicoceras mosbyense* Cobban, 1953. 13–16, USNM 423757; 23–25, USNM 423758; 26, 27, USNM 423759; 28–30, USNM 423760; 31, 32, USNM 423761; 33, 34, USNM 423762; 35, 36, USNM 423763; 37, 38, USNM 423764, all from USGS Mesozoic locality D8314, *M. mosbyense* zone.

Figs. 16, 28, 29 are $\times 2$; fig. 30 is $\times 3$; the remainder are $\times 1$.



Material. Five well-preserved, uncrushed specimens from a limestone concretion. Much of the shell material is retained.

Dimensions (costal)

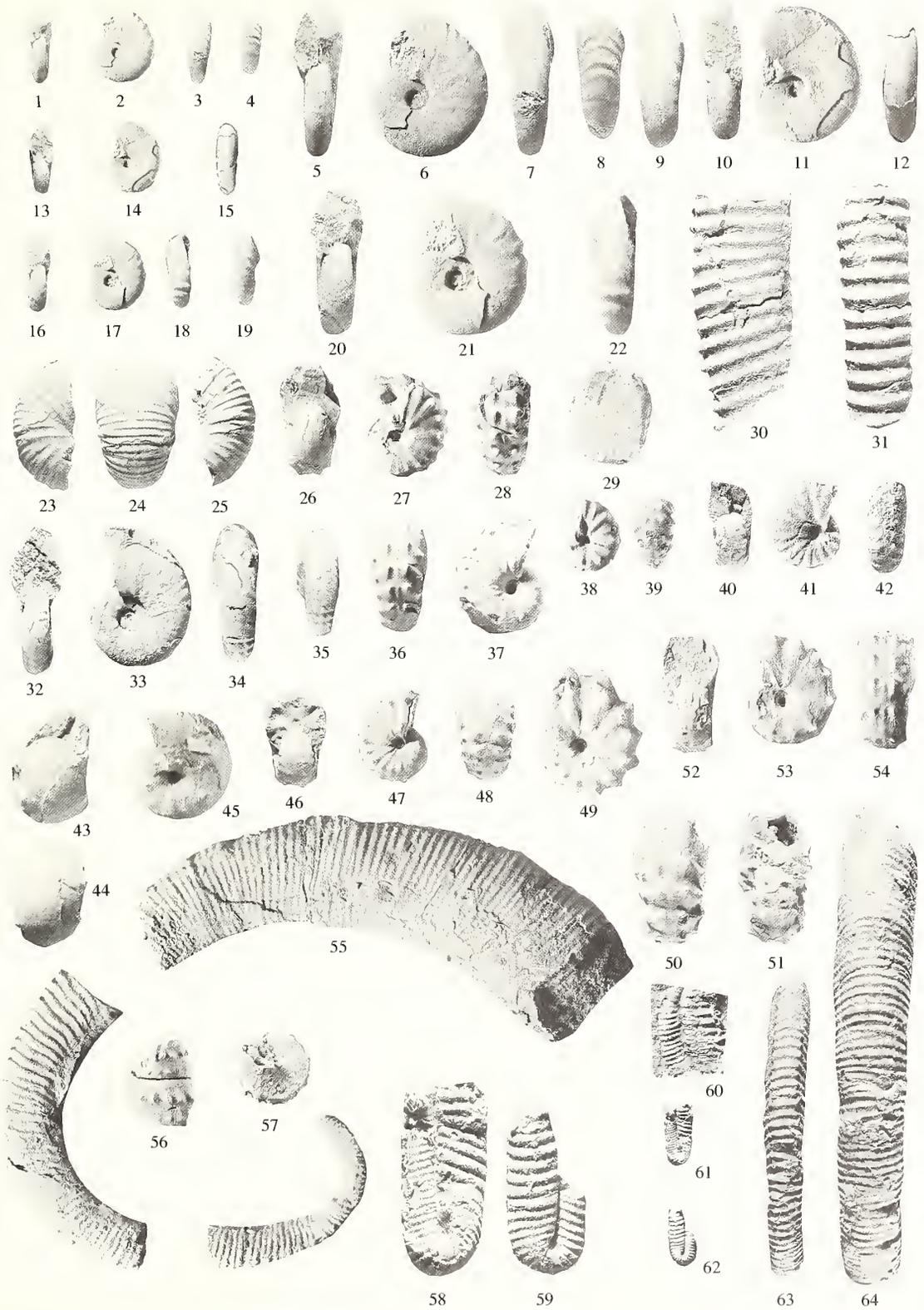
	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
USNM 423748	24.3 (100)	12.6 (51.9)	12.5 (51.4)	1.0	3.4 (14.0)
USNM 423750	25.3 (100)	12.2 (48.2)	14.4 (56.9)	0.85	2.5 (10.0)
USNM 423749	32.7 (100)	15.7 (48.0)	16.3 (49.8)	0.96	6.4 (19.6)

Description. Coiling involute with small umbilicus of moderate depth. Umbilical wall flattened, umbilical shoulder broadly rounded. Intercostal whorl section oval with greatest breadth low on the flanks. Costal section with greatest breadth at umbilical bullae, whorl breadth to height ratio 0.85–1.0, with rounded, convergent flanks and venter concave between outer ventrolateral clavi. There are 20–22 ribs per whorl between 14 and 35 mm diameter. Primary ribs arise at the umbilical seam and may or may not develop from umbilical bullae, from which ribs arise singly or in pairs; intercalated ribs arise around mid-flank. Conical inner ventrolateral tubercles are present at the smallest diameters visible but are lost by 18 mm diameter in larger specimens. All ribs bear strong outer ventrolateral clavi, linked across the venter by a strong transverse rib. A weak siphonal tubercle is present to as much as 25 mm diameter.

Discussion. These specimens closely resemble inner whorls of *Metioceras latoventer* Stephenson, 1953, (p. 209, pl. 53, figs. 1–9; pl. 54, figs. 9–11) from the Woodbine Formation of north Texas in their whorl inflation, ribbing style and presence of a siphonal clavus. The Wyoming specimens differ, however, in the very early loss of inner ventrolateral tubercles, which persist to the end of the adult phragmocone in the Texas material. The early loss of these tubercles is like that of the early whorls of *M. praecox* Haas, 1949, (p. 15, pls. 5–7, text-figs. 5–9). The present material probably represents an undescribed form that we are referring to as sp. A.

EXPLANATION OF PLATE 6

- Figs. 1–22. *Alzadites incomptus* gen. et sp. nov. 1–8, paratype USNM 423726; 10–15, paratype USNM 423727; 9, 16–22, holotype USNM 423725. All specimens are from USGS Mesozoic locality D12052, *Sciponoceras gracile* zone.
- Figs. 23–25. *Scaphites* (*Scaphites*) sp. USNM 423802, from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.
- Figs. 26–28. *Plesiacanthoceras* cf. *bellsanum* (Stephenson, 1953). USNM 423741, from USGS Mesozoic locality D5947, *Dunveganoceras pondi* zone.
- Figs. 29–31. *Hamites salebrosus* Cobban, Hook and Kennedy, 1989. USNM 423786, from USGS Mesozoic locality D8314, *Metioceras mosbyense* zone.
- Figs. 32–35. *Sumitomoceras* sp. USNM 423747, from USGS Mesozoic locality D12052, *S. gracile* zone.
- Figs. 36, 37, 52–54. *Plesiacanthoceras wyomingense* (Reagan, 1924). 36, 37, USNM 388161; 52–54; USNM 388159, from USGS Mesozoic locality 22871, *P. wyomingense* zone.
- Figs. 38–42. *Metioceras* sp. A. 38, 39, USNM 423751; 40–42, USNM 423752, from USGS Mesozoic locality D5947, *D. pondi* zone.
- Figs. 43–51. *Dunveganoceras pondi* Haas, 1949. 43–45, USNM 423744; 46–48, USNM 423745; 49–51, USNM 423746; all from USGS Mesozoic locality D4466, *D. pondi* zone.
- Figs. 55, 63, 64. *Idiohamites bispinosus* sp. nov. Paratype USNM 423793, from the Bighorn Basin of Wyoming, *D. pondi* zone.
- Figs. 56, 57. *Carthaginites aquilonius* sp. nov. Holotype USNM 423801, from USGS Mesozoic locality 12650, *M. mosbyense* zone.
- Figs. 58–62. *Metatyphoceras* spp. 58, 61, USNM 423787; 59, 62, USNM 423789, both from the Lower Turonian part of the Greenhorn Formation on the northeastern flank of the Black Hills in western South Dakota. 60, USNM 423788, from USGS Mesozoic locality D8314, *M. mosbyense* zone.
- Figs. 5–12, 20–22 are $\times 2$; figs. 43–45, 58, 59 are $\times 3$; the remainder are $\times 1$.



Occurrence. Known only from a single concretion at USGS Mesozoic locality D5947 in the NW $\frac{1}{4}$ sec. 14, T. 47 N., R. 65 W., Weston County, Wyoming. Upper Cenomanian zone of *Dunveganoceras pondi*.

Metoicoceras aff. *praecox* Haas, 1949

Plate 5, figs. 6–9; Plate 7, figs. 3–5, 14–16

Compare:

- 1949 *Metoicoceras whitei* Hyatt *praecox* Haas, p. 15, pls. 5–7; text-figs. 5–9.
- 1952 *Metoicoceras praecox* Haas; Cobban and Reeside, p. 1017.
- 1970 *Metoicoceras praecox* Haas; Ilyin, text-fig. 2E.
- 1977a *Metoicoceras* cf. *M. praecox* Haas; Cobban, p. 25, pl. 16, fig. 25; pl. 21, figs. 8 and 9.
- 1981 *Metoicoceras praecox* Haas; Kennedy, Juignet and Hancock, p. 58.

Types. The holotype of *M. praecox* is AMNH 26415, the original of Haas 1949, pl. 5, figs. 1, 5, 8; there are five paratypes, all from the basal part of the Cody Shale 9.7 km east and 11.2 km north of Greybull, Wyoming, in the north-central part of Township 53 N., Range 92 W.

Material. Four specimens, USNM 423753 to 423756, from USGS Mesozoic locality D4462, *Dunveganoceras pondi* zone.

Description. The earliest stages are shown by USNM 423755 and 423756, 18 and 19.5 mm in diameter respectively (Pl. 7, figs. 3–5, 14–16). Coiling is very involute, with a tiny, near-occluded umbilicus. The whorl section is depressed, polygonal in costal section. At the smallest diameter visible there are no umbilical bullae. Faint, straight prorsiradiate ribs arise low on the flank and terminate in conical inner ventrolateral tubercles; the venter is smooth. As size increases the ribs strengthen and total 13 per half whorl. They are alternately long and short, and by 16 mm diameter, weak umbilical bullae appear. The inner ventrolateral tubercles, which dominated ornament at the smallest diameter visible, decline in importance, outer ventrolateral clavi appear and strengthen, and are linked to the inner ventrolateral tubercle by a blunt rib. A low, broad swelling links the outer ventrolateral clavi and bears a weak siphonal clavus (Pl. 7, figs. 5 and 16). Larger specimens show a change to the style of ornament typical of middle growth, with bullate prorsiradiate primary ribs separated by shorter intercalatories to give an estimated 12 ribs per half whorl. The inner ventrolateral clavi are lost by a whorl height of 7 mm, although the outer ventrolateral clavi remain prominent, and the siphonal clavus is present to an estimated 25 mm diameter (Pl. 5, figs. 6–9).

Discussion. The earliest development of ornament of *M. praecox* has not been described, but the innermost whorls of a topotype have the same development of ornament as that of the specimens from locality D4462 except that the inner ventrolateral tubercles are lost at a smaller diameter. Ribs on the inner whorls of topotypes are also broader and more rounded than those on similar-sized specimens from locality D4462. Two of the four specimens from this locality have parts of body chambers, and it is possible that we are dealing with some diminutive species closely allied to *M. praecox*. Until more conclusive material is available, we are referring the specimens from locality D4462 to *M.* aff. *praecox*.

Occurrence. Known from a single limestone concretion in the Belle Fourche Shale in the NE $\frac{1}{4}$ sec. 24, T. 47 N., R. 65 W., Weston County, Wyoming. Probably low in the Upper Cenomanian zone of *Dunveganoceras pondi*.

Metoicoceras mosbyense Cobban, 1953

Plate 5, figs. 13–16, 23–38; Plate 7, figs. 1 and 2

- 1953 *Metoicoceras mosbyense* Cobban, p. 48, pl. 6, figs. 1–14; pl. 7, figs. 1–3.
- 1953 *Metoicoceras muelleri* Cobban, 1953, p. 49, pl. 6, figs. 15, 16; pl. 8, figs. 1–7; pl. 9.
- 1957 *Metoicoceras defordi* Young, p. 1169, pl. 149, figs. 1–8; text-fig. 1A, E, G, I.
- non 1960 *Metoicoceras muelleri* Cobban; Wiedmann, p. 720.
- non 1964 *Metoicoceras muelleri* Cobban; Wiedmann, p. 115.

- non 1967 *Metoicoceras* aff. *mosbyense* Cobban; Collignon, p. 35, pl. 19, fig. 3.
 1970 *Metoicoceras muelleri* Cobban; Ilyin, text-fig. 2b.
 1973 *Metoicoceras* cf. *M. defordi* Young; Cobban and Scott, p. 75.
 1977 *Metoicoceras muelleri* Cobban; Kauffman, p. 258, pl. 21; pl. 22, figs. 17, 18.
 non 1978 *Metoicoceras muelleri* Cobban; Wiedmann and Kauffman, pl. 6, fig. 3.
 1979 *Metoicoceras defordi* Young; Merewether, Cobban and Cavanaugh, pl. 2, figs. 17, 20–22.
 non 1980 *Metoicoceras muelleri* Cobban; Wiedmann, pl. 6, fig. 3.
 1989 *Metoicoceras mosbyense* Cobban; Cobban, Hook and Kennedy, p. 43, figs. 85c–t, 86l, m.

Type. The holotype is USNM 108315, from the Mosby Sandstone Member of the Belle Fourche Shale of east-central Montana, *Metoicoceras mosbyense* zone.

Material. USNM 423757 to 423765, from USGS Mesozoic locality 8314. *M. mosbyense* zone.

Discussion. The present collections show the early development from 8 mm diameter onwards. At this size the coiling is very involute, with a tiny, near-occluded umbilicus (Pl. 5, figs. 13–16, 23–32; Pl. 7, figs. 1 and 2) flank ribs, no umbilical bullae and strong, conical inner ventrolateral tubercles, and weaker, clavate outer ventrolaterals. There is no trace of a siphonal row. As size increases the dominance of the inner ventrolateral tubercles declines and the outer ventrolaterals become more important, while shorter ribs with outer ventrolateral tubercles only alternate with the primaries for a short interval, although all ribs have a complete set of inner and outer ventrolateral tubercles beyond 12 mm diameter.

The largest specimens in the collection are 54 and 62 mm diameter. The former is a compressed individual that has lost its inner ventrolateral tubercles (Pl. 5, figs. 35 and 36); the latter is stouter with more robust ornament and feeble inner ventrolateral tubercles visible to 22 mm whorl height (Pl. 5, figs. 37 and 38).

The early ontogenetic stages of *M. mosbyense* are immediately separable from those of *M. latoventer* and *M. praecox*, which have siphonal tubercles. They are more like those of *M. geslinianum* (d'Orbigny, 1850), where shorter intercalated ribs without inner ventrolateral tubercles may also be present below diameters of 8 mm, and there is an earlier growth stage with prominent spinose inner ventrolateral tubercles only (Pl. 7, fig. 13).

As discussed by Cobban, Hook and Kennedy (1989), mature *M. mosbyense* are dimorphic with the type material of *mosbyense* representing the probable microconch and the type material of *M. muelleri* which is larger, more involute and weakly ornamented, as the macroconch. *M. defordi* Young, 1957 (p. 1169, pl. 149, figs. 1–8; text-fig. 1A, E, G, I) from the Upper Cenomanian of Apache County, Arizona is based on microconchs that we cannot separate from those of *M. mosbyense* and we regard it as a synonym.

Occurrence. *Metoicoceras mosbyense* zone of Montana and Wyoming, south to southwest New Mexico and Arizona, where it is commonly identified as *M. defordi* Young, 1957. Wiedmann (1964, 1980) records the species (as *M. muelleri*) from northern Spain, but his figured specimen belongs to some other species.

Genus CRYPTOMETOICOCERAS nov.

Derivation of name. *Kryptos* (Greek): hidden, referring to the obscure origins of the genus.

Type species. *Cryptometoicoceras mite* gen. et sp. nov., *Dunveganoceras pondi* zone, Wyoming.

Diagnosis. Very small, adult at 12 mm or less. Very involute, with tiny occluded umbilicus. Whorl section as wide as high with flattened, subparallel flanks and broadly arched venter. Phragmocone ornamented by distant, low, broad ribs that terminate at conical inner ventrolateral tubercles at the ventrolateral shoulder. Inner ventrolateral tubercles decline on adult body chamber, small rounded outer ventrolateral tubercles present on first part, thereafter disappearing. Last part of body chamber before aperture with tiny clavi on sharp ventrolateral angles linked across venter by low,

blunt, convex ribs. Suture very simple with elements only slightly incised. E is broad, E/L comparable and asymmetrically bifid, L broad and bifid, L/U₂ and auxiliary saddles on umbilical lobe entire.

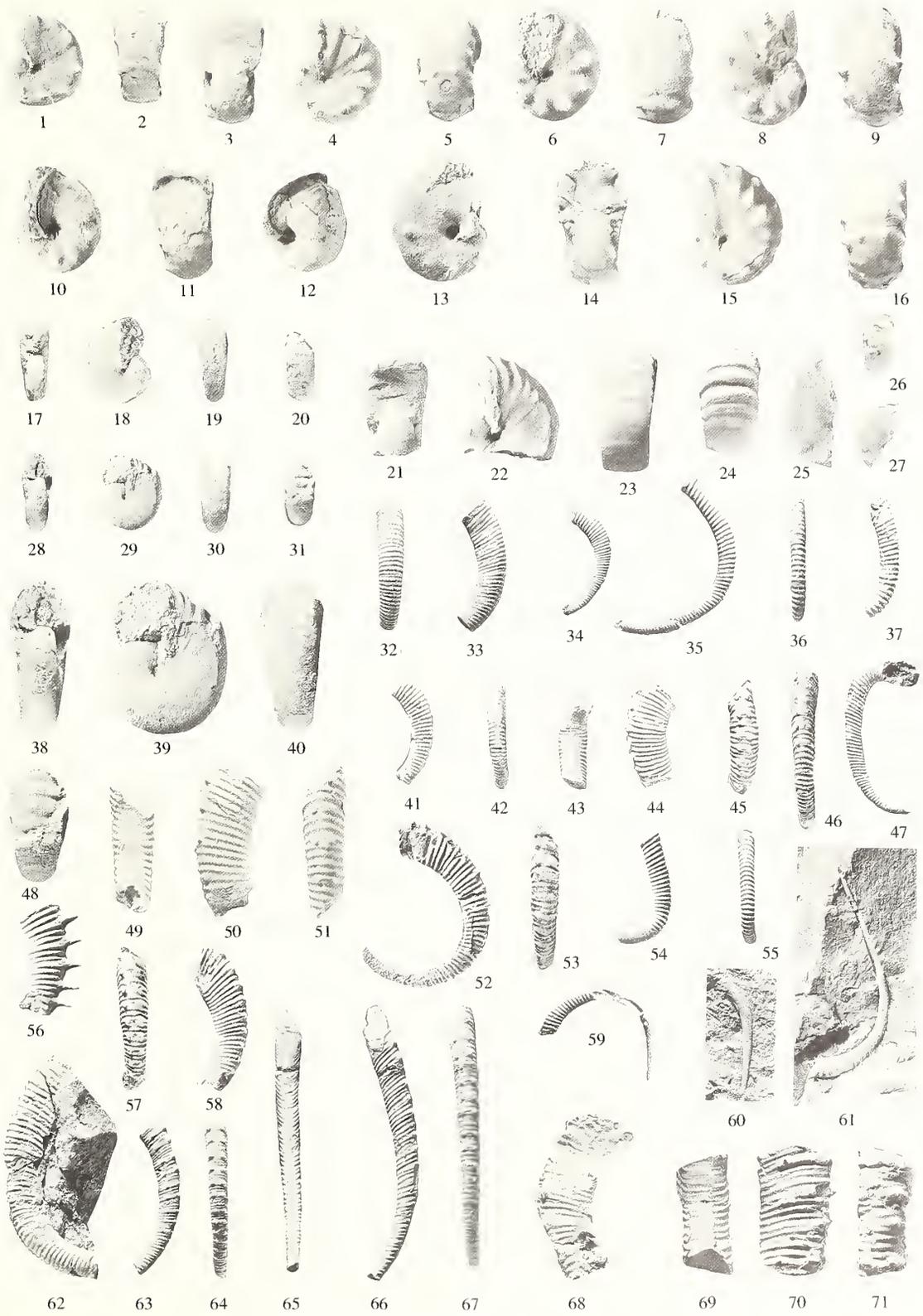
Discussion. This remarkable genus is interpreted as a progenic dwarf derivative of *Metoicoceras praecox*, described above, with which it co-occurs. The earliest ornamented stages of *M. praecox* have conical inner ventrolateral tubercles only, after which outer ventrolateral and siphonal clavi appear (Pl. 7, figs. 3–5, 14–16). In *Cryptometoicoceras* all of the phragmocone corresponds to the first stage, the outer ventrolaterals are only transiently present on the first part of the adult body chamber, after which the distinctive mature ornament appears (Pl. 7, figs. 21–27). The adult *Cryptometoicoceras* is only 12 mm in diameter, the largest *M. praecox* seen are up to 138 mm in diameter.

There can be no doubt that these specimens of *Cryptometoicoceras* are adult, for they show modified body chamber ornament and the holotype has the last few sutures crowded together.

There are obvious similarities to *Nannometoicoceras* Kennedy, 1988 (p. 63, pl. 11, figs. 1–24; text-fig. 8A) with *Metoicoceras acceleratum* Hyatt, 1903 (p. 127, pl. 14, figs. 1–11) from the Upper Cenomanian *Sciponoceras gracile* zone of north-east Texas as type species, a progenic dwarf derivative of *Metoicoceras geslinianum* (d'Orbigny, 1850). Being derived by paedomorphic processes from the same genus they both have adult phragmocones with features of the nuclei of their ancestor. But whereas *Cryptometoicoceras* has only flank ribs and conical inner ventrolateral tubercles, *Nannometoicoceras* has weak to strong, flexuous primary ribs with up to three

EXPLANATION OF PLATE 7

- Figs. 1, 2. *Metoicoceras mosbyense* Cobban, 1953. USNM 423765, from USGS Mesozoic locality 12650, *M. mosbyense* zone.
- Figs. 3–5, 14–16. *Metoicoceras* aff. *praecox* Haas, 1949. 3–5, USNM 423755; 14–16, USNM 423756, both from USGS Mesozoic locality D4462, *Dunveganoceras pondi* zone.
- Figs. 6–9, 13. *Metoicoceras geslinianum* (d'Orbigny, 1850). 6–9, USNM 423773, from USGS Mesozoic locality 23062; 13, USNM 423722, from the Britton Formation 2.25–2.7 km (1.5–1.8 miles) southeast of Britton, Ellis County, Texas, both *Sciponoceras gracile* zone.
- Figs. 10–12. *Buccinanmonites minimus* gen. et sp. nov. Holotype USNM 423770, from USGS Mesozoic locality 23062, *S. gracile* zone.
- Figs. 17–20. *Nannometoicoceras nanos* sp. nov. Holotype USNM 423768, from USGS Mesozoic locality 12740, *M. mosbyense* zone.
- Figs. 21–27. *Cryptometoicoceras mite* gen. et sp. nov. 21–24, holotype, USNM 423766; 25–27, paratype USNM 423767, both from USGS Mesozoic locality D4462, *D. pondi* zone.
- Figs. 28–31, 38–40, 48. *Nannometoicoceras? glabrum* sp. nov. Holotype USNM 423769, from USGS Mesozoic locality D12052, *S. gracile* zone.
- Figs. 32–37, 54, 55, 59–62. *Hamites cimarronensis* (Kauffman and Powell, 1977). 32, 33, USNM 423774; 34, USNM 423775; 35, USNM 423776; 36, 37, USNM 423777; 54, 55, USNM 423779; 59, USNM 423780; 60, USNM 423781; 61, USNM 423782; all from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.
- Figs. 41–47, 49–53, 56–58, 65–68. *Idiohamites bispinosus* sp. nov. 41, paratype USNM 423794; 43–45, paratype USNM 423795; 46, 52, 53, paratype USNM 423796; 47, paratype USNM 423778; 49–51, paratype USNM 423797; 56, paratype USNM 423798; 57, 58, paratype USNM 423799; 65–67, holotype USNM 423792; 68, paratype USNM 423800. Figs. 41–45, 49–51 are from USGS Mesozoic locality D4466, *D. pondi* zone. Figs. 46, 52, 53, 56–58 are from USGS Mesozoic locality D5947, *D. pondi* zone. Figs. 65–67 are from USGS Mesozoic locality 22871, *P. wyomingense* zone. Fig. 68 is from USGS mesozoic locality D4466, *D. pondi* zone.
- Figs. 63, 64, 69–71. *Idiohamites pulchellus* sp. nov. 63, 64, holotype, USNM 423790; 69–71, paratype USNM 423791, both from USGS Mesozoic locality 22871, *P. wyomingense* zone.
- Figs. 1–5, 15–16, 21–25, 38–40, 48–51, 60, 61 are $\times 2$; figs. 6–13 are $\times 3$; the remainder are $\times 1$.



KENNEDY and COBBAN, Cenomanian ammonites

intercalatories, conical inner *and* outer ventrolateral tubercles, the latter projected adaperturally of the former, or tubercles only. Body chambers of *Nannometoicoceras* have primary ribs that are bullate or not with 2–3 intercalatories between, and conical to clavate inner and clavate outer ventrolateral tubercles that persist to the end of the body chamber.

Occurrence. *Dunveganoceras pondi* zone, Wyoming.

Cryptometoicoceras mite gen. et sp. nov.

Plate 7, figs. 21–27

Types. Holotype is USNM 423766; paratype USNM 423767, from USGS Mesozoic locality D4462, *D. pondi* zone.

Derivation of name. *Mite*, small.

Diagnosis. With the characters of the genus.

Description. The holotype is an incomplete adult lacking the adapical part of the body chamber. Its essential characteristics are incorporated in the generic diagnosis. Paratype USNM 423767 is a body chamber fragment of comparable size to the holotype. It has ribs at the adapical end with both inner and outer ventrolateral tubercles, those at the adapical end have lost the outer ventrolateral tubercles and are markedly strengthened, suggesting that this specimen too is an adult.

Occurrence. As for types.

