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Cover: The Coralline Crag (Pliocene) bryozoan *Cribrilina* sp. showing a group of ten feeding zooids each with an ovicell and paired adventitious avicularia on either side of the orifice. This specimen was figured as *Lepralia punctata* Hassall in G. Busk's Palaeontographical Society monograph of *Crag Polyzoa* (1859, pl. 4, fig. 1). It is reillustrated here by means of a new technique, scanning electron microscopy of the uncoated specimen using back-scattered electrons. × 75.

CLASSIFICATION OF THE ECHINODERMATA

by ANDREW B. SMITH

ABSTRACT. A critical review of past attempts to classify echinoderms is presented and it is shown that, in retrospect, fossil groups have been incorporated into classifications in an arbitrary manner that has confused rather than clarified. The search for relationship through the recognition of pattern in character distribution has become progressively divorced from the production of classification schemes, and the most recent classifications are the most ambiguous about relationships. Furthermore, the increased knowledge we have gained about fossil echinoderms has added very little to our understanding of how extant groups are interrelated and, indeed, has sometimes been interpreted misleadingly. It is argued that fossils cannot generally provide insight into the relationships of living groups except where characters have been lost through developmental foreshortening. The most important taxonomic information that palaeontology can provide concerns the pattern of character acquisition within the stem group, although it can also be useful in providing the latest date by which a split occurred, and in checking statements of homology and identifying synapomorphic characters that have been lost in one or other sister group. It is concluded that the higher classification of the Echinodermata should be based first and foremost on the distribution of characters gleaned from the study of embryology and comparative anatomy in living echinoderms. Fossil groups can then be added to this classification in their appropriate place.

An analysis of character distribution amongst the five extant classes of echinoderm shows that the Eleutherozoa form a monophyletic group whose primitive sister group is the Pelmatozoa. Within the Eleutherozoa, asteroids are the primitive sister group to the group (ophiuroids + echinoids + holothuroids) for which the name *Cryptosyringida* is proposed. The relationship of holothuroids within the cryptosyringids is more ambiguous but it is concluded that echinoids and holothuroids are sister groups and more closely related to one another than either is to the ophiuroids. A phylogenetic classification is proposed and this provides the primary framework into which fossil groups can be incorporated by using the concept of stem and crown groups. The position of principal fossil groups within this classification is briefly outlined and outstanding problems for future research are identified.

WITHIN the last few years, systematics