Genus NANNOMETOICOCERAS Kennedy, 1988

Type species. *Metoicoceras acceleratum* Hyatt, 1903, p. 127, pl. 14, figs. 1–11. Upper Cenomanian *Sciponoceras gracile* zone of north-east Texas.

Nannometoicoceras nanos sp. nov.

Plate 7, figs. 17–20

Derivation of name. *Nanos* (Greek): a dwarf.

Types. Holotype is USNM 423768, from USGS Mesozoic locality 12740, *Metoicoceras mosbyense* zone.

Diagnosis. Adult at 12–13 mm diameter. Late phragmocone and early body chamber with conical inner and outer ventrolateral tubercles. Late body chamber with smooth flanks and strong, nontuberculate ventral ribs.

Description. Holotype is a complete adult no more than 13 mm diameter. Coiling very involute with minute, near-occluded umbilicus. Whorl section compressed (whorl breadth to height ratio 0.6 approximately), with flattened, subparallel flanks, narrowly rounded ventrolateral shoulders and a flattened venter. No umbilical bullae on phragmocone or body chamber. Weak, distant, long and short ribs alternate more-or-less regularly. All terminate in a conical inner ventrolateral tubercle, of which there are five or six on the first half of the outer whorl. Corresponding to these are minute, feebly clavate, outer ventrolateral tubercles. Tubercles disappear on last section of body chamber, where there are five broad, blunt ventral ribs preserved just before the adult aperture. Last few sutures are crowded, indicating maturity, and are very simple, with narrow E/L and broad, bifid L.

Discussion. Small size, absence of umbilical bullae and of strong flank and ventral ribs on the greater part of the body chamber immediately distinguish *N. nanos* sp. nov., from the type species *N.*

acceleratum (Kennedy, 1988, p. 67, pl. 11, figs. 1–24; text-fig. 8A). There are obvious similarities to *Cryptometoiceras mite* gen. et sp. nov. (p. 411, Pl. 7, figs. 21–27) which has the same terminal body chamber ornament, but *N. nanos* sp. nov. has inner and outer ventrolateral tubercles on the phragmocone whereas *C. mite* lacks the outer ventrolateral. The adult phragmocone of *N. nanos* sp. nov., closely resembles that of juvenile *Metoiceras mosbyense* (Pl. 7, figs. 1 and 2) of which it is presumed to be a progenic dwarf derivative.

Occurrence. As for type.

Nannometoiceras? glabrum sp. nov.

Plate 7, figs. 28–31, 38–40, 48

Derivation of name. *Glaber* (Latin): smooth.

Type. Holotype is USNM 423769 from USGS Mesozoic locality D12052, *Sciponoceras gracile* zone.

Diagnosis. Small, adult at 11 mm diameter. Phragmocone and early body chamber with distant, conical, outer ventrolateral tubercles followed by a shallow ventral constriction, four on the first half of the outer whorl. Middle section of body chamber with low folds and constrictions, final part with four coarse ventrolateral and ventral ribs, the venter markedly flattened before the adult aperture.

Description. Holotype is adult at 11 mm diameter. Coiling is very involute with a tiny umbilicus. Whorl section compressed with a broadly rounded venter on the phragmocone. Phragmocone and early body chamber smooth except for distant, conical, outer ventrolateral tubercles, four on the first half of the outer whorl. Venter of middle part of body chamber with low folds. Last part of body chamber has flattened venter in costal section, with four coarse, ventral and ventrolateral ribs separated by deep, wide interspaces. Ribs are transverse on the venter, concave on the ventrolateral shoulder, and connected to the umbilicus by a delicate lira.

Sutures not seen.

Discussion. Absence of inner ventrolateral tubercles distinguish this species from all other *Nannometoiceras* and from *Cryptometoiceras mite* gen. et sp. nov. The absence of inner ventrolaterals suggests that, given additional material it might merit subgeneric status within *Nannometoiceras*. There is no clear indication of its evolutionary origins.

Occurrence. As for type.

Genus BUCCINAMMONITES nov.

Derivation of name. *Buccina* (Latin): trumpet, in reference to the trumpet-like flared aperture.

Type species. *Buccinammonites minimus* gen. et sp. nov., *Sciponoceras gracile* zone, southeastern Montana.

Diagnosis. Minute, adult at 4.5 mm diameter. Very involute with tiny umbilicus. Whorl section depressed with flattened subparallel flanks, venter broadly rounded. Five ribs per half whorl on the phragmocone are broad and coarse and terminate in strong conical inner ventrolateral tubercles. This style of ornament persists onto the first part of the adult body chamber. Aperture preceded by narrow crowded ribs with minute ventrolateral tubercles. Mouth border with flare that extends out for 30% of the whorl height in a trumpet-like aperture. Suture with very simple, little-incised bifid elements.

Discussion. Minute size, simple ornament and the extraordinary flared aperture distinguish *Buccinammonites* gen. nov., from all other described taxa. The coiling and proportions of the

phragmocone whorls recall those of *Cryptometoicoceras* gen. nov., but the body chamber ornament is utterly distinctive. Like *Nannometoicoceras* and *Cryptometoicoceras*, the phragmocone ornament of *Buccinanmonites* indicates that it is a progenic dwarf derivative of some other metoicoceratine, but whether this was *Metoicoceras* (Pl. 7, figs. 1–9, 14–16) where the earliest ornamented stage has only flank ribs and inner ventrolateral tubercles or the already dwarf *Nannometoicoceras* or *Cryptometoicoceras*, we cannot say.

Occurrence. As for genus.

Buccinanmonites minimus gen. et sp. nov.

Plate 7, figs. 10–12

Derivation of name. *Minimus* (Latin): least.

Types. Holotype USNM 423770, paratype USNM 423771, from USGS Mesozoic locality 23062, *Sciponoceras gracile* zone.

Diagnosis. With the characters of the genus.

Discussion. The holotype is a complete adult showing all the diagnostic features of the species. Paratype USNM 423771 is incomplete at 4.8 mm diameter and has shallow constrictions.

Occurrence. As for types.

Suborder ANCYLOCERATINA Wiedmann, 1966, p. 54

Superfamily TURRILITACEAE Gill, 1871, p. 3

Family HAMITIDAE Gill, 1871, p. 3

Genus HAMITES Parkinson, 1811, p. 145

(= *Torneutoceras* Hyatt, 1900, p. 586 (objective synonym); *Stomohamites* Breistroffer, 1940, p. 85; *Hamitella* Breistroffer, 1947, p. 100 (84) *nom. nov. pro. Helicoceras* d'Orbigny, 1842, p. 611, *non* Koenig, 1825, pl. 19).

Type species. *Hamites attenuatus* J. Sowerby, 1814, p. 137, pl. 61, figs. 4 and 5, by the subsequent designation of Diener 1925, p. 65.

Hamites cimarronensis (Kauffman and Powell, 1977)

Plate 7, figs. 32–37, 54, 55, 59–62

1953 *Hamites?* sp. Stephenson, p. 197.

1977 *Stomohamites simplex cimarronensis* Kauffman and Powell, p. 97, pl. 9, figs. 1, 3, 4; text-figs. 5 and 6.

1990 *Hamites cimarronensis* (Kauffman and Powell, 1977); Kennedy and Cobban, p. 140, pl. 15, figs. 11, 13, 15, 17, 19–21.

Type. Holotype is USNM 167160, the original of Kauffman and Powell 1977, pl. 9, fig. 1, from USGS Mesozoic locality 30235 in Cimarron County, Oklahoma, and from the Hartland Member of the Greenhorn Limestone, late Cenomanian.

Material. More than 100 fragments from USGS Mesozoic localities D5947, D4462, D4466 and D22871, *Plesiacanthoceras wyomingense* to *Dunveganoceras pondi* zones.

Discussion. Fragments of this species are very common in the present collections. The very earliest developmental stages generally lack the protoconch and consist of a straight, smooth, slowly expanding shaft up to 12 mm long (Pl. 7, figs. 59–61). This shaft is terminated by a curved section,

at which point ribbing develops. The largest fragment seen has a whorl height of 10 mm, and is part of a curved portion (Pl. 7, fig. 62). It and fragments of intermediate size suggest an elliptical coiling with at least three shafts. Ornament consists of fine, dense, prorsiradiate ribs that are weakest on the dorsum and strongest over the venter, straight to feebly convex, with a rib index of 6–8. Most of the material is much smaller than that of the European *H. simplex* d'Orbigny, 1842 (p. 550, pl. 134, figs. 12–14) making comparison difficult, but large fragments are always much more densely ribbed than the comparable stage of *H. simplex*.

Occurrence. Widespread in the US Western Interior from Montana and Wyoming south to New Mexico and northeast Texas, ranging from *Conlinoceras tarrantense* to *Dunveganoceras pondi* zones.

Hamites salebrosus Cobban, Hook and Kennedy, 1989

Plate 6, figs. 29–31

1989 *Hamites salebrosus* Cobban, Hook and Kennedy, p. 57, fig. 95bb, cc, ii.

Type. Holotype is USNM 423786 from USGS Mesozoic locality D12069 in Apache County, New Mexico, Twowells Sandstone Tongue of Dakota Sandstone, *Metoicoceras mosbyense* zone.

Material. USNM 423786 from USGS Mesozoic locality D8314. *M. mosbyense* zone.

Description and Discussion. Specimen is a body chamber fragment 46 mm long with a maximum preserved whorl height of 17.5 mm. The whorl section is a compressed oval with a whorl breadth to height ratio of 0.7. The rib index is 5, the ribs weakened somewhat on the dorsum but strengthening across the flanks, where they are straight and prorsiradiate, and passing straight across the venter. Large size, coarse ribbing, compression and low rib density distinguish *H. salebrosus* from all other described species.

Occurrence. *Calycoceras canitaurinum* and *M. mosbyense* zones, New Mexico, Arizona and Wyoming.

Genus METAPTYCHOCERAS *Spath*, 1926, p. 80

Type species. *Ptychoceras smithi* Woods, 1896, p. 74, pl. 2, figs. 1 and 2, by original designation.

Metaptychoceras spp.

Plate 6, figs. 58–62

Compare:

1977 *Hemiptychoceras* sp. Kauffman and Powell, p. 99, pl. 9, fig. 5; text-fig. 7.

Material. USNM 423788, from USGS Mesozoic locality D8314, *M. mosbyense* zone; USNM 423787 and 423789 from the Greenhorn Formation of western South Dakota.

Discussion. USNM 423788 is an external mould of two shafts, with a maximum preserved length of 7.5 mm. The smaller shaft is curved and ornamented by strong, straight, weakly prorsiradiate ribs; the rib index is 4–5. The larger shaft has coarser ribs; the rib index is 5. *Metaptychoceras* is generally uncommon in the US Western Interior. It occurs in the middle Cenomanian of Oklahoma (Kauffman and Powell 1977) and Wyoming (the present record), *C. canitaurinum* zone of New Mexico, *S. gracile* zone of Colorado and northeast Texas, lower Turonian of the Dallas area in Texas and the northeast flank of the Black Hills in western South Dakota (Pl. 6, figs. 58, 59, 61, 62) and is locally frequent in the upper Turonian in the Waco area in central Texas and Chispa Summit in Trans-Pecos Texas.

Family ANISOCERATIDAE Hyatt, 1900, p. 587
 (= Algeritidae Spath, 1925, p. 190)
 Genus IDIOHAMITES Spath, 1925

Type species. *Hamites tuberculatus* J. Sowerby, 1818, p. 30, pl. 216, figs 4 and 5, by original designation.

Idiohamites pulchellus sp. nov.

Plate 7, figs. 63, 64, 69–71

1973 *Idiohamites* sp. Cobban and Scott, p. 50, pl. 13, figs. 1–4.

Derivation of name. Diminutive of *pulcher* (Latin): beautiful.

Types. Holotype is USNM 423790, paratype is USNM 423791, from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Diagnosis. Compressed *Idiohamites* with narrow prorsiradiate ribs, rib index 9. Periodically strengthened ribs have sharp lower lateral and ventrolateral tubercles, typically with 3–4 non-tuberculate ribs between.

Discussion. The holotype is a slightly curved fragment 25 mm long and shows a transition from an initially bituberculate section. Paratype USNM 423971 is much larger, with a whorl height of 11.5 mm and a rib index of 9, showing the same differentiation into stronger tuberculate ribs separated by up to five non-tuberculate ones. *I. pulchellus* sp. nov., is easily distinguished from *I. bispinosus* sp. nov., to be described below, which is the only other species known from the Western Interior, and which lacks lateral tubercles.

Occurrence. *Conlinoceras tarrantense* and *Acanthoceras muldoonense* zones of southeastern Colorado, *Plesiacanthoceras wyomingense* zone of Montana.

Idiohamites bispinosus sp. nov.

Plate 6, figs. 55, 63, 64; Plate 7, figs. 41–47, 49–53, 56–58, 65–68

Types. Holotype is USNM 423792, from USGS Mesozoic locality 22871, *P. wyomingense* zone. Paratypes USNM 423796, 423798 and 423799 are from USGS Mesozoic locality 5947; paratype USNM 423800 is from USGS Mesozoic locality D4466; paratypes USNM 423794, 423795 and 423797 are from USGS Mesozoic locality D4462; paratype USNM 423793 is from the Bighorn Basin of Wyoming; all from the *Dunveganoceras pondi* zone.

Diagnosis. Planispirally coiled in an open ellipse. Whorl section compressed oval with crowded, prorsiradiate, feebly convex ribs. One, sometimes two, linked ribs bear sharp ventrolateral tubercles on moulds that are the bases of septate spines linked across the venter by a pair of looped ribs. There are 1–3 non-tuberculate ribs between the tuberculate ones.

Discussion. Specimens range from 2 to 10 mm whorl height. At the smallest sizes there may be some irregularities in ribbing with up to five non-tuberculate ribs between tuberculate ones, and the very earliest stages may lack tubercles. The septate spines are perfectly preserved in USNM 423798 (Pl. 7, fig 56).

What may be an adult of the species is represented by USNM 423793, from the Upper Cenomanian *Dunveganoceras pondi* zone near Greybull, Wyoming (Pl. 6, figs. 55, 63, 64). The three fragments illustrated were originally part of a single specimen. The smallest piece closely resembles the type series. The middle piece, from a whorl height of 8.5 to 13 mm has a rib index of 8, the ribs

flexuous and prorsiradiate, and nearly all with a ventral tubercle. The largest fragment, preserved to a whorl height of 22 mm has a rib index of 16, with tuberculate ribs separated by up to three non-tuberculate ones on the first part, after which the ribs are all non-tuberculate for the final 65 mm.

Absence of lateral tubercles easily distinguishes *I. bispinosus* sp. nov., from *I. pulchellus* sp. nov., the only other species known from the Western Interior.

Occurrence. *Plesiacanthoceras wyomingense* and *Dunveganoceras pondi* zones of Wyoming and Montana.

Family TURRILITIDAE Gill, 1871, p. 3
 (= Pseudhelicoceratinae Breistroffer, 1953, p. 1350)
 Genus CARTHAGINITES Pervinquière, 1907, p. 96

Type species. *Turrilites (Carthaginites) kerimensis* Pervinquière, 1907, p. 101, pl. 4, fig. 18.

Carthaginites aquilonius sp. nov.

Plate 6, figs. 56 and 57

Derivation of name. *Aquilonius* (Latin): northerly.

Type. Holotype is USNM 423801 from USGS Mesozoic locality 12650, *Metoicoceras mosbyense* zone.

Description. Specimen consists of one and a quarter whorls, with a maximum preserved whorl height of 6.9 mm. Apical angle low, with seam between successive whorls only slightly indented. 17–18 low, broad, prorsiradiate ribs arise at the upper edge of the outer whorl face and strengthen into small, sharp tubercles a little above the middle of the outer whorl face. A broad, smooth, depressed zone separates these from a row of small, blunt, aperturally displaced tubercles low on the outer whorl face. These show feeble spiral elongation and lie at a sharp angulation in the whorl profile and pronounced facet that extends to the lower edge of the outer whorl. The sharp edge between outer and lower whorl faces is feebly crenulate, the crenulations corresponding in position and number to the lowest row of tubercles.

Discussion. The imperfectly exposed suture shows E/L occupying the upper outer and part of the upper whorl face, confirming this as a *Carthaginites* rather than *Neostlingoceras*. The presence of strong tubercles immediately distinguishes it from *C. krorzaensis* Dubourdieu, 1953 (p. 66, pl. 49, figs. 49–52; text-fig. 20). *C. kerimensis* Pervinquière, 1907, (p. 101, pl. 4, fig. 18) is based upon a minute specimen with only 6–7 mid-flank tubercles per whorl, and no lower row. *Carthaginites virdense* Cobban, Hook and Kennedy (1989) has 12–13 tuberculate ribs in the upper row, and those in the lower row twice as numerous.

Superficially similar is *Neostlingoceras kottlowski* Cobban and Hook, 1981 (p. 26, pl. 4, figs. 1–28), which has a third row of tubercles on the underside of the whorl.

Occurrence. As for type.

Superfamily SCAPHITACEAE Gill, 1871, p. 3
 (*nom. transl.* Wright and Wright, 1951, p. 13, *ex* Scaphitidae Gill, 1871, p. 3)
 Family SCAPHITIDAE Gill, 1871, p. 3
 Subfamily SCAPHITINAE Gill, 1871, p. 3
 (*nom. transl.* Wright, 1953, p. 473, *ex* Scaphitidae Gill, 1871, p. 3)
 Genus and subgenus SCAPHITES Parkinson, 1811, p. 3.

Type species. *Scaphites equalis* J. Sowerby, 1813, p. 53, pl. 18, figs. 1–3.

Scaphites (Scaphites) sp.

Plate 6, figs. 23–25

Material. USNM 423802, from USGS Mesozoic locality 22871, *Plesiacanthoceras wyomingense* zone.

Description. Specimen is a wholly septate fragment of less than half a whorl with a maximum preserved whorl height of 9 mm. Coiling very involute, with a depressed, reniform whorl section. Narrow primary ribs arise at the umbilical seam and secondary ribs are inserted between them, both high and low on the flank. Ribs are narrow, straight and prorsiradiate, and cross the venter nearly straight. The last half of the fragment bears small, conical, ventrolateral tubercles on four out of nine primary ribs. Each tubercle gives rise to a pair of ribs that loop across the venter to the tubercle on the other flank.

Discussion. This is the only *Scaphites (Scaphites)* known from the Western Interior below the zone of *Sciponoceras gracile* (see Cobban, 1952 for details).

Occurrence. As for material.

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AN APPLICATION OF CRITICAL POINT DRYING TO THE COMPARISON OF MODERN AND FOSSILIZED SOFT TISSUES OF FISHES

by DAVID M. MARTILL *and* LIZ HARPER

ABSTRACT. Critical-point-dried samples of recent biological soft tissues can be used to make accurate comparisons with exceptionally well-preserved fossil material. This technique has distinct advantages over thin sections of biological tissues, as palaeontologists are often more familiar with observing three-dimensionally preserved material. This technique offers important opportunities for comparative taphonomic and anatomical studies, especially for palaeontologists working with exceptionally well-preserved soft tissues such as may be found in early diagenetic concretions.

CRITICAL point drying (CPD), the drying of biological tissues at the critical temperature and pressure of carbon dioxide, is a technique which allows the examination in three dimensions of soft tissues under a vacuum, and hence is ideal for scanning electron microscopy (SEM). The technique produces a minimum of artefacts during the drying process compared with freeze drying and drying in air, and the CP-dried tissues may be coated with a variety of electrically conductive materials.

Biological specimens dried in air are greatly distorted by surface tensional processes, unless they are composed of particularly rigid biopolymers such as chitin. CPD involves taking the liquid in which a specimen is immersed to its critical point; that is the temperature (T_c) and pressure (P_c) at which the liquid changes imperceptibly from a liquid to a gas (or vice versa). At this point, surface tension is zero, and fluid may be released from the tissue causing a minimal amount of morphological change. The procedure is based on Anderson (1951), who also describes in more detail the principles behind the method. An alternative to CPD is freeze drying (Boyde 1974). Freeze drying offers excellent opportunities for examining fractured surfaces, but it also has a number of serious drawbacks, including severe tissue damage due to ice crystal formation (Hayat 1978), and we do not recommend its use here.

We demonstrate an application of CPD to a palaeontological problem, an attempt to resolve an early diagenetic event preserved in pre-compaction concretions. Martill (1988) suggested that the preservation of phosphatized soft tissues in Cretaceous fishes from the Santana Formation of Brazil took place very rapidly, and prior to burial. Since burial rates in the deposit are unknown, however, the time interval in which phosphatization took place is also unknown. The soft tissues discovered by Martill show a number of features related to the decomposition and collapse of the tissues. Thus it was believed that phosphatization accompanied active decay rather than post-dating a physico-chemically induced interruption of the decomposition process, but this supposition remained to be tested.

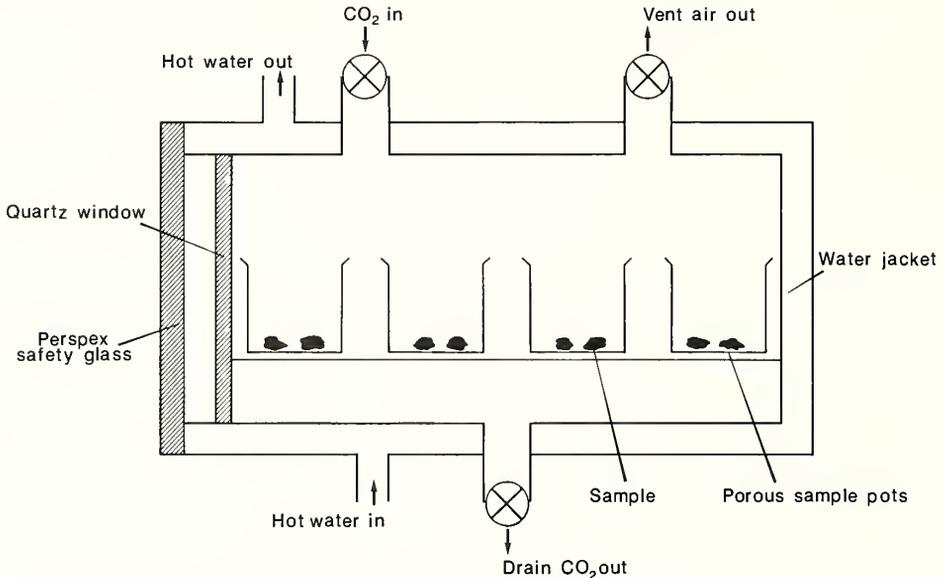
On this basis, it should be possible to mimic decomposition processes taking place on the sea floor under laboratory conditions, to sample the decaying tissue at various intervals, and observe changes in tissue morphology with time. CP-dried samples of partly decomposed tissue could then be examined using the SEM, and direct comparisons made between recent and fossil material.

METHOD

A rainbow trout (*Salmo gairdneri* Richardson), 20 cm in length, was killed and placed in a bath of fresh sea water with a specific gravity of 1.02 (normal salinity). Samples of striated muscle, gill filament with secondary lamellae, and ovaries were removed at death. Further samples were removed at hourly intervals up to 4 hours.

and then at 6 hours, 24 hours, 48 hours, and 7 days. The experiment was carried out at room temperature in a fume cupboard.

The samples of tissue were immediately fixed for 1.5 hours in 1% osmium tetroxide buffered in phosphate at pH 7.2 to prevent further post-mortem degradation. After two washes in the buffer the tissue was dehydrated by immersion in a series of acetones (30%, 50% – 10 minutes each, then 70%, 85%, 90%, 95%, and 100% for 15 minutes each). The 100% acetone wash was repeated. At this stage all the water in the tissue had been replaced by acetone (alternative methods of dehydration use ethanol or freons, as described by Cohen 1979). The samples were then placed in porous vessels flooded with acetone, and loaded into the CP-drying bomb (text-fig. 1). This was then filled with liquid carbon dioxide and flushed through three or four times over a 3.5 hour period to expel all the acetone from the samples, replacing it with CO₂. The half-filled bomb was gently heated to bring the CO₂ to its critical point and then vented ($T_c = 31^\circ\text{C}$, $P_c = 72.9$ atmospheres). Biological tissues cannot be CP-dried using water as the ambient fluid as the higher temperature and pressure required is not practical (water $T_c = 374^\circ\text{C}$, $P_c = 217.7$ atmospheres). The CP-dried samples were sputter-coated with gold and examined using a Hitachi S-520 SEM at 20 kV.

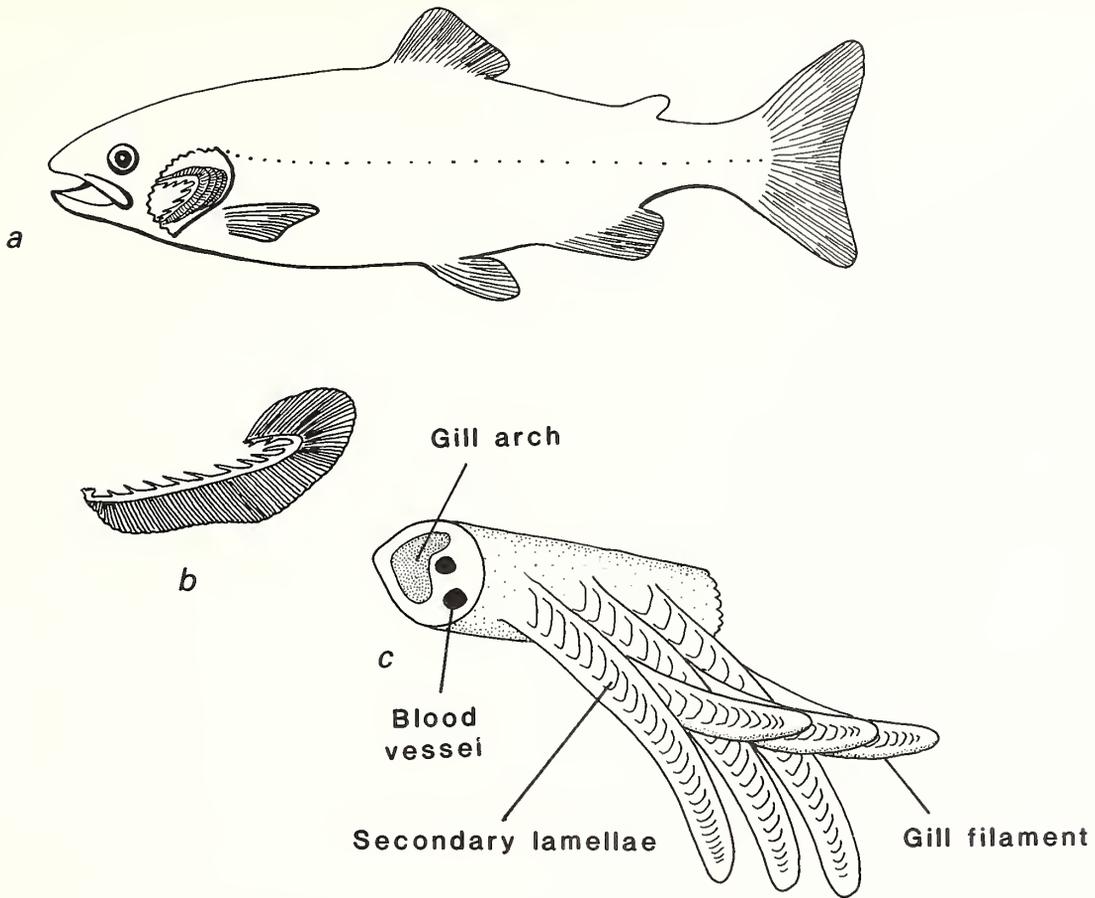


TEXT-FIG. 1. Schematic diagram of the critical point-drying bomb. Samples are placed in porous beakers supported on a boat. The apparatus is heated by a hot water circulatory system. CO₂ enters through a regulatory valve. The operation can be observed through a clear Perspex safety shield in front of a silica window.

Fossilized soft tissues were obtained from teleost fish in pre-compaction concretions from the Santana Formation (Lower Cretaceous, Aptian/Albian), of the Chapada do Araripe, Ceara, north-east Brazil. They were prepared by partial digestion in 10% acetic acid so that the fish skeleton remained partly within the concretion. This allows the soft tissues to be more readily identified since they remain *in situ* within the fossil. The fossil material was also sputter-coated with gold and examined on the same SEM, but at 15 kV to minimize beam damage (*note*: high kV at high magnifications have been found to damage some phosphatized soft tissues).

RESULTS

The morphology of all the recent CPD soft tissues examined changed with time after death. Here we discuss only the gill filaments and associated secondary lamellae (text-fig. 2). In the recent samples, secondary lamellae of the gills at time zero are erect and well spaced (plate 1, fig. 1). At high magnification, detail on the surface of individual cells is seen at time zero, but this begins to break down after only one hour (plate 1, fig. 8). As time of decay progresses, individual secondary



TEXT-FIG. 2. Diagram showing position of secondary lamellae and gill filaments in the rainbow trout (*Salmo gairdneri*). *a*, Trout with operculum removed to reveal gill arches. *b*, Single gill arch with gill filaments. *c*, Detail of gill arch with three filaments showing position of secondary lamellae. Based loosely on Hughes and Morgan (1973).

lamellae collapse, possibly due to lack of blood pressure and also because of gravity (plate 1, fig. 3). This collapse produces a prominent kink at the base of each lamella (plate 1, fig. 9). After two hours, the epithelial cells of the recent secondary lamellae begin to detach, leaving only a connective tissue lining (plate 1, fig. 6). Epithelial tissue covering the gill ray begins to detach from the gill ray after four hours. A similar detachment is also seen in the fossil material (plate 1, fig. 4). Gills sampled after seven days show very little identifiable soft tissue remaining. However, bone surfaces show numerous colonies of microorganisms, including spherical and rod-shaped bacteria (plate 1, fig. 10).

A large number of the fossil gills show kinks at the base of each lamella (plate 1, fig. 7a, b), although many of the fossil secondary lamellae are preserved fully erect and well spaced (plate 1, fig. 2a, b). Individual epithelial cells are only rarely preserved in the fossil material, but they can sometimes be seen on the surface of gill rays. They do not show details of cell wall ultrastructure, but this may be because of an inability of this preservational style to resolve these features.

DISCUSSION

Timing of phosphatization

Results of the experimental decomposition of the trout show that very rapid morphological change occurs in delicate soft tissues such as gill filaments and secondary lamellae. The exceptional preservation of these tissues in fossil fish from the Santana Formation, together with the preservation of artefacts brought about by decomposition, show that phosphatization was clearly an extremely early and rapid diagenetic event. Temperature and salinity are likely to have been major influences controlling the rate of reactions and hence rate of decay of the fossil fish. The temperature of the Santana sea floor has yet to be determined isotopically, but its position within the palaeo-tropics, and its generally shallow aspect suggest warm, rather than cold, bottom-water conditions. Present-day salinity has been assumed for the Santana Formation for the purpose of this experiment, although a number of authors have considered the salinity to range from fresh to hypersaline (see Martill 1988 for a review).

Comparisons between Recent and fossil material at normal salinity and room temperature suggest that phosphatization must have taken place within the first five hours of death of the fish, although preservation of epithelial cells in place suggests a possibly earlier event, *c.* 1–2 hours. This indicates that very high concentrations of dissolved phosphate were available for rapid precipitation on to nucleating sites. Although the oxygen level of the Santana sea floor is not known precisely, the presence of arthropods and rare molluscs shows that anoxia had not been reached. However, Allison (1988) has shown that most carcasses in marine environments undergo anoxic decomposition even in well-oxygenated water. We therefore assume that oxygen levels are not as important as hitherto believed.

Use of CPD by palaeontologists

This example shows how critical point drying can be used to help solve a specific palaeontological problem, in this case, one of taphonomic and diagenetic importance. However, there are numerous other taphonomic, taxonomic, and palaeobiological applications for the technique. Palaeobotanists

EXPLANATION OF PLATE I

Comparison between fossil soft tissues and recent trout gills after various times of decomposition. (Fossil material prefixed DM is currently held by the first author at the Open University, but will be transferred to the University of Leicester, Department of Geology.)

Fig. 1. Section of CPD fresh trout gill filament with erect secondary lamellae, $\times 150$.

Fig. 2. DM 50. *a*, Section of fossil gill filament from Santana Formation, $\times 150$. *b*, Detail of four erect fossil secondary lamellae showing preservation fabric of phosphatic microspheres, $\times 700$.

Fig. 3. Three CPD trout gill filaments after one hour of decomposition. Two of the filaments show detached portions of epithelial cells revealing connective tissue lining of blood vessels, $\times 70$.

Fig. 4. DM 63. Fossil gill filaments showing same features observed in fig. 3, $\times 70$.

Fig. 5. CPD trout gill filament after one hour of decomposition, with post-mortem break-up following boundary between epithelial cells, $\times 300$.

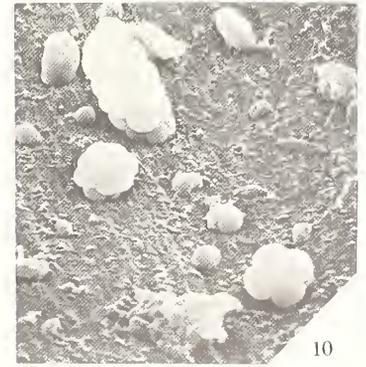
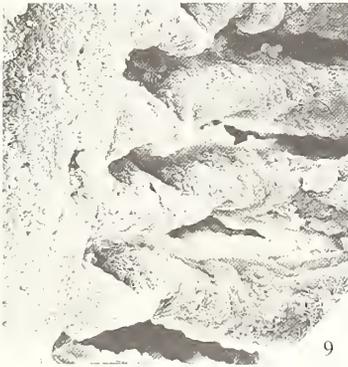
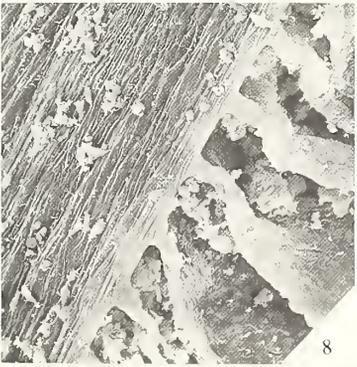
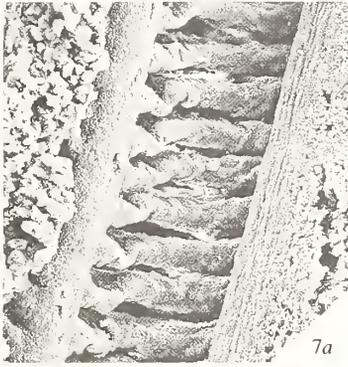
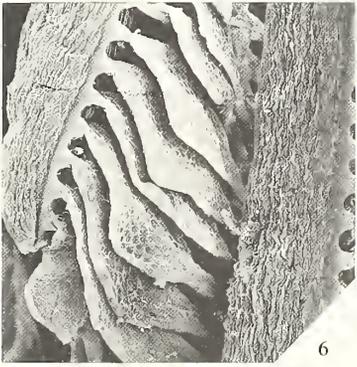
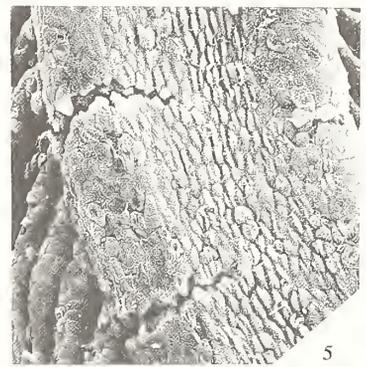
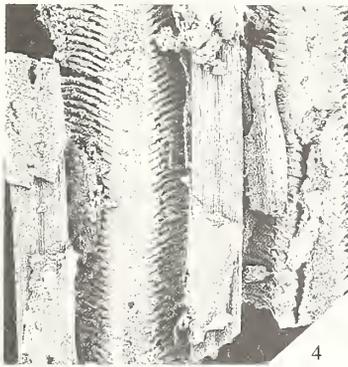
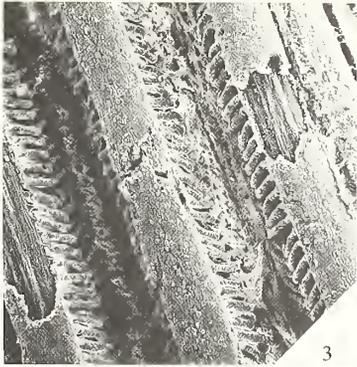
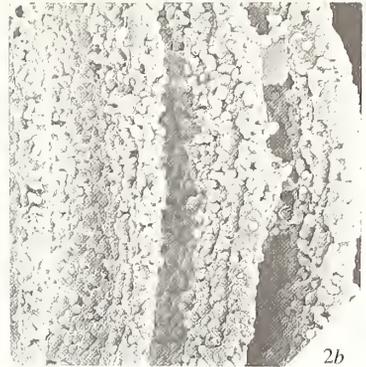
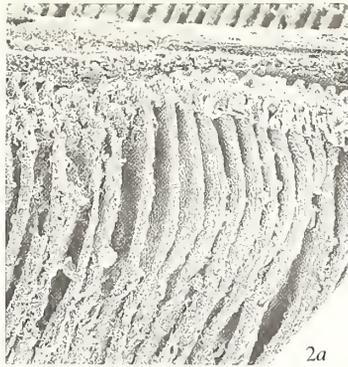
Fig. 6. CPD trout gill filament with secondary lamellae after four hours of decomposition. The epithelial cells have detached from the lamellae leaving only a connective tissue lining. Collapse has produced kinking of the lamellae at their bases. Some shrivelling of the connective tissue lining of the blood vessel has taken place, $\times 200$.

Fig. 7. DM 101. *a*, Fossil gill filament showing similar features to those seen in figure 6, $\times 400$. *b*, Detail of secondary lamellae/blood vessel junction, $\times 1000$.

Fig. 8. CPD trout gill after one hour of decomposition, showing collapsed epithelial cells, $\times 2000$.

Fig. 9. CPD trout gill filament showing detail of secondary lamellae/blood vessel junction, after four hours decomposition, $\times 400$.

Fig. 10. CPD trout gill after seven days of decomposition. All gill tissue has decomposed, only isolated colonies of bacteria remaining on exposed bone surfaces.



familiar with CPD (e.g. Hill 1987) have used it successfully for comparative anatomical studies. Wherever fossil material requires comparison with recent material, especially at high magnifications, this technique allows direct comparisons of three-dimensional material to be made. Very few artefacts are introduced during preparation, although it should be pointed out that there may be some shrinkage of the tissue, and at very high magnifications it is sometimes possible to see osmium tetroxide crystallized on some surfaces from over-osmication.

CP-dried material stored in anhydrous conditions has a long shelf life. Bivalve mollusc material prepared by Harper has persisted for at least 12 months without discernible deterioration.

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COMPUTER-AIDED RESTORATION OF A LATE CAMBRIAN CERATOPYGID TRILOBITE FROM WALES, AND ITS PHYLOGENETIC IMPLICATIONS

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ABSTRACT. Tectonic deformation is liable to affect the diagnostic characters of fossils, but its effects can be removed with the help of a computer-graphic technique, which is here applied to trilobites for the first time. *Dikelocephalus? discoidalis* Salter, 1866, with its putative synonym *D.? celticus* Salter, 1866, is known only from distorted specimens collected from the upper part of the *Parabolina spinulosa* Biozone in the Dolgellau Formation (upper Cambrian) of North Wales. It has been reconstructed by removing tectonic deformation. *D.? discoidalis* is now referred to *Cermatops* Shergold, a member of the Subfamily Iwayaspidinae; this group is considered to be a paraphyletic subgroup within the Family Ceratopygidae.

IN north-west Europe the Late Cambrian faunas are dominated by olenid trilobites, a specialized group that was adapted to oxygen-deficient environments (Henningsmoen 1957), whereas such cratonic realms as North America, Australia, northern China and Siberia, each supported a diverse and partly endemic suite of genera (Palmer 1977). Besides the agnostids, one of the most widely distributed trilobite groups is the Family Ceratopygidae, members of which are known from most areas yielding late Middle Cambrian to Tremadoc faunas, though despite much recent work the full biostratigraphical potential of the group has yet to be realized. *Proceratopyge* is recorded in the English Midlands (Rushton 1983) and *Ceratopyge* itself from the Tremadoc of North Wales but until now no ceratopygids have been recorded from the Merioneth Series in Wales. However, we here refer Salter's *Dikelocephalus?* species from the Merioneth Series of North Wales to the ceratopygid genus *Cermatops* Shergold, 1980. Dikelocephalids are common only in North American Trempealeauan deposits from shallow shelf environments (Taylor 1977). Their supposed presence in black shales from North Wales was remarkable, both on account of the slope setting there and because the European *P. spinulosa* Biozone is correlated with the lower Franconian *Taenicephalus* Biozone of North America, well below the Trempealeauan. The new assignment negates a suggestion by Conway Morris and Rushton (1988, fig. 3) that dikelocephalids migrated from outer-shelf environments onto the North American craton, but fits well with the known biogeography of ceratopygid trilobites.

OCCURRENCE

Salter's '*Dikelocephalus*' material came from the locality 'Ogof-ddû', 1 km east of Criccieth, Gwynedd, North Wales, *D.? discoidalis* being based on cephalon and *D.? celticus* and *D.? sp.* on pygidia. Ogof-ddû refers to the cliff-section Rhiw-for-fawr (around National Grid reference SH 5135 3795) that extends from the top of the Ffestiniog Flags Formation, through the whole Dolgellau Formation, to the lower part of the Tremadoc (Fearnside 1910, p. 153); the section encompasses several trilobite biozones. In 1951 officers of the British Geological Survey (BGS) examined the section bed-by-bed and collected fossils throughout; Stubblefield (1953) reported preliminary results. Review of the BGS collection shows that the lowest 13 m of the Dolgellau Formation is referable to the *Parabolina spinulosa* Biozone. Material of '*Dikelocephalus*' (now *Cermatops*) was collected only from 8.5 to 9.0 m above the base, that is, entirely within the upper part of the *P. spinulosa* Biozone. The *Cermatops* are associated with the following fossils:

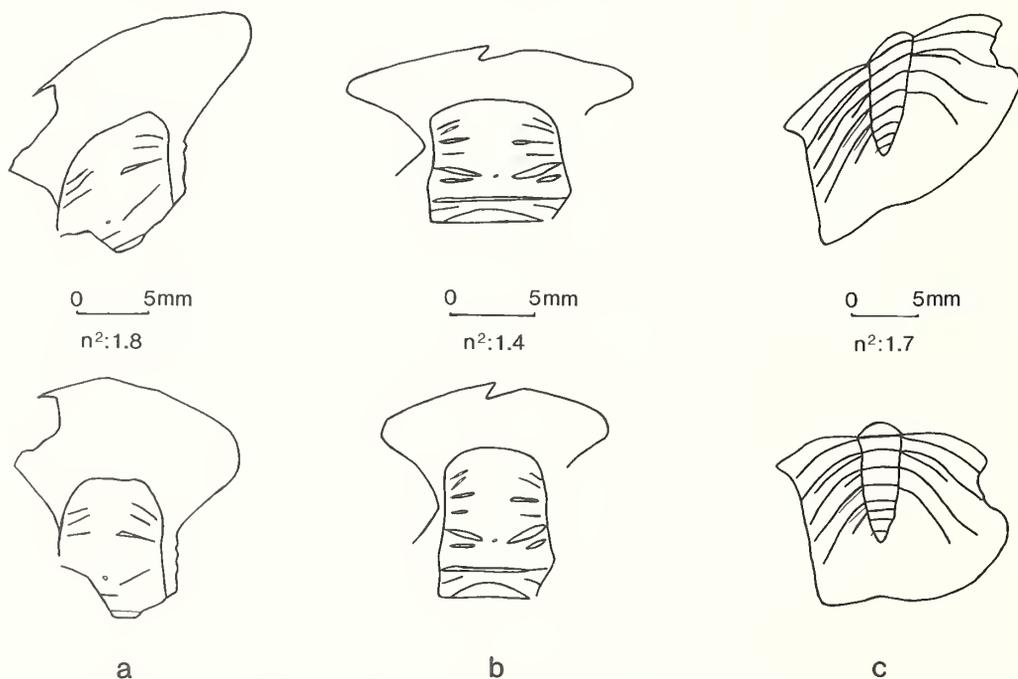
Homagnostus obesus laevis Westergård, *Pseudagnostus cyclopyge* (Tullberg), *Parabolina* cf. *spinulosa* (Wahlenberg), *Parabolinites*? sp., *Lingulella* sp., *Orusia lenticularis* (Wahlenberg) [abundant] and *Stenotheca* sp.

Fearnside collected a pygidium referable to *Cermatops discoidalis* (Pl. 2, fig. 9) from the stream section below Penmorfa Church (Salter 1866, p. 250).

The only other material known to us was collected by Shackleton (1959, p. 222) from the cliff above Cwm-y-ffynnon (SH 5403 5141), 7.5 km west-south-west from the summit of Snowdon and about 14 km N of Ogof-ddû, where rare *Cermatops* fragments are associated with abundant *O. lenticularis* and *Homagnostus*, *Pseudagnostus*, *Parabolina* aff. *mobergi* Westergård, *Parabolinites*? sp. and *Maladoidella*? *abdit*a (Salter). Apart from the abundance of *O. lenticularis* this fauna does not yield clear evidence of the *P. spinulosa* Biozone, but fragments of *P.* aff. *mobergi* are present at the top of the *P. spinulosa* Biozone at Ogof-ddû.

CORRECTION OF DISTORTION

Salter's (1866) *Dikelocephalus*? from the Dolgellau Formation are strongly deformed. To assess the generic position of these forms it was desirable to restore the original shape, and to this end we used a computer-graphic method employed at the British Museum (Natural History). The technique involved the digitization of camera lucida or photographic images of the specimens; the digitized images were then displayed on a monitor and progressively adjusted until bilateral symmetry was achieved (see Jefferies *et al.* 1987 for details). The validity of this method was tested using slabs in which various specimens were preserved in different orientations; some had the sagittal axis parallel to the principal component of strain (x axis of the strain ellipse) whereas in others it was perpendicular or oblique. Bilateral symmetry was restored to each specimen individually and values of n^2 (the proportionate increase of the y co-ordinate relative to the x co-ordinate) compared.



TEXT-FIG. 1. Examples of computer restorations giving bilateral symmetry. Above – camera lucida sketches; below – after restoration. n^2 represents the factor required to restore symmetry to each drawing.

Within individual slabs the value of n^2 required for each specimen was identical; this validated the use of bilateral symmetry as a criterion for restoring the shape.

The program gave an approximation to the original shape (see text-fig. 1) but did not produce perfect restorations; in many cases the x - y plane of the strain ellipse was not exactly the same as the dorso-ventral plane of the specimens, and in some cases pyrite crystals caused local inhomogeneities of strain. Several specimens had been cracked during compression and prior to tectonic distortion. These factors did not, however, significantly limit the use of the method in determining a generalized representation of the overall shape, and this proved important for taxonomic assessment.

The bilaterally symmetrical restorations of cranidia and pygidia provided by the computer method were scaled to a standard size using a Rost planvariograph. These images were superimposed and an overall representation of original shape inferred (see text-fig. 2). Because of the complexity of post-mortem deformation, particular weight was given to those specimens which showed least original distortion (for example the pygidium in Pl. 2, fig. 9). The three specimens of free cheeks were not analysed on the computer because two of the specimens were comparatively undistorted and also because their shape could largely be inferred from the cranidial restoration. As the sagittal axis of the single hypostome was parallel to the x axis of strain, it was not possible to restore its shape; the outline of the hypostome in the reconstruction is therefore dotted. In the absence of complete specimens the relative size of cranidium and pygidium was estimated from the size-ranges of the specimens available. Particular features, such as the sculpture and median tubercle, were included in the reconstruction only if they were recognized in at least two specimens.

SYSTEMATIC PALAEOONTOLOGY

- Superfamily ASAPHACEA Burmeister, 1843
 Family CERATOPYGIDAE Linnarsson, 1869
 Subfamily IWAYASPIDINAE Kobayashi, 1962
 Genus CERMATOPS Shergold, 1980

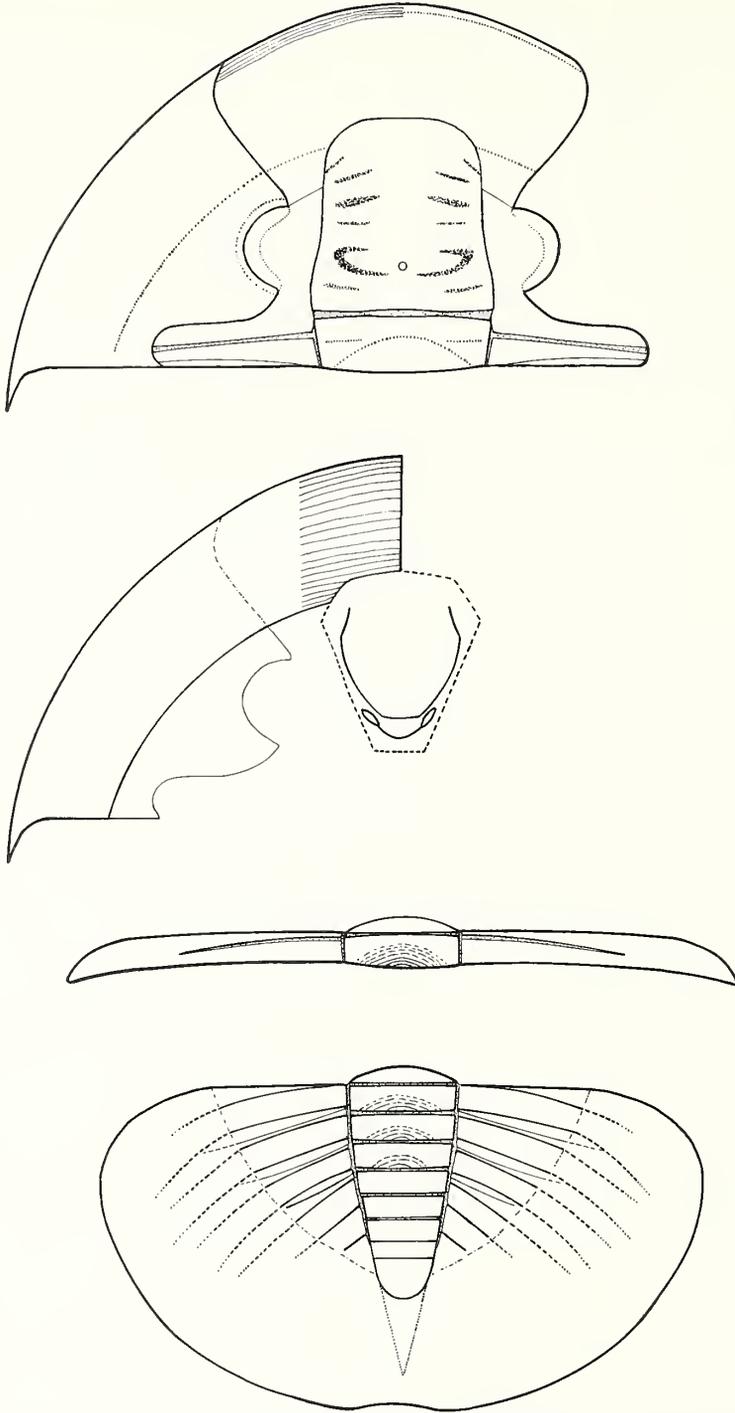
Type species. *C. vieta* Shergold (1980, p. 87, pl. 34, figs. 3–11). [Names with *-ops* are treated as masculine so the specific name is changed here to *vietus*.]

Diagnosis. Ceratopygid trilobites without macropleural pygidial spines (Subfamily Iwayaspidinae), having a subquadrate glabella showing several pairs of furrows and muscle-scars anterior of S1; palpebral lobe does not reach axial furrow; pygidium transversely semi-oval, the pleural segments having reduced propleural bands. The generic and subfamilial classifications are discussed below.

Cermatops discoidalis (Salter, 1866)

Plates 1 and 2; text-figs. 1, 2, 3a, 4

- 1866 *Dikelocephalus?* (*Centropleura?*) *celticus*, n. sp.; Salter, p. 304, pl. 5, figs. 21 and 22.
 1866 *Dikelocephalus?* (*Centropleura?*) *discoidalis*, n. sp.; Salter, p. 304, pl. 5, figs. 18, 18a, 19.
 1866 *Dikelocephalus?* (*Centropleura?*) sp.; Salter, p. 305, pl. 5, fig. 20.
 1868 *Dikelocephalus?* *Celticus* Sal., *D.?* *discoidalis* Sal.; Belt, p. 6 [gives horizon, but incorrectly].
 1914 *Dikelocephalus celticus* Salter, *D. discoidalis* Salter; Walcott, pp. 350, 366 [mentioned as generically indeterminate].
 1919 *Dikelocephalus discoidalis* Salter; Lake, p. 115, pl. 14, figs. 2–5 only [not figs. 6 and 7, ? = *Lakella invita* (Salter)].
 1919 *Dikelocephalus celticus* Salter; Lake, p. 116, pl. 14, figs. 8–10.
 1935a *Briscoia celticus* (Salter), *B. discoidalis* (Salter); Kobayashi, pp. 51–52 [transferred to *Briscoia*].
 1946 *Dikelocephalus celticus* Salter; Lake, p. 343 [discusses similarity to *Briscoia*].
 1953 '*Dikelocephalus?* *celticus* Salter; Stubblefield, p. 56 [discusses horizon].
 1988 *Briscoia?* *celtica* (Salter, 1866); Morris, p. 38 [listed].
 1988 *Briscoia?* *discoidalis* (Salter, 1866); Morris, p. 38 [listed].



TEXT-FIG. 2. Restoration of *Cermatops discoidalis* (Salter), about $\times 3$. Dorsal view of cranium: the dorsal terrace-ridges are shown on the left side of the preglabellar field, the border furrow is indicated on the right. Ventral view of right free cheek and hypostome; terrace-ridges are shown on a representative area; hypostomal outline inferred (dashed), course of dorsal suture indicated (pecked). Dorsal view of thoracic segment. Dorsal view of pygidium.

Type material. The lectotype of *D. ? discoidalis*, selected by Morris 1988, p. 38, is BGS GSM 10214 (Pl. 1, fig. 3); it is the original of Salter's fig. 18 and Lake's fig. 2. Paralectotypes include cranidia GSM 10209 (Lake's fig. 3), 10210 (Salter's fig. 19 and Lake's fig. 4) and 10216; and free cheeks GSM 10213, 10213A (Salter's fig. 18a and Lake's fig. 5) and 10215. The lectotype of *celticus*, selected by Morris 1988, p. 38, is GSM 10206A (Pl. 2, fig. 3) and 10206 (counterparts), the original of Salter's fig. 22 and of Lake's fig. 9. The paralectotypes include the original of Salter's fig. 21 (GSM 10208), and possibly the unfigured specimens GSM 10212, BGS GSD 4587 and two pygidia collected by Homfray (Sedgwick Museum SM A932). Other material. From Ogoferddu: GSM 85214 (Wyatt-Edgell Coll.), SM A50349-50354 (Fearnside's Coll.), and about forty specimens and fragments collected by S. W. Hester for the Geological Survey in 1951, numbers prefixed Hr. From Penmorfa, SM A51599 (Fearnside's Coll.). From Cwm-y-flynnon, five specimens presented to the BGS by Professor R. M. Shackleton.

Description. Glabella widest (tr.) at midlength (sag.) of L1 (= posterior lateral glabellar lobe). Lateral margins subparallel anterior of S1 (posterior lateral glabellar furrow). Glabella with rounded anterolateral corners and straight anterior margin. S1 furrows crescentic, strongly curved, half of glabellar width, shallow adaxially, deeply incised in distal third, not connecting with axial furrow, anterior part weaker than posterior. S2 deepest distally, transverse, crossing one-fifth of glabellar width; S3 oblique inwards and forwards, one-fifth of glabellar width, deepest at mid-length (tr.). L3 short (exsag). Shallow intercalated furrows subparallel to SO across distal quarter of L1. Median tubercle within bifurcation of S1. Shallow furrows intercalated within L2 and anterior of S3. Glabella lacks sculpture. Occipital furrow deepest distally, shallow in axial third. A low ridge arches anteriorly from posterior border of occipital ring, occupying medial four-fifths of occipital width and extending three-quarters of occipital length (sag.). Shallow transverse furrows run adaxially, about one-third of occipital width (tr.). Axial furrow shallow in front of glabella.

Preglabellar field broad, over half as long as pre-occipital glabella, and over twice as wide as occipital ring. Border low, short (sag.), anterior margin slightly angular axially. Terrace-ridges on border face anteriorly. Anterior border furrow crescentic, weakly defined. Preocular sutures diverge forwards at 45 degrees to the sagittal line, then curve in and extend along anterior margin of cephalon. Paradoublural line runs obliquely backwards from anterolateral corner of glabella, subparallel to weak eye ridge. Fixigena narrowest (tr.) opposite L3. Palpebral lobe arcuate, one quarter the length of cranium, widest (tr.) opposite L2. Palpebral area slopes steeply into axial furrow. Palpebral furrow weakly developed. Posterolateral border area wider (tr.) than occipital ring, straight, narrow (exsag). Postocular suture transverse, subparallel to posterolateral margin. Posterior marginal furrow deeply incised. A shallow furrow runs outwards parallel to posterior margin for four-fifths of width of posterolateral border. Estimated length of cephalic axis in various specimens is 5–15 mm.

Free cheeks arcuate, border smooth. Genal spine short, its base much narrower (tr.) than width of doublure. Median suture present. Portion of ocular platform within paradoublural line one-fifth of fixigenal medial width (tr.), bounded adaxially by upraised flange. Adaxial margin of doublure sub-parallel to cephalic margin; a slight flexure in its anterior portion presumably accommodated the anterior edge of the hypostome. Doublure extends about three-quarters of the distance from margin to ocular incisure. About twenty terrace-ridges present on doublure, continuous, gently sinuous, steeper slopes facing abaxially, most closely spaced at inner and outer margins.

Associated hypostome elongate. Anterior border and anterolateral wing not preserved. Lateral border narrow (tr.) dipping steeply into border furrow; posterior border flatter, longer (sag.) than wide. Median body ovoid. Anterior lobe inflated, posterior lobe gently convex. Median furrow complete, connecting with border furrow. Maculae prominent, ovoid. Sculpture not observed.

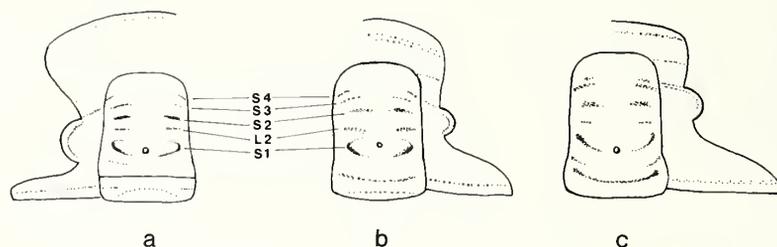
Number of thoracic segments unknown. Associated thoracic segment shows articulating furrow deeply incised distally, more shallowly in medial third. An arcuate set of fairly continuous terrace-ridges covers the posterior part of the axial ring. Axial furrows parallel to sagittal axis. Pleura gently curved posteriorly. Pleural furrows deeply incised.

Pygidium sub-elliptical, wider than long. Margin entire, with slight post-axial emargination developed in larger specimens. Axis narrow, convex, tapering evenly posteriorly, about three-quarters of pygidial length and about one quarter of maximum pygidial width. Articulating half ring short (sag.), crescentic. Axis generally of six rings and terminal piece, a poorly defined seventh ring present in some specimens. A set of arcuate posteriorly facing terrace-ridges, similar to those on the thoracic segment, run from posterior border of axial rings. Ring furrows deeply incised distally, shallow adaxially. Axial furrow deeply incised. Post-axial ridge narrow (tr.) where present, extends to posterior margin. Interpleural furrows narrow, firmly incised, extending almost to pygidial margin. Pleural furrows broad, shallow. Five to seven pleurae present, sixth and seventh poorly defined. First pleura contains equally divided pro- and opisthopleurae; pleural and interpleural furrows

geniculate at paradoublure line. Subsequent pleura show relative reduction of length and width of propleura. Propleura absent from fifth (and subsequent) pleura, where pleural furrows are undifferentiated from interpleural furrows. Terrace-ridges weakly developed on propleurae. Doublure wide, extending inwards to posterior end of axis, and inwards from anterolateral pygidial margin for half pleural width (tr.). Terrace-ridges of doublure have high relief, steeper slopes facing outwards, distributed most densely along adaxial portion. Estimated length of various pygidia is 5–25 mm.

Interpretative remarks

1. Lateral glabellar furrows. The glabellar furrows of *C. discoidalis* are difficult to interpret because they are variously altered and masked by tectonic compression. Lake thought that the S1 furrow was transcurrent, as in other *Dikelocephalus*. Such a feature is seen only in the most compressed cranidium (Pl. 1, fig. 6), and is contradicted by other specimens and our reconstruction. Salter correctly described the obliquity of the furrows – S1 sloping inwards and backwards, S2 transverse, S3 inwards and forwards – though neither his figures nor Lake's show this clearly. Our interpretation (text-fig. 3) is based especially on the lectotype (Pl. 1, fig. 3) and on the new material

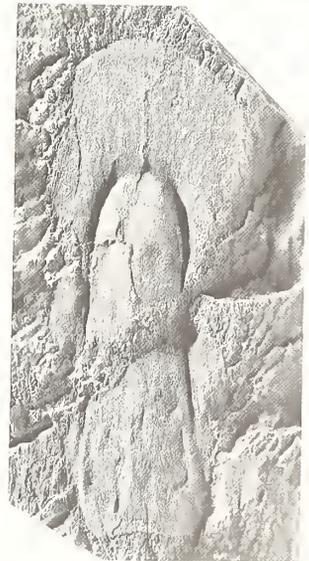
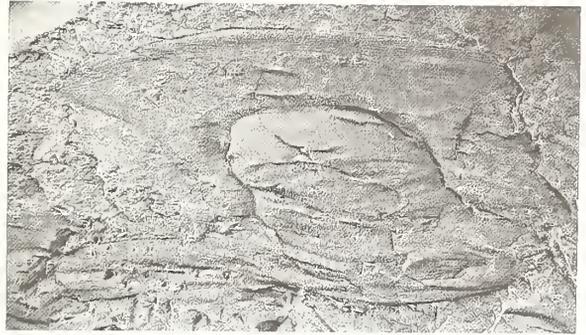


TEXT-FIG. 3. Suggested interpretation of glabellar furrows in *a* *Cermatops discoidalis* and *b* *C. vietus*. *c* is *C.? tenacella*, based on Xiang and Zhang 1985, pl. 41, fig. 11.

(e.g. Pl. 1, fig. 4). The strongest furrow, with inner ends opposite the glabellar tubercle, is interpreted as S1, as is typical of the Ceratopygidae. The comparatively well-marked furrows opposite the anterior half of the palpebral lobes are homologized with S2 of the primitive asaphine pattern (Fortey and Chatterton 1988). The furrow interpreted as S3 is weaker and lies anterior to the front of the palpebral lobe; it is seen in several specimens but is obscured by a misleading crease in GSM 10209 (Pl. 1, fig. 1). A short furrow close to the axial furrow and just in front of S3 is referred to as S4 – a similar furrow is seen in *Guozia crassa* (text-fig. 5h). Some specimens show weak transverse furrows on glabellar lobes L1 and L2. Those on L1 are present in some iwayaspidines, as remarked

EXPLANATION OF PLATE I

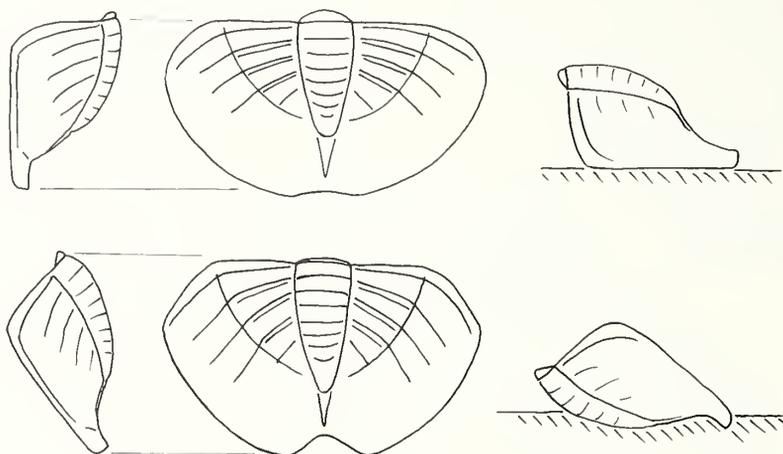
Figs. 1–9. *Cermatops discoidalis* (Salter, 1866), all from the *Parabolina spinulosa* Biozone of Ogof-ddü, west of Criccieth, North Wales (National Grid ref. SH 5157 3787 approx.). All these specimens are in the collections of the Biostratigraphy Research Group of the British Geological Survey (BGS), Keyworth, Nottingham. All were whitened before photography and, unless otherwise indicated, are internal moulds. 1–6, 9, cranidia. 1, GSM 10209, $\times 3$; an *Orusia lenticularis* lies to the right of the glabella. 2, Hr 927A, $\times 3$. 3, Lectotype, GSM 10214, $\times 3$. 4 and 5, Hr 948, showing glabellar furrows, and latex cast of counterpart Hr 948A, showing palpebral lobes. Both $\times 4$. 6, GSM 10210, $\times 4$. 7 and 8, free cheeks; 7, GSM 10213, showing the doublure forward of preocular suture and behind it a pyrite infilling between the doublure and the dorsal surface. 8, latex cast of Hr 937, showing small genal spine (slightly retouched). 9, Hr 927B, $\times 3.2$. On the same block as Fig. 2, but oriented at right angles to it. The originals of Figs. 3, 6, 7 were illustrated by Salter 1866, pl. 5, figs. 18, 19, 18a; those of Figs. 1, 3, 6, 7 were illustrated by Lake 1919, pl. 14, figs. 3, 2, 4, 5 respectively.



below, and in some olenids (Rushton 1982). The L2 furrows are weak in *C. discoidalis* but there is a pair of stronger impressions in a similar position in *C. vietus* (Shergold 1980, pl. 34, figs. 3 and 6).

2. Association of the pygidium. Salter assigned the cephalon and pygidium to different species for reasons of caution. Their association in the newer material and their congruence with other Iwayaspidinae indicates that Lake was right to suppose that they belonged to one species.

3. Pygidial shape. The pygidia that Salter described as *D.?* *celticus* differ from those of *D.?* sp. because the length/width ratio is greater, the posterior margin is indented and the pleural furrows are more swept back. Lake thought that these were the same species differently compressed; we believe that he was correct. The differences are readily understood if the pygidium was considerably convex and the posterior margin was arched upwards rather than indented. Viewed from above the pygidium is relatively short, the anterior margin straight, the pleurae direct and the posterior arch nearly invisible (text-fig. 4). This is the '*D.?* sp.' configuration. Viewed obliquely from above and behind, however, the projected length is greater, the anterior margin and pleurae sweep backwards and the posterior arch is more visible (text-fig. 4) – the '*celticus*' configuration. One reason why the pygidium should appear in two forms is that moulted pygidia could come to rest either on the doublure or upside-down on the dorsal surface; flattening by compaction would then give projections corresponding to the two appearances described above.



TEXT-FIG. 4. Sketches to illustrate the differing appearances of the pygidia of *Cermatops discoidalis* according to whether they were deposited dorsal side up (above) or inverted (below).

EXPLANATION OF PLATE 2

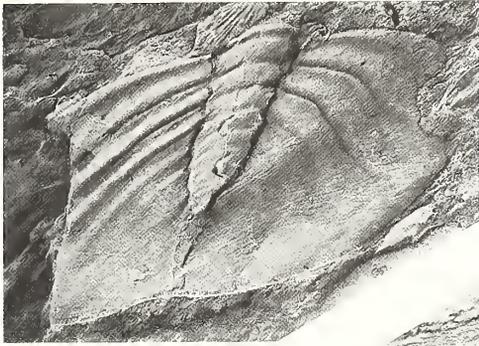
Cermatops discoidalis (Salter, 1866). All are from Ogof-ddŷ, west of Criccieth, North Wales (National Grid ref. SH 5157 3787), except for Fig. 9 which is from Penmorfa Church 2 km west of Tremadog, North Wales (about SH 5418 4030). Figs. 5, 7 and 9 are in the Sedgwick Museum, Cambridge (SM); all the other specimens are in the collections of the Biostratigraphy Research Group of the British Geological Survey. All were whitened before photography and, unless otherwise indicated, are internal moulds. 1–5, 7, 9, 10, pygidia; 6, hypostome; 8, thoracic segment. 1, Hr 925 (external mould), $\times 3$. 2, GSM 10212, $\times 3$. 3, GSM 10206A, $\times 3$. 4, GSM 10211, $\times 4$. 5, two pygidia showing terrace-lines on the doublure; SM A.50349, $\times 3$. 6, fragmentary hypostome, Hr 923, $\times 6$. 7, SM A.933, $\times 4$. 8, thoracic segment, GSM 10216, $\times 2$. 9, least distorted pygidium, SM A.51599, from Penmorfa, $\times 4$. 10, latex cast of GSM 10208, $\times 2$. The originals of Figs. 3, 4, 10 were illustrated by Salter 1866, pl. 5, figs. 22, 20, 21, and by Lake 1919, pl. 14, figs. 9, 10, 8 respectively.



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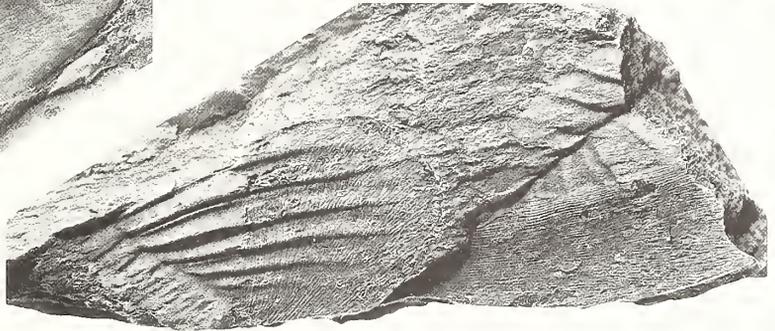
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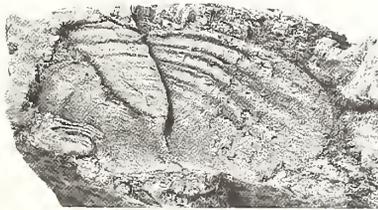
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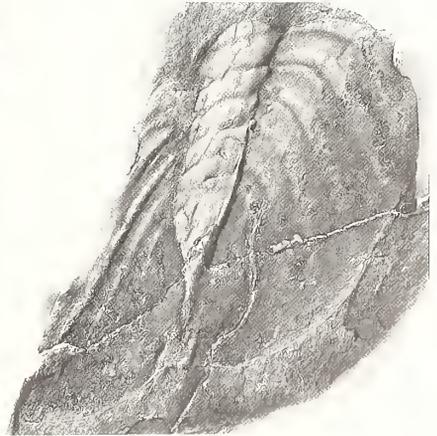
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10

Specific differentiation. The cephalon of *C. discoidalis* differs most obviously from *C. vietus* in having larger eyes, a longer and wider frontal area with more divergent preocular sutures and a smaller genal spine. The same cranial features distinguish it from *C. ? tenacella* (Xiang and Zhang 1985, pl. 41, fig. 11). The pygidium of *C. discoidalis* differs from those of *C. vietus* and *C. sp.* of Shergold (1980, pls. 34 and 35) because it has several clearly defined axial rings (six or more rather than three or four). *C. discoidalis* also has a slight posterior indentation in the pygidium.

Generic position. Shergold referred only *C. vietus* and some unnamed pygidia to *Cermatops*. *C. discoidalis*, as reconstructed here, shows many similarities with *C. vietus* and these we consider to outweigh the obvious differences.

Glabellar structure. In ceratopygids S1 has an unusual crescentic or longitudinal form, and most iwayaspidines show this and a conventional S2 and S3. Both *C. vietus* and *C. discoidalis*, unlike other iwayaspidines, show four pairs of furrows anterior of S1, though their homologies with S2, S3 etc. are not established with certainty. Shergold remarked that the glabellar furrows of *C. vietus*, which are weak, cannot be distinguished from faint muscle scars on the glabellar lobes (Shergold 1980, pl. 34, fig. 3). Furrows are present in a corresponding position in *C. discoidalis*, and an interpretation is given in text-fig. 3. Similar structure is also visible in the holotype of *Sayramaspis tenacella* Xiang and Zhang, 1985 and this may also be referable to *Cermatops*, though the pygidium (at present unknown) is needed to provide confirmation. The form of the S1 furrows and the presence of a median glabellar node in *C. discoidalis* indicate that it is not closely related to the Dikelocephalidae, in which S1 is commonly transcurrent and there is no preoccipital node.

Pygidial structure. The pleural regions of the pygidium are well segmented but behind the anterior segment the propleural band (the anterior part of an individual segment) is reduced, both longitudinally and transversely (Pl. 2, fig. 2). This is seen also in *Tamdaspis* (Ergaliev 1980, pl. 19, fig. 8) and, less distinctly, in *Guozia* (Xiang and Zhang 1985). Both these genera differ from *Cermatops* in their glabellar form.

A similar pygidial structure was independently derived in the Dikelocephalidae, for example *Briscoia septentrionalis* Kobayashi, 1935a (Palmer 1968, pl. 15, figs. 3 and 4). Pygidia of remarkably similar form have also been described in the family Aphelaspidae under the generic names *Duibianaspis* Lu and Lin (1984, pl. 7, figs. 8, 9, 12, 13) and *Pseudaphelaspis* (*Arrhenaspis*) Qian (1985, pl. 6, figs. 4–7). (Note that the name of the type species of the latter genus, *P. (A.) latelimbata* Qian, 1985, is unavailable, being a primary junior homonym of *Pseudaphelaspis latelimbata* Lu and Lin, 1984.) In each of these genera the pygidium was associated with a typical aphelaspid cranium, and if they are correctly so assigned the genera are synonymous. However, those authors have not considered the possibility that the pygidia belong to *Cermatops* or *Tamdaspis*. Compared with the pygidia of *Cermatops*, that attributed to *Duibianaspis typicalis* Lu and Lin, 1984 has a blunt axis that is barely half the pygidial length, and that attributed to *P. (A.) 'latelimbata'* Qian, 1985 is proportionally much wider, and recalls *Tamdaspis*.

The pygidium from the *Elvinia* Zone in a borehole in Montana, figured by Lochman (1964, pl. 11, fig. 7) as *Pterocephalia sanctisbae* Roemer, differs from other figured pygidia of that species but bears a great likeness to *C. discoidalis*, though it differs in having the ventral terrace ridges half as densely spaced. The generic assignment of this pygidium is uncertain because none of the associated cranium is likely congeneric with it.

Family relationships. *Cermatops* is regarded as a member of the Iwayaspidinae (Shergold 1980). This group shares several characters, for example the form of the glabellar furrows, the presence of a median preoccipital tubercle and a median suture, with primitive Asaphidae (in the sense of Fortey and Chatterton 1988) and the Ceratopygidae, but it lacks any convincing autapomorphy; it is a paraphyletic group, and we find the usual difficulties in assessing the relationships of the taxa within such a group.

The genera referred to the Iwayaspidinae commonly have a narrow cephalic border (compared with typical Asaphidae), a distinct preglabellar field and genal spines that are narrower at their base

than the width of the cephalic doublure; the thorax varies, with 8–10 segments. These features are not seen in the Asaphidae but are met with in the Ceratopygidae. Therefore we agree with Shergold (1980, p. 86) and Fortey and Chatterton (1988, p. 196) that the Iwayaspidinae are better referred to the Ceratopygidae than the Asaphidae.

The typical Ceratopygidae (Subfamily Ceratopygidae) are characterized especially by the presence of marginal spines in the pygidium that are derived from macropleural segments. The capacity to develop such spines is taken as an autapomorphy for the subfamily, although it is evident that not all such spines are homologous (for example they are developed from the tenth post-cephalic segment in *Proceratopyge* but the eighth in *Dichelepyge*). Fortey and Chatterton (1988) justifiably referred the Macropyginae to the Ceratopygidae; this subfamily is characterized by bacellar lobes on the cephalon and an exceptionally elongate pygidium (text-fig. 5i, j).

Several genera have been referred to the Iwayaspidinae, as follows: the type genus *Iwayaspis* Kobayashi, 1962 (type species *I. asaphoides* Kobayashi) has been regarded as a junior synonym of *Pseudoyuepingia* Chien, 1961 (type species *P. modesta* Chien), e.g. by Jago 1987. Other genera are *Yuepingia* Lu, 1956 (type species *Y. niobiformis* Lu), *Aplotaspis* Henderson, 1976 (*Charchagia erugata* Whitehouse, 1939), *Cermatops* Shergold, 1980, *Guozia* Xiang and Zhang, 1985 (*G. crassa* Xiang and Zhang) and *Sayramaspis* Xiang and Zhang, 1985 (*S. angustaxis* Xiang and Zhang). *Haniwooides* Kobayashi, 1935b, based on *H. longus* Kobayashi, is imperfectly known but is probably an iwayaspidine; it generally resembles *Yuepingia* apart from the apparent absence of a median glabellar tubercle. *Haniwooides? varius* Shergold, 1980 (and probably also *H.? puteolatus* Kobayashi, 1962), though doubtfully referred to the genus, has all the features of an iwayaspidine. *Norinia* Troedsson, 1937 has the typical arrangement of glabellar furrows but has a relatively short, undifferentiated preglabellar field, and it may be better referred to the Asaphidae. *Charchagia* Troedsson, 1937 has the axial features effaced and is therefore difficult to evaluate, as already noted by Troedsson.

Tamdaspis Lisogor, 1977 can be interpreted as an advanced Iwayaspidine but, depending on how its special features such as the baculae are evaluated, it may be regarded as a primitive member of the Macropyginae (text-fig. 5i and j). *Psiloyuepingia* Qian and Qiu, 1983 (in Qiu *et al.* 1983) is doubtless a synonym of *Tamdaspis*. We exclude *Pseudohysterolenus* Harrington and Leanza, 1957 because it differs from all iwayaspidine genera in the posterior position of the glabellar node. We also exclude *Metayuepingia* Liu (in Zhou *et al.* 1977), *Yuepingioides* Lu and Lin, 1984 and *Parayuepingia* Zhou *et al.*, 1982) from the Iwayaspidinae. All have short frontal areas, little or no preglabellar fields, and in the first two forms the genal angle is rounded.

Most of the above taxa have been proposed since publication of the Treatise Volume O (Moore 1959), and examples are illustrated here in text-fig. 5. Although many of their features are primitive with respect to the Asaphacea a few characters may be regarded as advanced when considering relationships within the group:

1. Reduction of the interocular cheeks. Early *Proceratopyge* and Asaphidae have the palpebral lobe separated from the glabella by a distance about equal to the length (sag.) of the occipital ring, and this is taken to be the primitive condition. In several species of Iwayaspidines and Ceratopygines the palpebral lobe is enlarged and approaches the glabella. As the anterior end of the palpebral lobe in all such forms lies near S3 and L4, those forms with a longer palpebral lobe necessarily have a more transverse postocular suture (Jago 1987, p. 227).

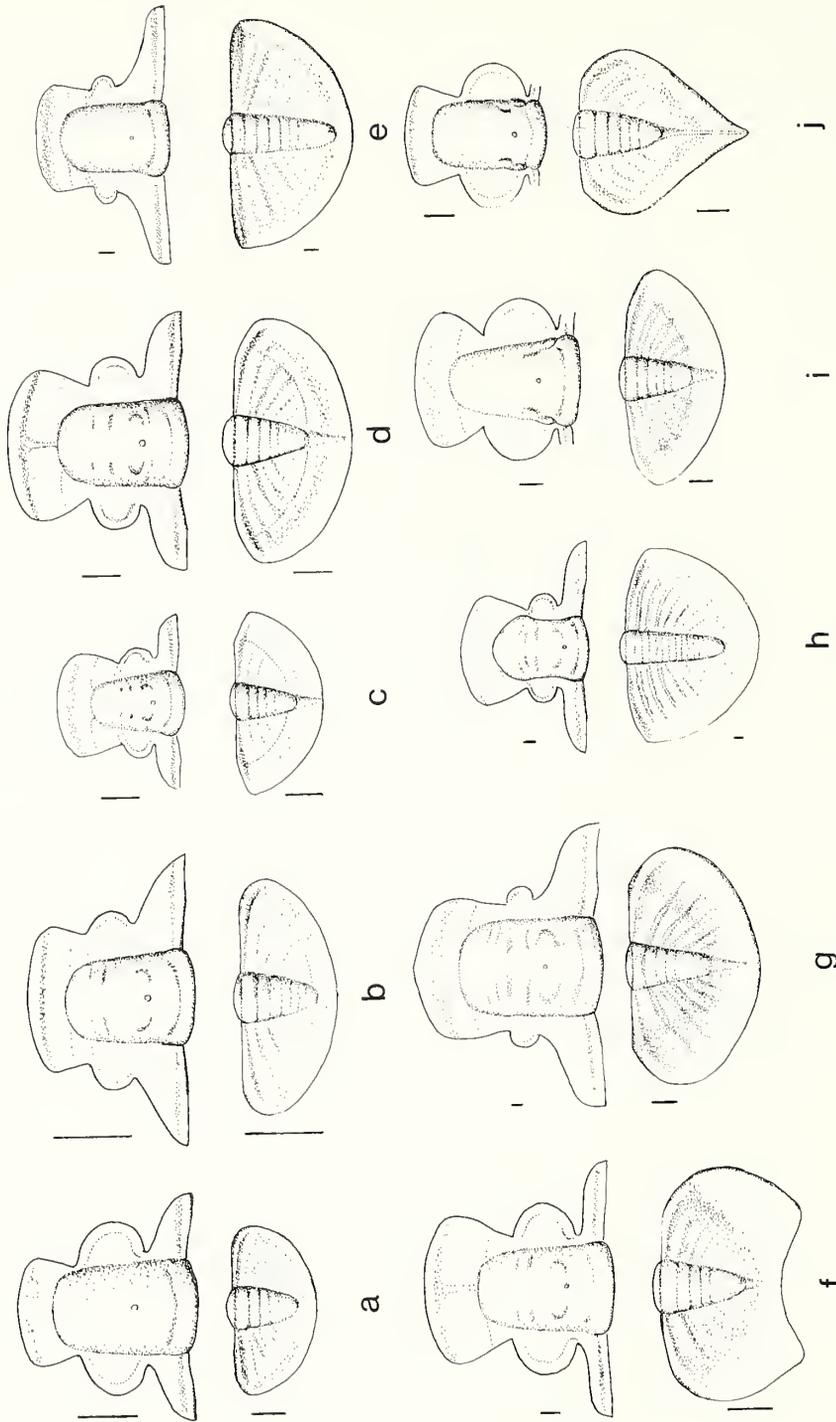
2. The development of bacellar lobes in the adult (as in *Tamdaspis*, text-fig. 5i).

3. The reduction of the propleural band in the pygidium (e.g. *Cermatops*, text-fig. 5g).

4. The development of a large posterior indentation in the pygidium (as in *Haniwooides? varius*, text-fig. 5f).

5. Effacement (e.g. in *Yuepingia*) is also regarded as a progressive feature but is so general as to be without classificatory value.

6. The presence of an auxiliary pair of glabellar furrows intercalated between S0 and S1 appears to be a specialized character but its distribution is sporadic. It is present in *Cermatops discoidalis* and in single species of *Guozia* (*G.? dubia*), *Yuepingia?* (*'Iwayaspis' caelata*, text-fig. 5d) and



TEXT-FIG. 5. Examples of Iwayaspidinae. *a.* *Yuepingia niobiformis*, after Lu 1956, pl. 1, figs. 6 and 8. *b.* *Pseudoyuepingia modesta*, after Chien 1961, pl. 3, fig. 5. *c.* *Aplotaspis erugata* (Whitehouse), after Henderson 1976, mainly pl. 48, fig. 17, and pl. 49, figs. 1 and 2. *d.* *Iwayaspidis* [= *Yuepingia*?] *caelata*, after Lazarenko, in Datsenko *et al.* 1968, pl. 16, figs. 6-10, drawn from photographs kindly supplied by Dr Lazarenko. *e.* *Sayramaspis yordanshanensis*, after Xiang and Zhang 1985, pl. 40, figs. 7-10. *f.* *Haniwooides*? *varius*, after Shergold 1980, pl. 34. *g.* *Giozia crassa*, 32, fig. 8 and pl. 33, fig. 10, and Xiang and Zhang 1985, pl. 43, figs. 1-5. *h.* *Cermatops vietus*, after Shergold 1980, pl. 34. *i.* *Giozia crassa*, after Xiang and Zhang 1985, pl. 43, figs. 5-7, and Ergaliev 1980, pl. 18, fig. 17 and pl. 19, fig. 8. *j.* *Aksapyge foveata* Lisogor (Subfamily Macropyginae, for comparison with *Tamdaspis*), after Apollonov *et al.* 1984, pl. 2, figs. 9-14. Scale bars represent 2 mm.

TABLE 1. Coding of characters for selected taxa of the Iwayaspidinae. They are mostly the type species of their respective genera, but *Sayramaspis yardanshanensis* and *Pseudoyuepingia whitei* (Webby *et al.* 1988) were preferred on account of their good preservation. The pygidium of *Haniwooides convexus* was used, as that of *H. longus* is not known.

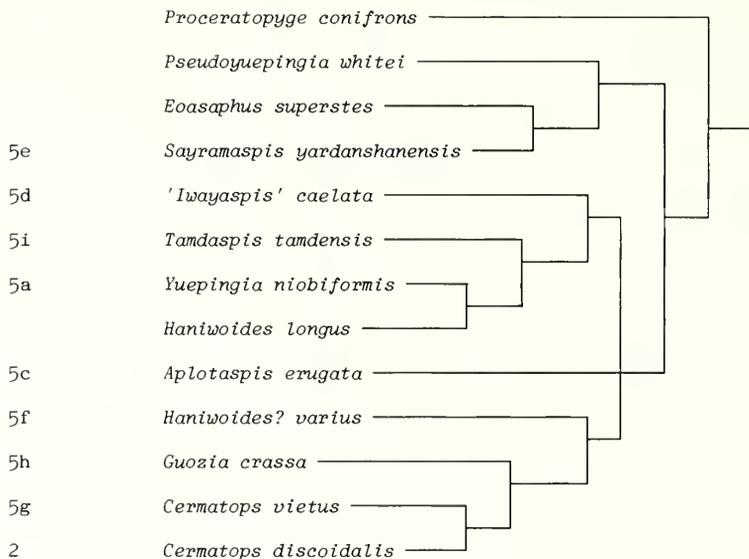
Character no.	1	2	3	4	5	6	7	8	9	10	11	12
<i>Eoasaphus superstes</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proceratopyge conifrons</i>	0	0	1	1	0	0	1	0	1	0	0	0
<i>Sayramaspis yardanshanensis</i>	0	0	2	0	0	0	1	1	0	0	0	1
<i>Pseudoyuepingia whitei</i>	0	0	1	0	1	0	1	0	0	0	0	9
' <i>Iwayaspis</i> ' <i>caelata</i>	0	0	1	1	0	0	1	0	1	0	2	1
<i>Yuepingia niobiformis</i>	0	0	2	0	0	0	1	0	0	1	2	0
<i>Aplotaspis erugata</i>	0	0	1	0	0	0	1	1	1	1	1	1
<i>Haniwooides longus</i>	0	1	2	0	0	0	0	1	0	1	1	1
<i>Tamdaspis tamdensis</i>	0	0	3	0	0	0	1	0	1	1	2	1
<i>Haniwooides?</i> <i>varius</i>	1	1	1	0	0	0	1	1	1	0	2	1
<i>Cermatops discoidalis</i>	1	1	1	1	1	1	1	1	0	1	2	1
<i>Cermatops vietus</i>	1	0	1	0	1	1	1	1	0	1	0	1
<i>Guozia crassa</i>	2	1	1	1	1	0	1	1	0	0	2	1

Character no.	13	14	15	16	17	18	19	20	21	22	23
<i>Eoasaphus superstes</i>	0	1	1	1	1	1	0	0	1	0	0
<i>Proceratopyge conifrons</i>	0	0	1	0	0	0	0	0	0	0	1
<i>Sayramaspis yardanshanensis</i>	1	0	0	0	1	1	0	0	0	0	0
<i>Pseudoyuepingia whitei</i>	1	1	0	0	0	0	0	0	1	9	0
' <i>Iwayaspis</i> ' <i>caelata</i>	1	0	9	1	2	0	0	0	1	0	0
<i>Yuepingia niobiformis</i>	0	0	9	2	2	2	0	0	0	0	0
<i>Aplotaspis erugata</i>	1	1	1	1	0	0	0	0	1	0	0
<i>Haniwooides longus</i>	9	0	0	2	2	2	0	0	1	0	0
<i>Tamdaspis tamdensis</i>	9	9	9	2	2	2	1	0	1	1	0
<i>Haniwooides?</i> <i>varius</i>	1	1	1	1	2	2	0	1	1	0	0
<i>Cermatops discoidalis</i>	1	1	1	1	2	0	0	1	1	1	0
<i>Cermatops vietus</i>	1	0	1	0	2	0	0	0	1	1	0
<i>Guozia crassa</i>	9	1	1	1	2	2	0	0	9	1	0

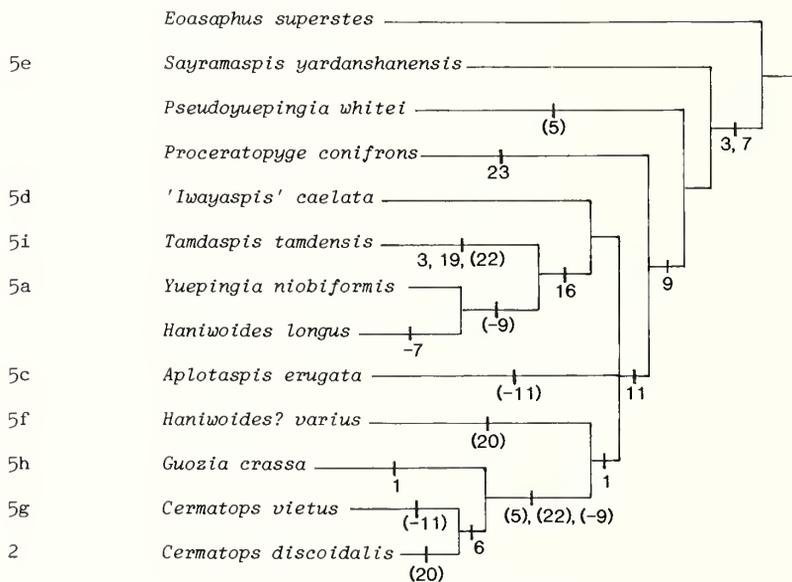
Characters 1–23, scored as follows.

1. Glabellar front: rounded 0, truncate 1, pointed
2. Glabellar sides: straight 0, concave 1.
3. Glabellar furrows: simple 0, asaphoid 1, effaced 2, only S1 developed 3.
4. Auxiliary furrow on L1: absent 0, present 1.
5. S4 furrow: absent 0, present 1.
6. Muscle-scars on glabella: absent 0, present 1.
7. Median glabellar tubercle: absent 0, present 1.
8. Occipital ring: simple 0, compound 1.
9. Plectral lines: absent 0, present 1.
10. Frontal area: border differentiated 0, not differentiated 1.
11. Preocular sutures: diverge at < 30° 0, 30°–60° 1, > 60° 2.
12. Paradoublural line on cranidium: absent 0, present 1.
13. Paradoublural line on free cheek: absent 0, present 1.
14. Length of genal spine: > half of rest of cheek 0, < half 1.
15. Width of genal spine at base: > width of doublure 0, < width of doublure 1.
16. Palpebral lobe length ÷ cephalic axial length: < 0.3 0, 0.3–0.4 1, < 0.4 2.
17. Distance of palpebral lobe from glabella: > length of occipital ring (SO) 0, = SO 1, < SO 2.
18. Ocular ridge: present 0, absent 1, palpebral lobe touches glabella 2.
19. Bacculae in adult: absent 0, present 1.
20. Pygidial margin: entire 0, emarginate 1.
21. Postaxial ridge: absent 0, present 1.
22. Pygidial pleurae: normal 0, propleurae reduced 1.
23. Pygidial marginal spines: absent 0, present 1. (Score 9 where a character cannot be coded.)

Text-fig.



Text-fig.



TEXT-FIG. 6. Relationships of selected taxa in the Iwaspidinae, as indicated by the PAUP program (see text). Top, consensus tree with *Proceratopyge conifrons* for out-group comparison. Below, alternative tree with a hypothetical ancestor for out-group comparison. *Eoasaphus* is the most primitive actual taxon analysed. Numbers refer to characters in Table 1; negative numbers indicate character reversals and numbers in parentheses indicate parallelisms.

Sayramaspis (*S. tenacella*, text-fig. 3c, possibly a species of *Cermatops*?). It is of uncertain value in classification.

7. The postaxial ridge is well developed in many Iwayaspidines but is absent in some genera (*Sayramaspis* and *Yuepingia*) and doubtfully present in others (*Pseudoyuepingia* and *Guozia*). The polarity of this feature is not clear.

To test the relationships of examples of the Iwayaspidinae twenty-three attributes of thirteen species were analysed using the PAUP (Phylogenetic Analysis Using Parsimony) program, as described by Fortey and Chatterton (1988). Table 1 shows the matrix of characters used. The type species of *Proceratopyge*, *P. conifrons* Wallerius (Westergård 1948), was included for out-group comparison because it is regarded as a primitive ceratopygine and is stratigraphically the earliest species.

When *Proceratopyge conifrons* was defined as the sister-taxon of the Iwayaspidinae, the program yielded two equally parsimonious but not very robust trees, differing only in the affiliation of *Aplotaspis*; the consensus tree is shown in text-fig. 6, top. An alternative analysis that compared the coded species with a hypothetical ancestor (which would score 0 in all columns of Table 1 – the Lundberg option) yielded a slightly different tree with the distal groupings unchanged but the basal dichotomies rearranged (text-fig. 6, below); this seems the more probable arrangement because it places *Eoasaphus*, which appears to lack the typical asaphine glabellar features, in the most primitive position. *P. conifrons*, which carries the autapomorphy of the Subfamily Ceratopyginae, branches off the tree above *Pseudoyuepingia*, in such a position that the Iwayaspidinae has to be regarded as a paraphyletic group. The results are viewed with caution because the attributes were mainly gleaned from descriptions and illustrations in the literature, and these are of uneven quality (a more reliable result could be obtained if the attributes were coded from actual specimens).

According to these analyses the Iwayaspidinae is a paraphyletic group of the Ceratopygidae that lacks the pygidial spines of the Ceratopyginae and the bacculae and median pygidial extension of the Macropyginae. The Iwayaspidinae fall into three groups: (1) primitive forms – *Eoasaphus*, *Pseudoyuepingia* and *Sayramaspis*; (2) a large-eyed group with *Haniwoides*, *Yuepingia* and *Tamdaspis*; (3) a more specialized group with *Cermatops*, *Guozia* and *H.? varius*. *Aplotaspis* appears as the sister taxon of (3) or of (2) + (3). We recognize that many of the features analyzed are not very compelling because several of them are known to have arisen independently in other groups. The most parsimonious of our cladograms includes several reversals of character-states: for example in *C. vietus* the small eyes and subparallel preocular sutures appear primitive in comparison with the rest of the taxa in its clade.

The analysis indicates that *Sayramaspis* is probably a synonym of *Pseudoyuepingia*, and *Yuepingia* of *Haniwoides*; these genera should be investigated further. If glabellar features are seen as most significant for classification *Tamdaspis* could be maintained as a distinct genus recognized by its bacculae (as well as its pygidial structure) and *Guozia* could likewise be separated from *Cermatops* by its distinctive glabellar shape.

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PRESERVATION OF AVIAN COLLAGEN IN AUSTRALIAN QUATERNARY CAVE DEPOSITS

by R. F. BAIRD *and* M. J. ROWLEY

ABSTRACT. The small well-preserved bones of ten avian fossils, species of the quail *Turnix*, from five Australian caves, ranging in age from 9000 to 38,000 years, were tested in a radioimmunoassay for collagen. Collagen was well preserved in all cave environments studied, whether 'wet' or 'dry', and nine of ten samples tested contained collagen, from 10% to 92% of the collagen content of fresh bone. The age of the bone was not clearly related to its collagen content, although the amount of collagen detected was significantly less in the older of the two samples for three of the five caves. The moisture content of the cave was not shown to affect the preservation of collagen. This study suggests that caves may provide a favourable environment for the preservation of collagen where fossils are physically well preserved.

PHYLOGENETIC relationships have traditionally been established using morphological criteria. Recently biochemical and immunological comparisons of proteins or of DNA have also been used in determining relationships (Wilson *et al.* 1977; O'Brien *et al.* 1985). Differences between morphologically and biochemically derived phylogenies therefore have caused debate on the applicability of each method (Hillis 1987). For example, re-evaluation of the morphological evidence for primate evolution in the light of data from comparisons of proteins or of DNA, suggests that gorillas, chimpanzees and man may have shared a common ancestor as recently as 5 million years ago, as predicted by molecular evidence, and not 15–20 million years ago as first suggested from morphological evidence (Lowenstein and Zihlman 1984). Similarly, phylogenies derived by Sibley and Ahlquist (1983) using DNA hybridization are stimulating a reassessment of the origins of many Australian birds. These techniques have been extended to examine relationships of recently extinct animals, such as the quagga *Equus quagga* (Higuchi *et al.* 1984) and the thylacine *Thylacinus cynocephalus* (Lowenstein *et al.* 1981), whose preserved skins have been used as a source of organic material, but for genuine fossils, phylogenies continue to be based on morphology.

Proteins may survive for considerable periods in fossils, however: bone collagen is one of the sources of ^{14}C used to date fossils, and the characteristic amino acids of collagen have been detected in dinosaur bones 200 million years old (Wyckoff 1980). Furthermore, material which reacts with specific antibodies to collagen has been detected in mammalian fossils millions of years old (Lowenstein 1980, 1981; Rowley *et al.* 1986).

During a study of the survival of collagen in Australian fossil sites (Rowley *et al.* 1986; Rowley unpubl. data) we gained the impression that caves provided a poor environment for the preservation of collagen. By contrast, bone morphology may be excellently preserved in most caves (Baird in press). We noted that most of the material examined for collagen had been from caves with abundant moisture. This study was therefore commenced to see whether, when well-preserved bones were selected, the moisture level within the cave could be shown to influence the survival of collagen. Bone samples from two 'dry' caves were compared with those from three caves which were considered to be 'wet'. The ability to predict which samples are most likely to contain collagen would reduce sample destruction and preparation time when collagen is used for phylogenetic studies.

MATERIALS AND METHODS

Environment

The caves from which material was studied include Clogg's Cave (EB-2: cave numbers from Matthews 1985: 148° 11' S, 37° 30' E) and McEachern's Cave (G-5: 141° 00' S, 37° 59' 30" E), Victoria; Koonalda Cave (N-4: 129° 50' S, 31° 24' E), South Australia; and Madura Cave (N-62: 127° 02' S, 32° 00' 30" E) and Devil's Lair (WI-61E: 115° 03' S, 34° 07' E), Western Australia. Both Clogg's Cave and Devil's Lair represent caves with moist environments ('wet' caves), and Madura Cave and Koonalda Cave represent caves with dry environments ('dry' caves). These are relative terms and imply no absolute definition, but generally wet caves have damp sediments, and may have water dripping or periodic inundations, while dry caves have dust. In many subaerial caves, if *high* humidity occurs for a long enough period, there is no preservation of bone whatsoever (RFB, pers. obs.), so that the determination of 'wet' and 'dry' applies only to those caves where bone survives.

The main taphonomic accumulator was the Barn Owl (*Tyto alba*, Tytonidae, Strigiformes) for all caves except G-5, which appears to be of fluvial/pitfall origin. The material from Koonalda Cave has been secondarily sorted by fluvial action (Baird 1986).

Bone samples

The taxa studied were *Turnix varia* (Painted Button-quail) for Clogg's Cave, McEachern's Cave and Devil's Lair, and *Turnix* sp. cf. *T. velox* (Little Button-quail) for Koonalda and Madura Caves (see Appendix). These species have been chosen because of the abundance of their elements in the deposits and the presence of this genus in a number of deposits.

A number of criteria were used in selecting material for study, including: the elements were all from the distal end of the humerus, the elements were complete before processing, the elements lacked damage or alteration to their surfaces, and the elements had a uniform light coloration. In some cases one or two of the criteria were not upheld because of the scarcity of material of appropriate geological age (i.e. different elements [youngest WI-61e = incomplete femur, and oldest = incomplete tarsometatarsus], incomplete elements [oldest N-4 = distal end humerus, youngest N-62 = proximal end humerus, and oldest N-64 = distal end humerus] and discoloured elements [oldest WI-61e = dark brown]). Table I gives the chronological distribution of the elements.

Preparation of the fossils

Fossils were ground to a fine powder, decalcified with 10 volumes of 0.5 M-EDTA, pH 7.5, then re-extracted with 10 volumes of 0.5 M acetic acid. The remaining bone powder was resuspended in 10 volumes of phosphate-buffered saline (PBS), pH 7.3, for testing. Extractions were carried out in siliconized glassware throughout, to minimize loss of protein on the sides of the tubes. Bones from modern *Turnix varia* and *Dromaius novaehollandiae* (Emu) were defatted by sequential extraction using acetone and ethyl ether, then air-dried and treated similarly to the fossils. All extractions were carried out at 4 °C.

Radioimmunoassay

A solid-phase radioimmunoassay for collagen was carried out on flexible polyvinyl microtitre plates. Wells were coated with 50 μ l of EDTA extract, acetic acid extract, or bone powder suspended in PBS and held overnight at 4 °C in a moist chamber. After coating with antigen, the plates were washed 3 times with PBS containing 1% skimmed milk powder and 0.05% Tween 20 (Blotto), and then washed 6 times with distilled water. The plates were then exposed to 200 μ l of Blotto for 2 hours at room temperature, to coat residual sites on the plastic, and again washed as above. The assay system was completed by adding 50 μ l of antiserum dilution to each well; the plates were kept overnight at 4 °C, and then washed as before. Antibody binding to the plates was detected using protein A from *Staphylococcus aureus*, labelled with 50 μ l 125 I, 50,000 cpm, with a specific activity of 40 μ Ci/ μ g, which was added to each well. The plates were kept overnight at 4 °C, washed as before, cut, and the activity bound to the wells was counted on a gamma counter. Under the conditions of the assay, the amount of radioactivity was proportional to the amount of collagen bound to the plate.

Each sample was tested in quadruplicate, using rabbit anti-collagen antiserum to measure specific binding to collagen, and normal rabbit serum to measure non-specific binding. In addition, each serum was tested on

uncoated wells of the plates, to determine the 'background' binding observed in the absence of fossils. Each sample was counted for 10 minutes, to increase the sensitivity of the assay. Modern *Turnix varia* and *Dromaius novaehollandiae* were included for comparison, and a control of soluble collagen from *Dromaius novaehollandiae* in PBS, in doubling dilutions from 5 $\mu\text{m}/\text{ml}$, was included on each plate.

Antibodies to collagen

Type I collagens were extracted from bird skins by pepsin digestion and purified by differential salt precipitation (Chung and Miller 1974). Rabbits were immunized subcutaneously with 5 mg of collagen in complete Freund's adjuvant initially, and in PBS 4 weeks later; antibodies reacted predominantly with native collagen and minimally with denatured collagen, as reported previously (Timpl 1982). The antiserum chosen for this study was a rabbit antibody to chicken collagen, selected because it contained the greatest reactivity to denatured collagen of any antiserum tested. Although it reacted most strongly with chicken collagen, it gave 85% of that reactivity with purified *Turnix* collagen.

RESULTS

The results of this study are summarized in Table 1. Samples of bone from modern *Turnix varia* and *Dromaius novaehollandiae* were included for comparison. However, the amount of collagen extracted from the sample of *Turnix varia* was approximately 60% of that extracted from the *Dromaius novaehollandiae* sample, and was lower than the amount obtained from some of the fossils. This bone was from a specimen that had been cleaned of flesh by exposure to dermestid beetles (*Dermestes maculatus*), in a warm moist atmosphere over several weeks. By contrast, the taphonomic accumulator for most fossils studied was the Barn Owl (*Tyto alba*), which implies that the bones would have been cleaned of flesh within hours, and excreted in a dry pellet. After preliminary drying, collagen is much more resistant to subsequent hydrolytic decomposition than is collagen, which remains moist (Wyckhoff 1972). The bone from the *Dromaius novaehollandiae* was from a freshly killed bird, which had been stored at -20°C since death. This difference in preparation may have affected the preservation of collagen. Therefore in Table 1 the amount of collagen found in the bones is expressed as a percentage of that extracted from the *Dromaius novaehollandiae* bone.

TABLE 1. Results of the analysis on collagen in avian fossils (*Turnix* spp.) of late Quaternary age from caves distributed across southern Australia. Results are expressed as mean counts per minute of radioactivity bound ± 1 standard deviation

Site	Cave environment	Age (years)	Bone sample		Collagen % (% of fresh collagen)
			Anti-collagen	NRS	
Fresh bone (<i>Dromaius novaehollandiae</i>)		—	18,100 \pm 2,300	500 \pm 110	—
No antigen		—	39 \pm 4	42 \pm 26	—
Clogg's Cave	Wet	8,720 \pm 230	11,160 \pm 3,400	210 \pm 120	64
		17,720 \pm 840	5,300 \pm 940	170 \pm 60	29
Devil's Lair	Wet	11,960 \pm 140	2,400 \pm 350	85 \pm 18	13
		32,480 \pm 1,250	4,500 \pm 450	160 \pm 4	25
Madura Cave	Dry	18,990 \pm 220	16,650 \pm 5,600	360 \pm 110	92
		37,880 \pm 3,520	67 \pm 2	45 \pm 6	—
Koonalda Cave	Dry	13,700 \pm 270	6,300 \pm 1,700	100 \pm 10	35
		> 20,600–< 21,550	1,800 \pm 370	68 \pm 9	10
McEachern's Cave	Wet	9,920 \pm 270	3,200 \pm 760	520 \pm 180	18
		14,880 \pm 240	3,700 \pm 1,400	450 \pm 160	21

Although the amounts of soluble collagen in the EDTA and acetic acid extracts were normally at or below 1% of the total, and therefore are not considered significant in the current study, those measurements from the McEachern's Cave elements yielded anomalously high counts (i.e. about 10% and about 5% of the total, respectively).

DISCUSSION

In previous studies on the preservation of collagen in fossils, samples of fossil bone obtained from cave deposits have contained very little collagen, irrespective of the age of the sample (Rowley *et al.* 1986; Rowley unpubl. data). This study was commenced to evaluate the effect of a damp cave environment on the preservation of collagen in bones. However, contrary to expectations, samples tested from both 'wet' and 'dry' caves contained significant residual collagen: one sample aged $18,990 \pm 220$ years contained 92% of the collagen detected in a modern bone sample. Therefore, the humidity of the cave does not appear to be a critical factor in the preservation of collagen. Other factors which we believed might have influenced collagen preservation included the geological age of the sample and its preservation history and size. The age of the bone was not clearly related to its collagen content, although the amount of collagen detected was significantly less in the older of the two samples for three of the five caves (Clogg's Cave, Madura Cave, and Koonalda Cave), and not significantly different for McEachern's Cave, the cave for which the age difference between levels was least. The effects of preservation remain untested since we purposely chose samples with similar taphonomic histories.

In contrast to our previous studies, however, these avian bones have been extremely well preserved, with an undamaged surface and minimal breakage. Such good preservation of small bones, each weighing less than 1 g, suggests that the microenvironments experienced by these bones may have been unusually favourable. Thus, Murray and Goede (1977) have shown that the preservation of elements in a cave environment is directly related to the weight and volume of the specimen. In our previous studies, the bones tested were much larger and less well preserved. Although good physical preservation is not an absolute indication of good preservation of collagen, and the only sample tested which did not contain measurable collagen was also rated as very well preserved, good structural preservation has previously been noted to be associated with preservation of amino acids of collagen (Wyckoff 1972).

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APPENDIX

Avian fossil material used during the course of this study, arranged with the youngest material from each locality above the older material. Cave numbers are from Matthews (1985). Abbreviations: com. = complete, dist. = distal, fem. = femur, hum. = humerus, incom. = incomplete, MV = Museum of Victoria, prox. = proximal, SAM = South Australian Museum, WAM = Western Australian Museum.

Identification	Element	Museum number	Cave	Cave no.
<i>Turnix</i> sp. cf. <i>T. velox</i>	Com. right hum.	SAM P.26117	Koonalda	N-4
<i>Turnix</i> sp. cf. <i>T. velox</i>	Dist. end right hum.	SAM P.261132	Koonalda	N-4
<i>Turnix varia</i>	Incom. right fem.	WAM 73.10.1451	Devil's Lair	WI-61c
<i>Turnix varia</i>	Incom. right tmt.	WAM 86.7.47	Devil's Lair	WI-61c
<i>Turnix varia</i>	Com. right hum.	MV P.183347	Clogg's	EB-2
<i>Turnix varia</i>	Incom. left hum.	MV P.1834377	Clogg's	EB-2
<i>Turnix</i> sp. cf. <i>T. velox</i>	Prox. end right hum.	MV P.184897	Madura	N-62
<i>Turnix</i> sp. cf. <i>T. velox</i>	Dist. end right hum.	MV P.184902	Madura	N-62
<i>Turnix varia</i>	Incom. right hum.	MV P.161181	McEachern's	G-5
<i>Turnix varia</i>	Com. right hum.	MV P.161131	McEachern's	G-5

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

by A. L. A. JOHNSON and C. D. LENNON

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 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.

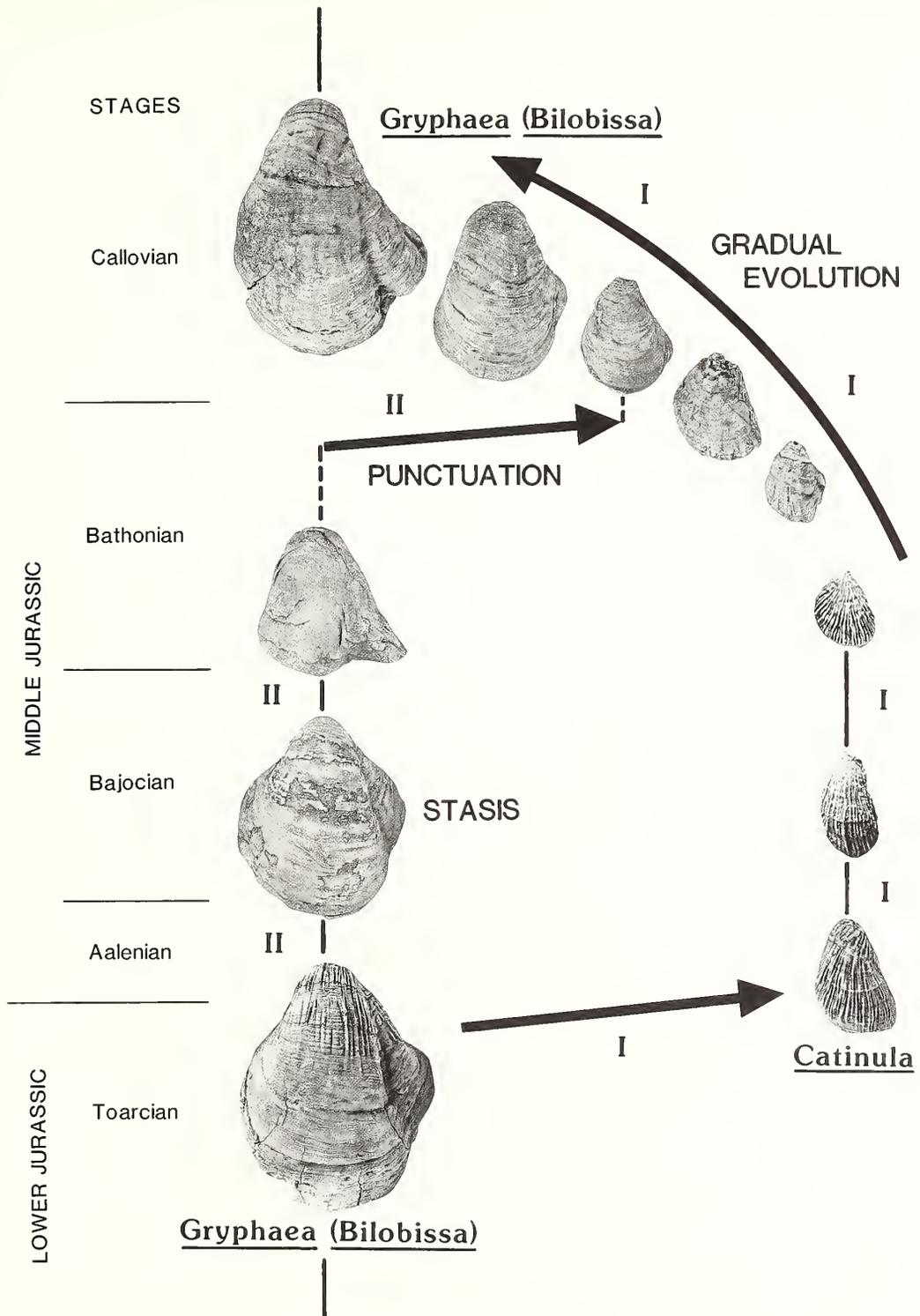
CONFLICTING HYPOTHESES FOR THE PHYLOGENY OF EUROPEAN MID-JURASSIC GRYPHAEATE OYSTERS

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 $\times 0.75$.



TEXT-FIG. 1. For legend see opposite.

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.

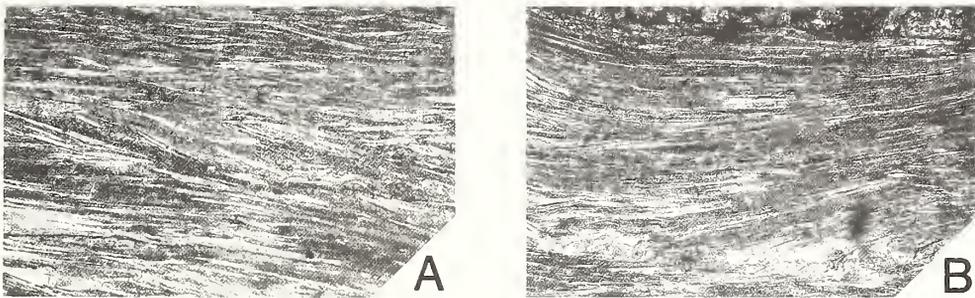
Summarizing, Sylvester-Bradley thought that '*Catinula*' evolved from *Gryphaea* (*Bilobissa*) in the Aalenian and subsequently evolved back into *Bilobissa* in the Callovian; Hallam thinks that these Callovian forms derive from a persistent (albeit in the Bathonian, exceedingly rare) *Bilobissa* lineage, 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 *Praexogyra* 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 *Praexogyra* species evolved from *Gryphaea* (*Bilobissa*) so the idea that *Praexogyra* descended from *Catinula*, put forward by Charles and Maubeuge (1953), can be discounted. Most

forms referred to *Praeexogyra* 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 'Liostrea', 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 (Pycnodontinae 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 *Catimula*. 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 *Catimula* 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 *Catimula*'. 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 *Catimula* 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 *Catimula*. 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/L, 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 (*temuiplicatus* 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.

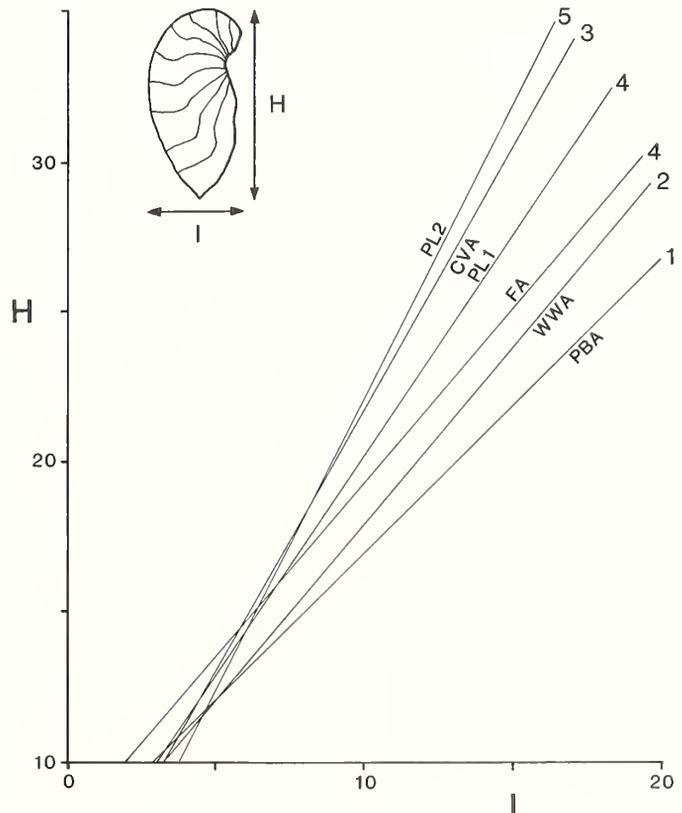
	Zones	Subzones	Populations
CALLOVIAN	Calloviense	Enodatum	KD1
		Calloviense	PL2
		Koenigi	FA PL1
	Macrocephalus	Kamptus	
		Macrocephalus	
BATHONIAN	Discus	Discus	CVA
		Hollandi	
	Aspidoides		
	Hodsoni		WWA
	Morrisi		
	Subcontractus		
	Progracilis		
	Tenuiplicatus		PBA

TEXT-FIG. 3. Stratigraphic position of Bathonian and early Callovian *Catimula* 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).

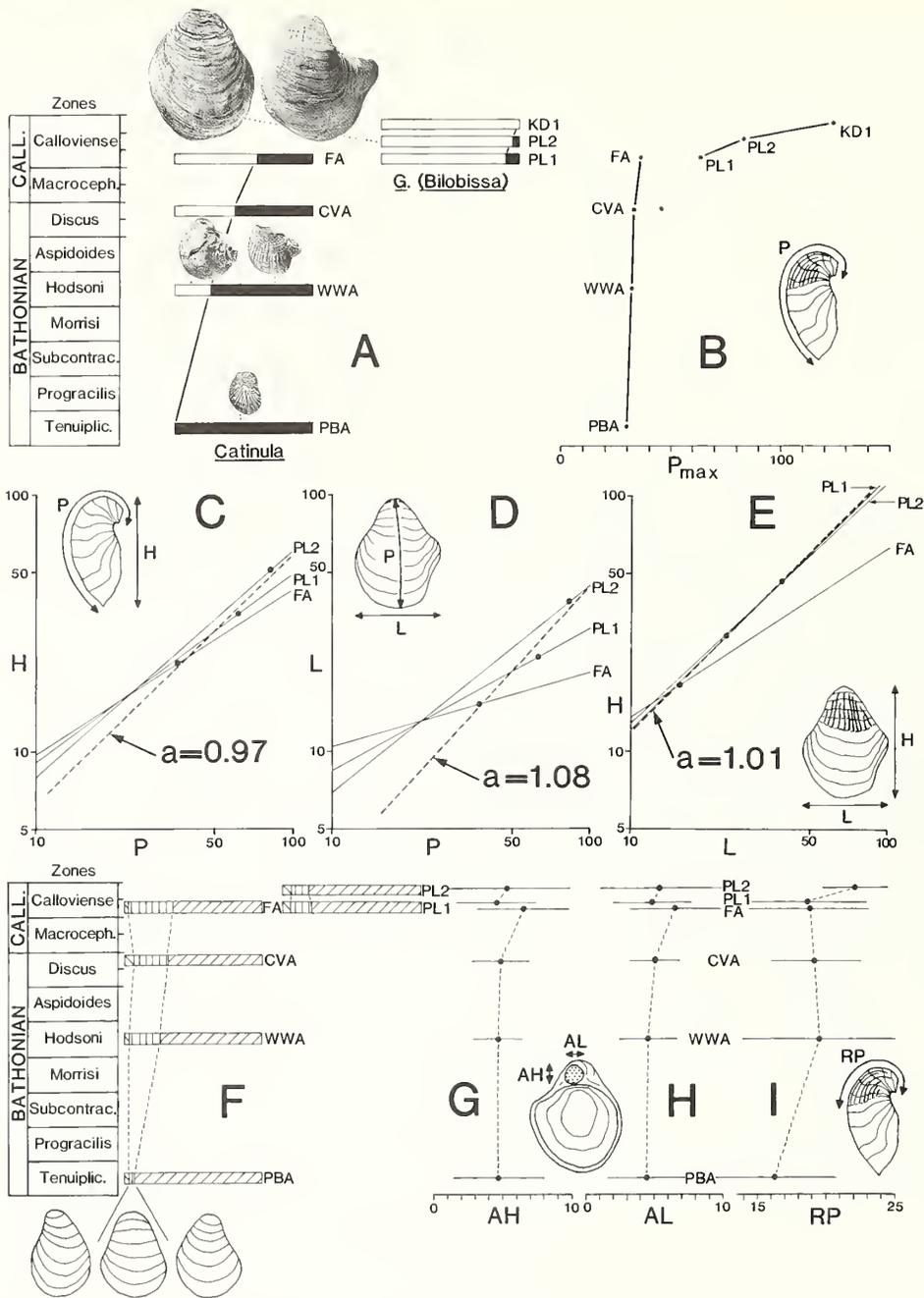
The proportion of ribbed to non-ribbed morphs shows a clear trend, a gradual decrease in the proportion of the former, through the sequence of populations (text-fig. 6A). A progressive increase in maximum peripheral height is also apparent (text-fig. 6B). However, in this case the rate of change is markedly 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*.

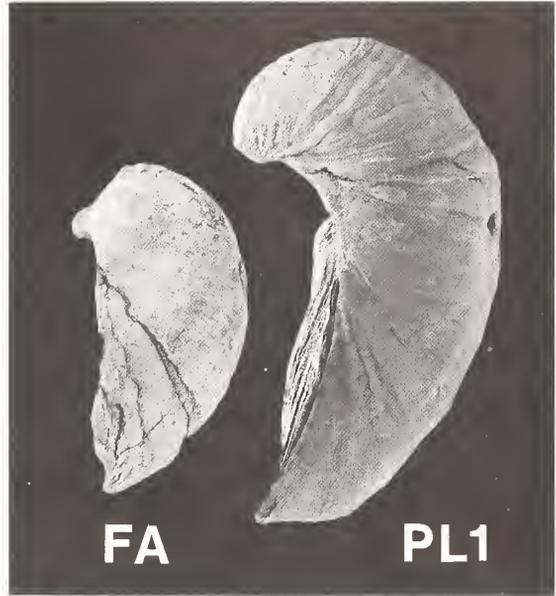
Gross shell dimensions. We pointed out above that Sylvester-Bradley’s angular measurement does not allow a true evaluation of relative incurvature (left valve ‘depth’; trend 3). Analysis of height (H) in relation to inflation (I), as carried out in connection with Brannan’s claims (see above), represents 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 *Catimula* 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 *Catimula* and *Bilobissa* populations (continuous lines). Dashed lines are regressions (slope $-a$ indicated) calculated from values (solid circles) corresponding to the

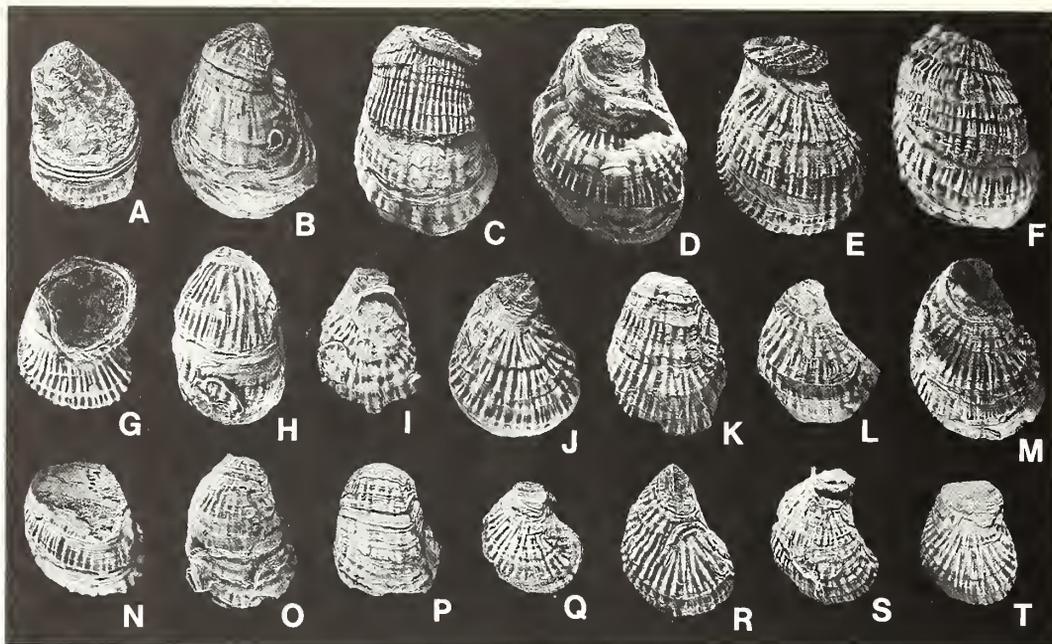
TEXT-FIG. 7. Anterior views of left valves from populations FA and PL1, showing the approach toward the fully developed gryphaeate coiling of the latter population within the former. LEIUG 104674 (FA), 104732 (PL1); $\times 1.7$.



(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 $\times 0.55$.



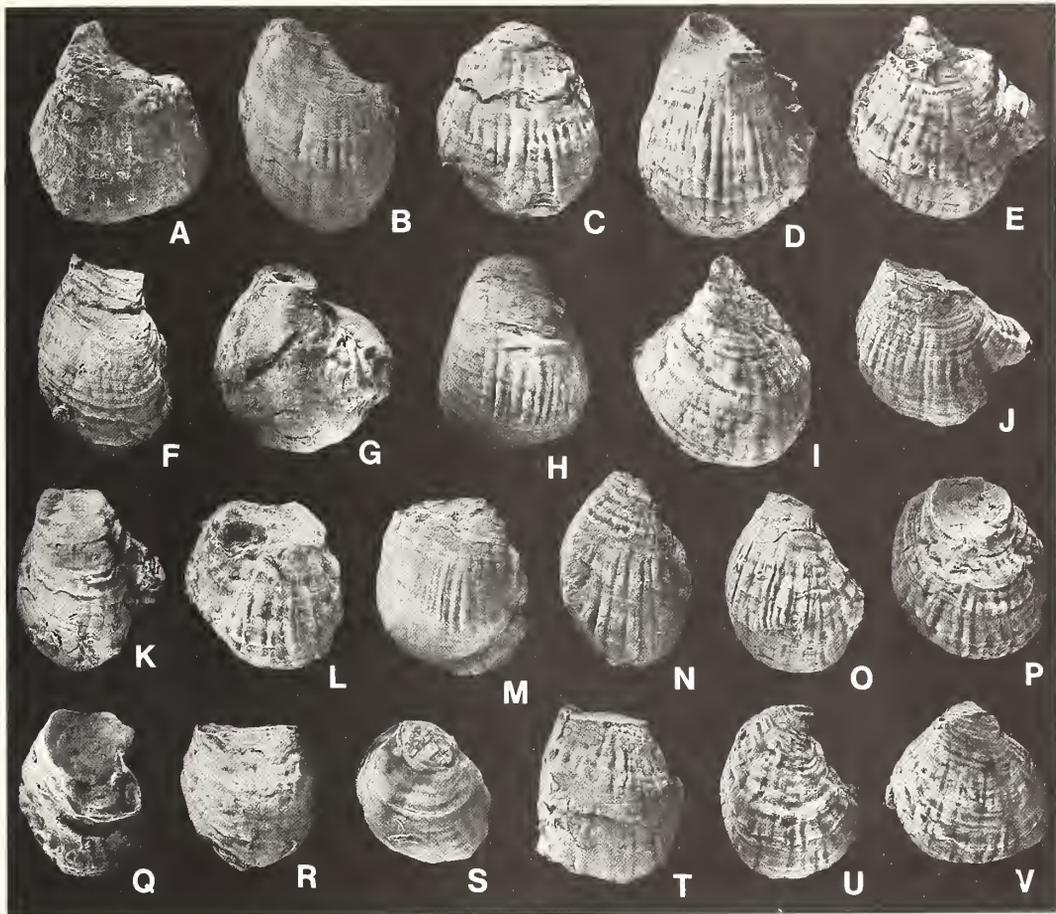
TEXT-FIG. 8. *Catinula* Rollier – population PBA (A–T: LEIUG 104604–104623 respectively): variation in external morphology of left valves. All specimens are ribbed morphs; $\times 1.7$.

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.

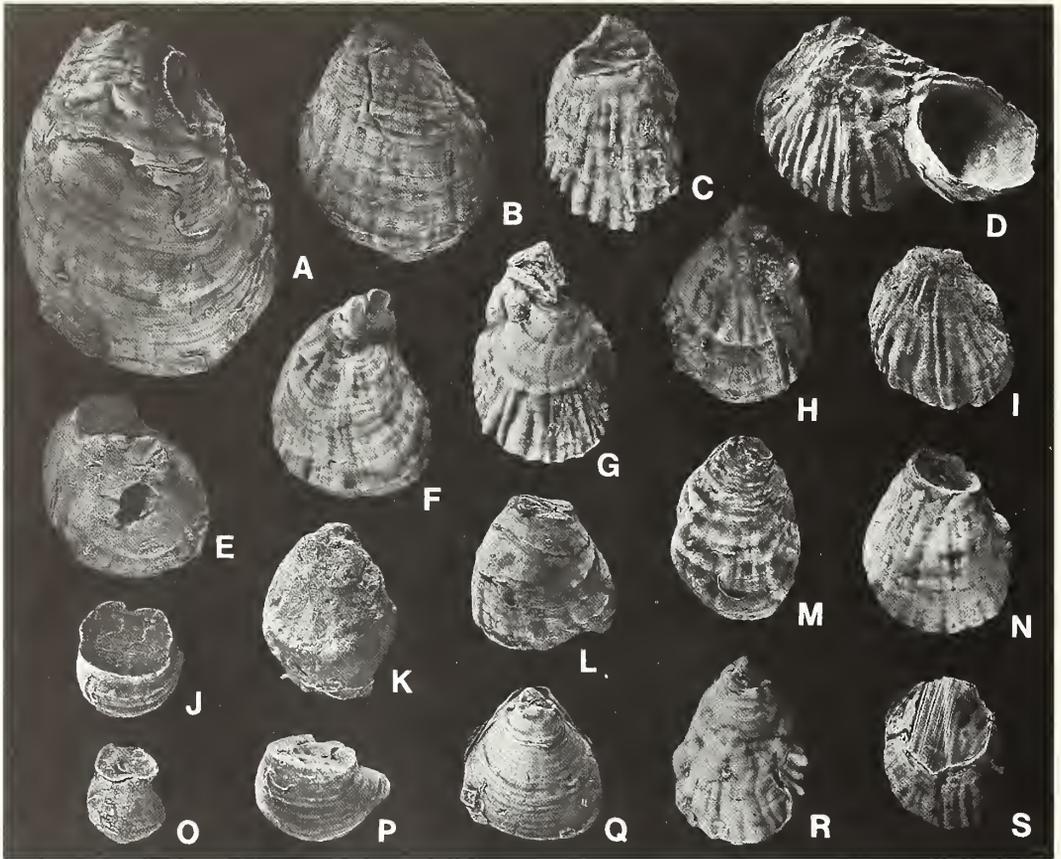


TEXT-FIG. 9. *Catimula* Rollier – population WWA (A–V: LEIUG 104373–104394 respectively): variation in external morphology of left valves. A, F, G, K, Q–S, ribbed morphs; remainder smooth; all $\times 1.7$.

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 *Catimula 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/Catimula* 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 *Catimula*. 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*.



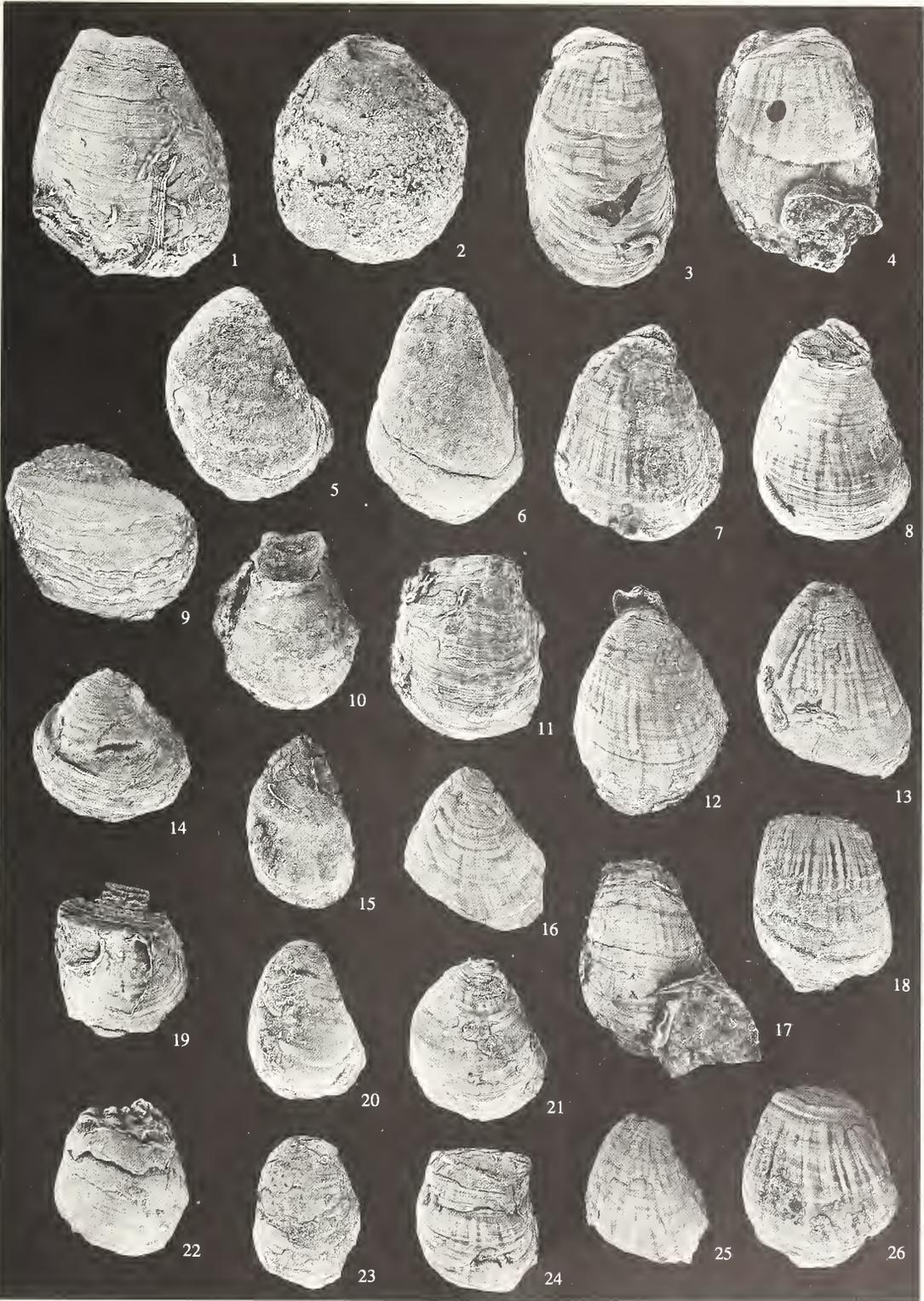
TEXT-FIG. 10. *Catinula* Rollier – population CVA (A–S: LEIUG 104474–104492 respectively): variation in external morphology of left valves. A, E, J–L, O–Q, smooth morphs; remainder ribbed; all $\times 1.7$. The exceptional size of the specimen figured as A may indicate that it is a contaminant.

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 $\times 1.7$.



CRC: Camarasa, Lérida, 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: Chateau 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.

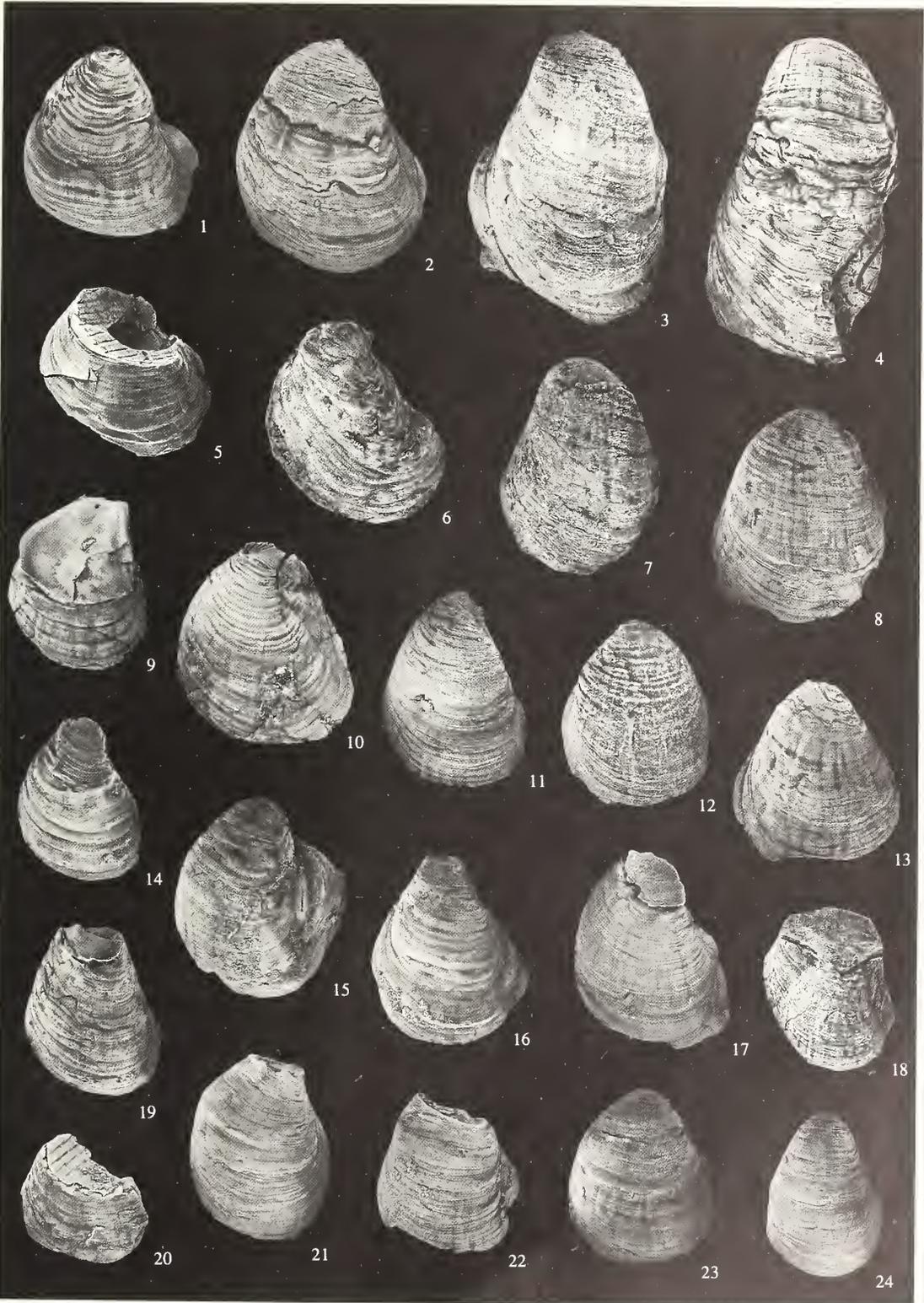
Sylvester-Bradley (MS notes) apparently considered that all the *G. (B.) pictaviensis* samples (last eight) were from the *levesquei* zone of the Toarcian. We have accepted the opinion of J. Gabilly (University of Poitiers; pers. comm., 1984), founded on detailed work in the Poitou region of France, 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 *Catimula/Bilobissa* lineage.

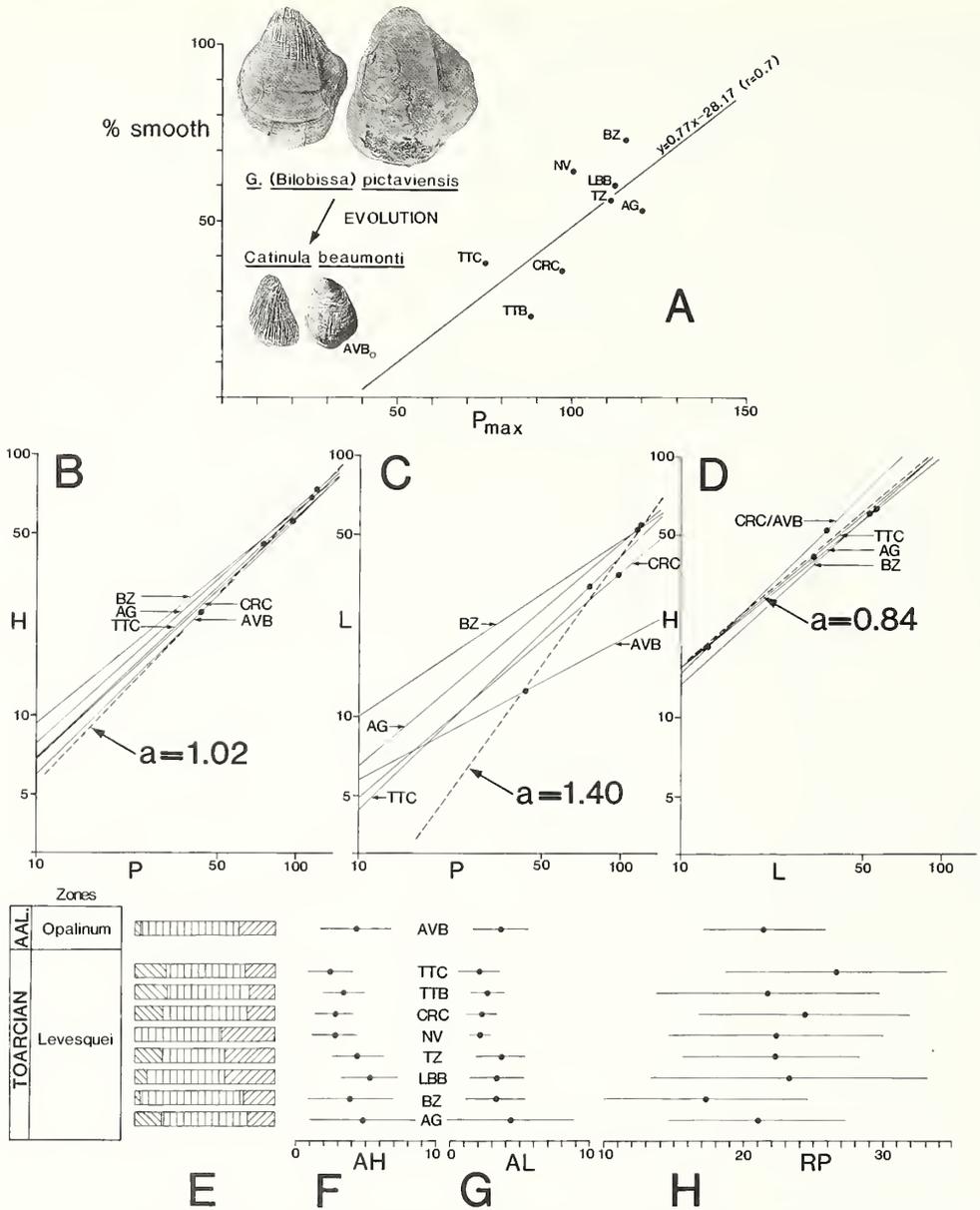
A regression calculated from the *G. (B.) pictaviensis* data passes remarkably close to the value for the *C. beaumonti* population (AVB). The whole array of data points can thus be interpreted in terms of a simple pattern of covariation. This, together with the near identity of ribbing form (see text-

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 × 1.7.



JOHNSON and LENNON, *Gryphaea (Bilobissa)*

Stages	Zones	<u>G. (Bilobissa)</u>	<u>Catinula</u>
CALLOVIAN	Jason		
	Calloviense	■	■
	Macrocephalus		
BATHONIAN	Discus		■
	Aspidooides		■
	Hodsoni		■
	Morrisi		■
	Subcontractus		■
	Progracilis		
	Tenuiplicatus	■	■
	Zigzag		■
BAJOCIAN	Parkinsoni		■
	Garantiana	■	■
	Subfurcatum		■
	Humphriesianum		■
	Sauzei	■	
	Laeviuscula		
AALENIAN	Discites		
	Concavum	■	
	Murchisonae	■	
TOARCIAN	Opalinum		■
	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:

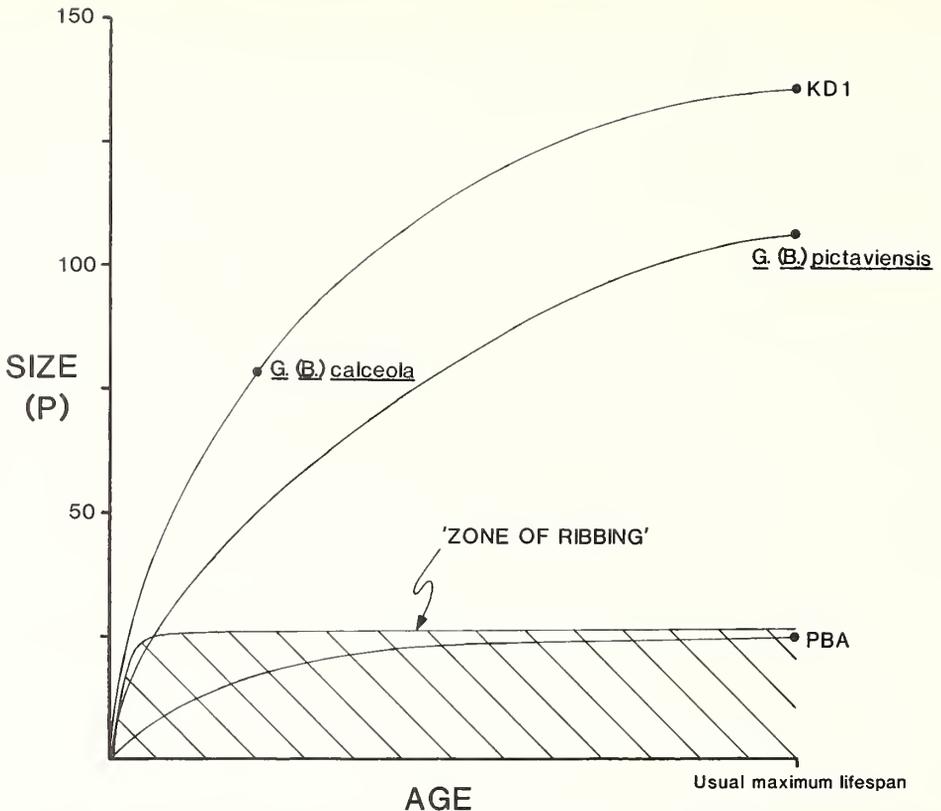
(1) ubiquitous ribbing in PBA (the most 'catinulate' population; smallest and with inferred slowest growth), combined with the late ontogenetic development of a smooth shell in the largest individuals in this population (text-fig. 8f);

(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 *Praeexogyra 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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THE TRILOBITE *PROTOLLOYDOLITHUS* FROM THE MIDDLE ORDOVICIAN OF NORTH PORTUGAL

by M. ROMANO

ABSTRACT. *Protolloydolithus* sp. nov., from beds of Llandeilo age in north Portugal, is described and figured. The genus was previously unknown from Iberia, and the present record indicates faunal links with southern Britain during middle Ordovician times. The appearance of the genus is linked to a transgressive event following an early Llandeilo lowering of the sea level.

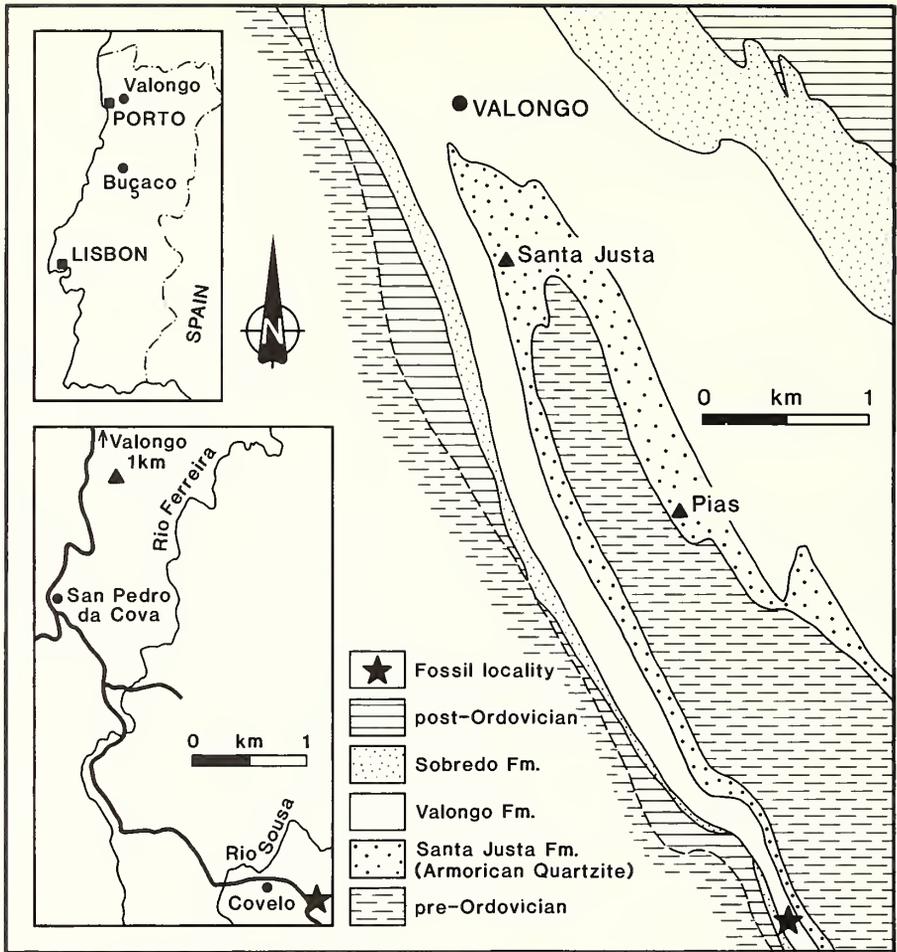
IN 1908 Delgado published extensive faunal lists from the Ordovician sequences of Portugal and recognized over thirty trilobite species from his 'Ordovician moyen' of the Valongo area of north Portugal. Many of these species have since been revised (see Henry 1980; Hammann 1974, 1983; Hammann *et al.* 1982; Gutiérrez-Marco *et al.* 1984, and references therein) and the dominantly mudrock sequence comprising Delgado's 'Ordovician moyen' (Valongo Formation of Romano and Diggins 1973-4) is now known to range in age from at least early Llanvirn to probably early Caradoc. No trinucleid trilobites were recorded by Delgado from north Portugal, but *Omnia* and/or *Deanaspis* occur in lower Caradoc strata in central Portugal and Spain (Hammann 1976; Rábano 1984; Young 1985). In Brittany, *Marrolithus* occurs in the upper part of the Postolonnec Formation (upper Llandeilo age, Henry 1980) but has not been recorded from coeval strata in central Portugal, despite the remarkable similarity of the two sequences (Henry *et al.* 1973-4; Henry and Romano 1978; Paris 1981; Romano and Henry 1982; Young 1988). Young (1985) regards their absence in central Portugal as being due to a hiatus on a topographic high.

REMARKS ON THE DISTRIBUTION OF *PROTOLLOYDOLITHUS*

A single specimen assigned to *Protolloydolithus* sp. nov. was collected from the upper part of the Valongo Formation near Covelo (text-fig. 1). The beds are within the top of the *Placoparia* (*Placoparia*) *tournemini* Biozone (rarely, specimens of the younger *P.* (*Coplacoparia*) *borni* also occur) of early Llandeilo age (Romano 1976). The specimen is unusual in that at present it is the oldest and only the second marrolithid known from rocks of middle Ordovician age in the Iberian/Armorican part of Gondwana, although rare specimens of 'Hanchungolithinae gen. et sp. inc.' occur in the *P. (C.) borni* Biozone of Spain (I. Rábano, pers. comm.). It is also the only record of *Protolloydolithus* outside Britain. The genus first appears in the lower Llanvirn of the Shelve inlier and South Wales with *P. ramsayi* (Hicks) and then *P. neintianus* (Whittard) (Thomas *et al.* 1984; Kennedy 1988). *P. salax* (Rushton and Hughes 1981) is known from the Llanvirn of the Great Paxton Borehole, Cambridgeshire, to be replaced in the lower Llandeilo of the Builtth area by *P. reticulatus* (Elles) (Hughes 1971).

AFFINITIES OF THE LOWER AND MIDDLE ORDOVICIAN TRILOBITE FAUNAS OF NORTH PORTUGAL

The trilobite faunas from the Arenig of southern Britain (Whittard 1966; Thomas *et al.* 1984; Fortey and Owens 1987) and the lower Llanvirn of North Portugal (Delgado 1908; Romano 1976, 1982a, b; Rebelo and Romano 1986) have much in common, namely *Neseuretus*, *Placoparia*, *Ectillaenus*, *Selenopeltis*, ?*Asaphellus*, *Colpocoryphe* and probably *Ogyginus* at generic level;

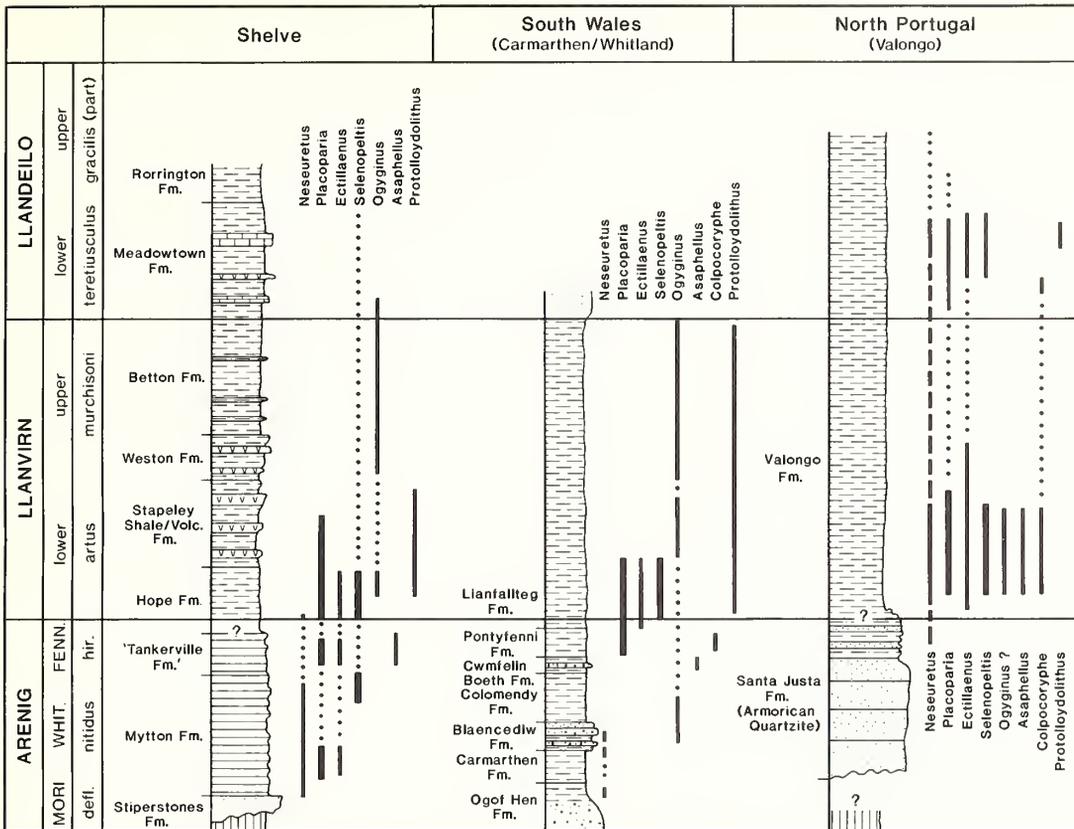


TEXT-FIG. 1. Locality maps and simplified geological map (after Delgado 1908) of Valongo area, north Portugal. Star indicates locality where *Protolloydolithus* sp. nov. was collected.

Placoparia (*P.*) *camabriensis* and ?*Selenopeltis macrophthalmus* at specific level. The ranges of these genera in the Shelve, Carmarthen/Whitland and north Portugal are shown in text-fig. 2.

The Arenig trilobite faunas of Shelve and Carmarthen have many taxa in common but also show important differences. Fortey and Owens (1987) pointed out that the varied trinucleid assemblages from the upper part of the Mytton Formation are absent in South Wales, and the Llanfallteg Formation fauna is not represented in the Shelve area. These authors explained the absence of the Llanfallteg fauna by suggesting that since the fauna and sediment of this unit represent a regressive phase, and as the Shelve area occupied an 'on-shelf' position, the Llanfallteg faunas did not reach the Shelve area.

The importance of transgressive/regressive events in controlling the distribution of shallow-water faunas is also well demonstrated in the composition of the north Portuguese faunas. Although approximately twenty-five and seventy species are present in the Shelve Arenig faunas and deeper-water equivalents in south Wales respectively (Whittard 1966; Fortey and Owens 1987), in north Portugal the shallower-water coeval Armorican Quartzite facies has yielded only *Neseuretus* (similarly for the Stiperstones Formation in the Shelve), and in Brittany some three species are



TEXT-FIG. 2. Simplified Ordovician sequences of Shelve Inlier, south Wales and north Portugal with ranges of selected trilobites (after Whittard 1966, 1979; Fortey and Owens 1987; Kennedy 1988; and author). Abbreviations: MORI. = Moridunian; WHIT. = Whitlandian; FENN. = Fennian. Thick vertical bars indicate similar species are present in all three areas.

recorded (Henry 1971, 1980). Fortey and Morris (1982), Fortey and Owens (1987) and Cocks and Fortey (1988) have previously pointed out the significance of *Neseuretus* in identifying inshore facies, although species of the genus also occur in deeper-water platform sites (Hammann 1983). Fortey and Owens noted that the diverse Arenig trilobite faunas of south Wales only appeared in the more shelfward sites of Gondwana during the Llanvirn or later. In north Portugal this is well shown by the appearance of a relatively diverse trilobite fauna of early Llanvirn age in mudrocks above the thinly bedded, heterolithic Armorican Quartzite sequences (text-fig. 2).

Deeper-water atheloptic assemblages (characterized by 'blind or nearly blind trilobites': Fortey and Owens 1987, p. 106), such as those from the Fennian of south Wales are not known in Portugal; these assemblages were considered to imply a water depth of 300 m or more (Fortey and Owens 1987, p. 106). Estimates based on sedimentological studies in central Portugal suggested that water depth there was probably no more than 80 m during the Llandeilo (Brenchley *et al.* 1986). Assuming a maximum average slope to the north of 0.1° for the Iberian Platform in Llandeilo times (Brenchley *et al.* 1986, p. 252), this would suggest that the water depth in north Portugal was in the order of 100–150 m, well above the inferred depth to support atheloptic assemblages.

The appearance of *Protolloydolithus* in the Llandeilo of north Portugal, along with a relatively sudden increase in diversity of the trilobite species, is related to another regressive/transgressive

couplet. The regressive event is documented in central Portugal (and Crozon Peninsula of north-west France) by the sandstones of the Monte da Sombadeira Formation (and Kerarvail Formation of north-west France), followed by a transgressive phase and the return to mudrock deposition with an increase in diversity and individual abundance of the benthos. This sandstone unit is not present in the deeper-water sequences of north Portugal, but work in progress at Valongo with Dr T. Young has identified slight lithological changes which, together with the faunal changeover, reflect the events recognized in central Portugal. However, the diverse Llandeilo faunas of north Portugal do not show such close affinities with the southern British faunas as was apparent in the early Ordovician. Only four trilobite genera are common to both regions in the Llandeilo: *Protolloydolithus*, *Selenopeltis*, *Ogyginus* and *Nobiliasaphus*. Of these, *Protolloydolithus* probably spread from the Builth area of Wales, while the other three were already endemic to Iberia (Delgado 1908; Romano 1982*b*; Romano *et al.* 1986). The reduced faunal affinities of southern Britain and north Portugal in the Llandeilo are considered to be the result of an increased separation of the two regions by middle Ordovician times and/or the relatively smaller magnitude of the transgression compared with that during the Llanvirn.

It is of interest to note that on a global scale Fortey and Cocks (1988) record an early Llandeilo regression followed by a major early Caradoc transgression. In Iberia there is evidence of two Llandeilo shallowing events: that represented by the Monte da Sombadeira Formation and a younger one which reached maximum shoaling during Cabril Formation times (Young 1988, p. 390). Both these formations (or equivalent units) are also recognized in Brittany and crop out in an area of over 75000 km². It therefore appears unlikely that the regressive sandstones of these two formations (and the intervening transgressive mudrocks with their relatively enriched benthos) represent a purely local tectonic effect. A more likely scenario is that the Llandeilo regression was composite, prior to the major early Caradoc transgression. Further detailed investigations into other middle Ordovician platform sequences may provide supportive evidence.

SYSTEMATIC PALAEOLOGY

Family TRINUCLEIDAE Hawle and Corda, 1847

Subfamily MARROLITHINAE Hughes, 1971

Genus PROTOLLOYDOLITHUS Williams, 1948

Type species. Trinucleus Ramsayi Hicks, 1875. Original designation by Williams 1948, p. 66. Lower Llanvirn, Ramsey Island.

Protolloydolithus sp. nov.

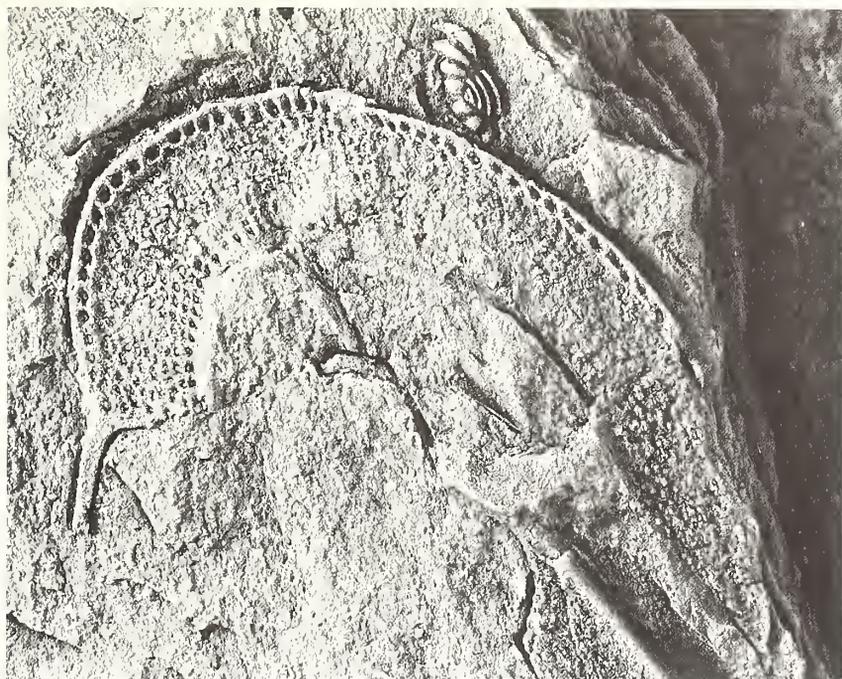
Text-fig. 3

Material. Single specimen (SG 6717); nearly complete but distorted fringe showing internal mould of part of upper lamella and external mould of part of lower lamella. Specimen housed in the museum of the Portuguese Geological Survey, Lisbon.

Horizon and locality. Upper part of Valongo Formation, c. 70 m below top of unit; top of *Placoparia* (*P. tournemini*) Biozone, lower Llandeilo. Locality 3/41 (see Romano 1976), a small quarry to the east of the road approximately 1 km ESE of Covelo (text-fig. 1).

Description. Cephalon approximately 14 mm wide across base of genal spines, margin apparently evenly rounded. Fringe more or less flat, although with slightly upturned outer arc of pits, of broadly constant width, but possibly narrows anteriorly in front of glabella. Preserved length of genal spine is 2.5 mm (but possibly at least 5 mm long), extending posteriorly and slightly outwards; lateral margins of fringe and genal spine are not in a straight line. Dorsal surface of spine is flat with very faint median furrow (possibly due to flattening).

Pits (E1) of outer arc larger than other pits; at least forty-five are visible but it is not possible to give an accurate fringe formula. Pits are largest anterolaterally and on the whole are fairly regularly disposed. Internal to E1 there is a well-marked girder, and a girder list which dies out before reaching genal spine. II arc



TEXT-FIG. 3. *Protolloydolithus* sp. nov. (SG 6717). Valongo formation, *Placoparia* (*Placoparia*) *tournemini* Biozone, Llandeilo. From small quarry approximately 1 km ESE of Covelo and 11 km SSE of Valongo. $\times 6.5$.

reasonably distinct, pits smaller and more numerous than in E1 (where preserved, six or seven E1 pits lie adjacent to ten I1 pits). Preservation is generally rather poor for the rest of the fringe, and apart from the distinct innermost arcs appears to consist of randomly arranged pits. However, nine or ten A 'arcs' may be present across the fringe between the cheeks and E1. In or F (flange) pits (Hughes *et al.* 1975) cannot be clearly distinguished although on the right-hand side there are possibly a few F pits. Laterally at least two regular inner arcs are present. The pits of these arcs show regular concentric and radial arrangement for at least fourteen radial rows, while two more external arcs are seen (where preservation allows) to continue this regular arrangement for at least six radial rows. Suggestion of very faint facial suture cutting across base of genal spine, running subparallel to distal part of posterior border margin.

Glabella and cheeks not preserved, although part of inner flange of fringe is present on right-hand side. Rest of exoskeleton unknown.

Discussion. The recognition of a single E1 arc, prominent girder and strong girder list, together with the generally irregular arrangement of the pits, indicates that the species may be assigned to *Protolloydolithus*. According to the diagnosis of the genus given by Whittard (1955, p. 40 and 1956, p. 41) and Hughes *et al.* (1975, p. 577), the present species shows some ?minor differences. I1 pits are not noticeably larger than the other inner pits; I pits are not all 'irregularly positioned'; F pits do not appear to be well developed. However, in *P. ramsayi* the I1 pits are not always significantly larger than the other pits (Whittard 1956, pl. V, fig. 11) and there is a tendency in *P. ramsayi* and *P. neintianus* for some regularity of inner I arcs anteriorly, and laterally in *P. salax*.

The specimen is considered to represent a new species since it does not closely resemble any described species of the genus. It is left unnamed at present as only a single specimen is known. The Llanvirn species *P. ramsayi*, *Protolloydolithus* sp. (Kennedy 1988) and *P. neintianus*, as well as the Llandeilo form *P. reticulatus* (Elles) (Hughes 1971) differ mainly from the Portuguese species in not possessing such well-ordered internal I arcs; in addition, the latter species has a much narrower fringe. The well-ordered pits indicate an advanced form (Dr J. K. Ingham, pers. comm.) and are

considerably better ordered than the arrangement seen in the broadly contemporaneous Builth species.

Acknowledgements. I should like to thank Dr J.-L. Henry for encouraging me to 'think again' about the specimen; Drs R. A. Fortey and J. K. Ingham for helpful discussions; Dr T. P. Young for reading the manuscript and photographing the specimen. Dr I. Rábano sent me information on Spanish middle Ordovician trinucleids. Mr M. Cooper redrew the diagrams, and Miss P. Mellor typed the manuscript.

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CADDISFLY PUPAE FROM THE MIOCENE INDUSIAL LIMESTONE OF SAINT-GÉRAND-LE-PUY, FRANCE

by MARGUERITE HUGUENEY, HENRI TACHET *and* FRANÇOIS ESCUILLIÉ

ABSTRACT. Trichoptera pupae are described for the first time in the Indusial Limestone Formation of Saint-Gérand-le-Puy, Allier, France. The caddisfly pupal cases, named *Indusia tubulosa*, constitute this limestone. The relationships of these pupae to extant families are analysed and they are placed in the Limnephilinae. Fossil preservation and palaeoenvironment are discussed.

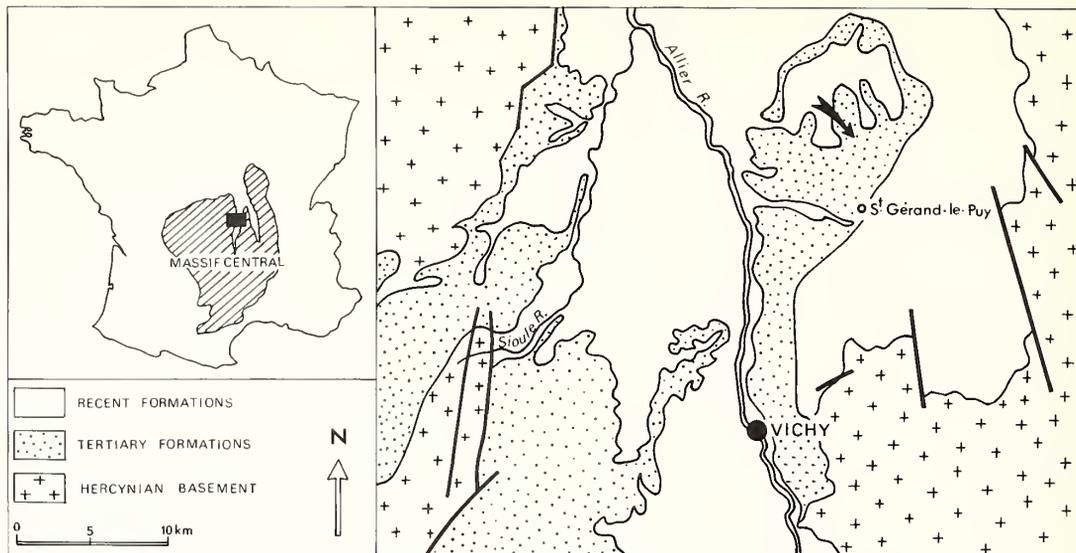
Bosc (1805) was the first author to mention the Indusial Limestone of Saint-Gérand-le-Puy and to describe the tubes of which it is composed as consisting 'de très-petits hélices fossiles agglutinés, tantôt en masse irrégulière, tantôt en forme de cylindres ouverts par un bout et fermés par l'autre, ou mieux, de cônes creux d'environ un pouce et demi de long sur cinq lignes de diamètre total, et un peu plus d'une ligne d'épaisseur'. He gave them the name of *Indusia tubulosa*, but was not able to establish if they were made by polychaete annelids or by caddisflies (Insecta: Trichoptera). Brongniart (1810) demonstrated the freshwater origin of the limestone and assigned a caddisfly larval origin to the tubes. As the knowledge on extant Trichoptera progressed, Oustalet (1870) classified these cases in the genus *Phryganea*; he even recognized two new species: *P. gerandiana* for the cases from Saint-Gérand and *P. corentiana* for those found in Gergovie (Puy-de-Dôme).

Up to now, no body part of Trichoptera had ever been described from Saint-Gérand, but recently two fossil pupae were found which prove that the tubes are really caddisfly cases. This study presents these new finds and provides evidence for systematic assignment and taphonomy, taking into account that much progress has been made in the taxonomical and biological knowledge of the Trichoptera since the first record.

GEOLOGICAL SETTING

The fossils were found at Le Vendant limestone quarry, Boucé commune, Allier Department, France, which is situated in the Limagne d'Allier basin in the Massif Central.

The Limagne d'Allier cuts a north-south furrow in the Hercynian basement of the Massif Central. The Allier River runs through this basin, which is 180 km long and roughly 35 km wide. Geophysical studies and boreholes demonstrate that, from the Eocene to the beginning of the Miocene, a series of small sedimentary basins, isolated from each other by tectonic or volcanic thresholds, opened from north to south in a plateau area and contained lakes of various sizes. Rapid subsidence led to the deposition of more or less thick sequences of clastic and carbonate sediments (Donsimoni and Giot 1977). Progressive migration from south to north during the Oligocene restricted the upper sequence (Upper Oligocene-Aquitainian) to the Vichy area; here, the fluvio-lacustrine sediments are characterized by the widespread development of stromatolitic limestones, which reached a maximum in the Saint-Gérand-le-Puy area. Algal growths in various shapes and sizes, from small ooliths and pisoliths to large spheroidal and columnar concretions, coalesced to form a limestone reef more than 20 m thick. This limestone often encloses an aggregate of tubes 3 or 4 cm long and 1 cm wide, generally covered by small mollusc shells and bound together by a



TEXT-FIG. 1. Location map: Le Vendant quarry is indicated by an arrow.

calcareous crust: since the tubes resemble caddis larvae cases, the limestone is known as the 'Calcaire à Phryganes' or the 'Indusial Limestone'.

The oldest bioherms are contemporaneous with the fossil mammal site of Cournon (Puy-de-Dôme), which is dated at about 30 Ma; the youngest correlate with the mammalian fauna of Marcoin (Puy-de-Dôme), which is older than the marine Burdigalian (> 21.9 Ma). Favourable conditions for caddises lasted for 8 million years. Later on, the lake progressively filled and the swamps dried up.

Le Vendant quarry belongs to the quarry group known since 1833 as Saint-Gérand-le-Puy, when Geoffroy-Saint-Hilaire recorded fossil vertebrate-bearing deposits there. These quarries have been exploited for more than 150 years, and the large and small mammals recovered are so numerous and important that these localities have been selected as a reference level for the fossil mammal biozonation of Europe (Mein 1976). They have also yielded an exceptional variety and abundance of fossil bird remains, mostly aquatic forms (Cheneval 1984), and are internationally recognized fossil bird localities, having no equivalent within or outside Europe. Nevertheless, caddisflies have never before been described from there.

SYSTEMATIC PALAEOLOGY

- Class INSECTA Linnaeus, 1758
 Order TRICHOPTERA, Kirby, 1813
 Family LIMNAPHILIDAE Kolenati, 1848
 Subfamily LIMNAPHILINAE Kolenati, 1859
 Genus INDUSIA Bosc, 1805
Indusia tubulosa Bosc, 1805
 Plate 1, figs. 1-4; Text-fig. 2A

- 1805 *Indusia tubulosa* Bosc, pp. 397-400, pl. 7, figs A-E.
 1810 *Indusia tubulata* Bosc; Brongniart, p. 357.
 1829 *Indusia tubulosa* Bosc; de Serres, p. 208.
 1833 *Indusia tubulata*; Geoffroy-Saint-Hilaire, p. 77.

- ?1871 *Phryganea Gerandiana* Oustalet, p. 102.
?1871 *Phryganea Corentiana* Oustalet, p. 101.
1969 *Indusia tubulosa* de Serres, *non tubulata* Brongniart; Fischer, p. 326.
1973 *Boscindusia tabulata* (sic) Bosc; Vialov, p. 586.

Emended diagnosis. See Vialov and Sukatsheva 1976.

Remarks. Bosc (1805) always referred to the fossils as 'Indusie tubuleuse'; the name of the taxon is latinized only in the title of his plate, which is placed much farther on in the volume. This fact led to errors on the valid specific name and the author's attribution of this binomial.

The International Code of Zoological Nomenclature (3rd edition, 1985) makes a clear distinction between the work of an animal (art. 23 f-iii) and its traces (art. 23 g-iii). In our opinion a fossil caddis case corresponds to the work of an animal and is not a trace fossil: normally, trace fossils are features independent of their producers; this is not at all the case for a caddis case, for the larva cannot live without it. So we consider that we have to refer to art. 23 f-iii and that the name *Indusia tubulosa*, created for the cases, is valid for the animals which made these cases.

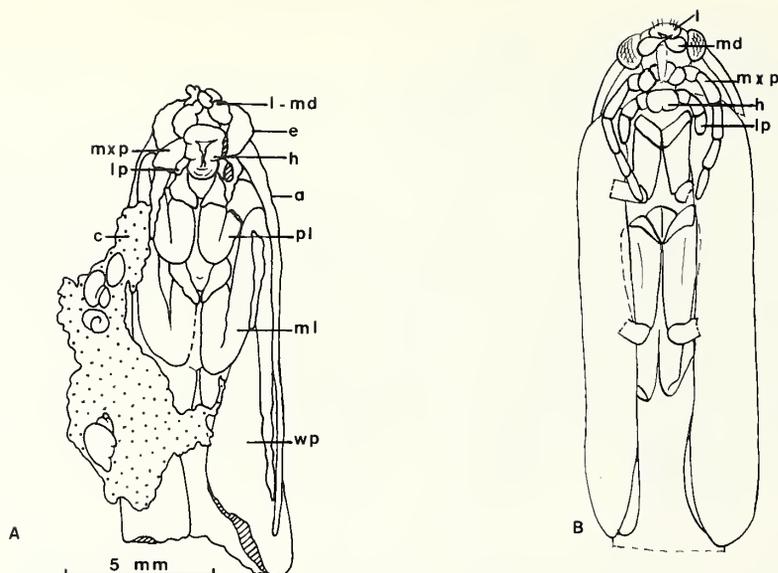
Repository. Centre des Sciences de la Terre, Université Lyon I, France; No. FSL 97698-97701.

Description. One of the two specimens is lying in its case and only its back is exposed. The other is free, but fragments of the case remain attached to it and only the ventral face can be observed clearly.

Head: eyes, antennae, labial and maxillary palpi and haustellum are well preserved. In front of the maxillary palpi, the head shows a bifid structure interpreted as the mandibulae spread out and joined to the labrum. The dimensions and the relative position of the labial and maxillary palpi are characteristic for pupae of the families Phryganeidae or Limnephilidae. Thorax: coxae and femora of the prothoracic legs and coxae of the mesothoracic ones are easily recognizable. The entire left mesothoracic leg, with all its distinct segments, is lying on the wing pad as in Recent Trichoptera pupae. Dorsal face: similar in shape and ornamentation to those of Phryganeidae and Limnephilidae.

Discussion. The pupae and the cases (indusia of the earlier authors) identify this form as a member either of the Phryganeidae or of the Limnephilidae. In these two families there exist genera whose larvae construct large cylindrical cases. In the extant Phryganeidae, the cases are constructed exclusively from plant material arranged in a spiral. The pupae of *Indusia tubulosa* are closer to those of the family Limnephilidae and even to the subfamily Limnephilinae. In the genus *Limnephilus*, the larvae build their cases from more diverse materials: owing to the availability of construction materials and behavioural preferences, they choose vegetable or mineral matter, or mollusc shells, or a mixture of these components. The fossil forms of Saint-Gérard seem to have preferred mollusc shells, ostracod carapaces or ooliths (Donsimoni 1975; Guillot 1979), but we observed also, in some fossil cases, vegetable fragments mixed with mollusc shells exactly as in the extant *Limnephilus*. In the Limnephilinae, different species can build similar cases but, reciprocally, different cases can be built by the larvae of a single species. So it is impossible to determine if the Saint-Gérard Limnephilinae represent one or more species and, without adult specimens, to decide whether the genus *Indusia* is a synonym of the genus *Limnephilus*, the cases of which are very similar to those of *Indusia*.

The author of the taxon *Indusia tubulosa* is Bosc (1805) and not Brongniart (1810) or de Serres (1829) as indicated by Fischer (1969) and Vialov and Sukatsheva (1976). The genus *Indusia* includes several fossil species (often only cases) from the Cretaceous and the Tertiary of Mongolia, Siberia and North America (Fischer 1969, Vialov and Sukatsheva 1976). As far as true Limnephilidae are concerned, the genus name *Phryganea* given by Oustalet (1871) to his new species is not correct, but as different species of Limnephilidae can build similar cases, it is impossible to decide if *I. gerandiana* and *I. corentiana* are synonyms of *I. tubulosa*.



TEXT-FIG. 2. A, *Indusia tubulosa* Bosc, 1805. FSL 97699. Ventral aspect of body. a, antenna; c, case; e, eye; h, haustellum; l-md, mandibulae joined to the labrum; lp, labial palp; ml, mesothoracic leg; mxp, maxillary palp; pl, prothoracic leg; wp, wing pad. The left maxillary and labial palpi and part of the left prothoracic leg are broken. B, *Limmephilus* sp. Ventral aspect of the anterior part of an extant pupa showing especially the masticatory apparatus.

TAPHONOMY AND PALAEOENVIRONMENT

This find of fossil caddis pupae is quite remarkable, considering this stage lasts only about two weeks in the trichopteran life cycle, and how fragile the animals are at that precise moment when the most intensive histolysis of the larval tissues takes place. When natural mortality of the pupa occurs, the dead tissues decay rapidly (in a few days) and only an empty, floppy pupal cuticle remains in the case. Evidently, the caddisflies were encrusted very rapidly, just before emergence, at the precise moment when the tissues became firm; but the tissues themselves are not preserved and the two specimens are natural moulds of external surfaces of the pupae.

On the other hand, since all the cases are the same size, Donsimoni (1975) believed, rightly in our opinion, that they are pupal case concentrations. It is unlikely that these concentrations are due to water currents because, just before the metamorphosis and even in stagnant conditions, the Trichopteran larvae fasten their cases on the substrate (here, rocky substrate or other cases) with silk threads. Under natural conditions, bacterial decay destroys the silk threads that bind the constitutive elements of the cases together in just a few months. In Saint-G erand, most of the cases

EXPLANATION OF PLATE I

Figs. 1-4. *Indusia tubulosa* Bosc, 1805. Indusial limestone of Saint-G erand-le-Puy (Le Vendant quarry), Aquitanian. 1a, b, FSL 97699, isolated pupa, $\times 3.6$; 1a, stereo-pair of ventral side; 1b, stereo-pair of lateral side. 2, FSL 97698, section of an indusial bioherm showing the caddisfly tubes, transversely or longitudinally cut, encrusted by repeated algal laminations, $\times 1$. 3, FSL 97700, isolated and non-encrusted tube from another more sandy part of the same quarry; this exceptional tube differs from the others by the helicoidal and regular arrangement of the *Pseudammicola gerannensis* (Rey, 1974) shells, $\times 1.6$. 4, FSL 97701, pupa preserved in its case, stereo-pair of dorsal side, $\times 2.5$.

Fig. 5. *Limmephilus* sp., extant larval case made from mollusc shells, $\times 2$.



are empty or filled with marly sediments. The rapidity of fossilization explains why they are preserved in such large quantities.

Virtually all the older records of Trichoptera, from Upper Cretaceous to Tertiary (the last partly contemporary with the Indusian Limestone fauna), are based on small adult remains from worldwide amber (Ulmer 1912; Botosaneanu and Wichard 1983), while *Indusia* are large. In amber, the case-makers are generally represented by extant genera of the families Phryganeidae, Calamoceratidae, Molannidae and Sericostomatidae. But the family Limnephilidae has not yet been reported. In Laurentiaux's opinion (1953) families recovered from amber could indicate a tropical or subtropical climate. Even if the lack of Limnephilidae in amber is due more to the adult way of life than to a real absence of the family at that time, we can suppose that the exceptional accumulation of the Limagne Indusian Limestone could be related to the Tertiary climatic changes (in particular progressive cooling). Indeed, whilst tropical or subtropical forms are represented in the rich vertebrate fauna of Saint-Gérard (crocodile, aninga, secretary bird, parrot, pangolin, tapir), palynology suggests the temperate deciduous forest region (*Ulmus*, *Ahnus*, etc.: Gorin 1975). At present the Limnephilinae are characteristic of holarctic temperate or cold habitats (Schmid 1955).

Most of the species recovered from amber, certainly adapted to higher temperatures, must have disappeared from the holarctic region and have been partly replaced by the Limnephilidae, more flexible in behaviour and with a greater ecological plasticity. Only the extant subfamily Limnephilinae includes species able to survive in temporary pools (Wichard and Reichel 1970; Wiggins 1973) due to an imaginal diapause. Moreover, the larvae of some species of this subfamily are the only Trichoptera to occur in brackish water (Sutcliff 1960; Leader 1971; Malicky 1974; Colburn 1983). In Saint-Gérard, skeletal elements of fossil flamingoes (*Phoenicopterus croizeti*, not very different from the extant *Phoenicopterus ruber*) are commonly found, and modern flamingoes are known to exploit food sources available only in brackish water, therefore salinity tolerance is also suggested by Donsimoni (1975) for the fossil *Indusia*. The fossil assemblage of Saint-Gérard, and especially the flamingoes, remind us of the modern community of the brackish Natron Lake in Africa, since one or two million *Phoeniconaias minor* and several thousand *Phoenicopterus ruber roseus* live there. Sedimentary conditions are strikingly similar (Hillaire-Marcel and Casanova 1987) but, as the distributional range of the Limnephilinae does not reach Africa, there is no opportunity for the development of trichopteran bioherms.

Due to the drying up of the lakes, the one or more Limnephilinae species of Saint-Gérard, with most probably a high degree of dependence on particular habitat features (salinity, volcanic particles supply, high algal productivity), have certainly disappeared, and this explains why we have no modern equivalent of the exceptional Indusian Limestone of Limagne.

CONCLUSION

Several taxonomic problems remain to be settled, since the two specimens lack crucial features. As the extant adult Limnephilinae, which show considerable flying ability, leave the aquatic environment just after emergence and return to it only to lay their eggs, it is very unlikely that we would find adult *Indusia* that would permit a more accurate determination; the discovery of prepupae is more likely and should complete the systematic information provided by the pupae.

Nevertheless, this discovery emphasizes the remarkable expansion of a trichopteran family which (certainly in response to Tertiary climatic changes) invaded the whole Northern Hemisphere, where it grew more and more numerous and diversified.

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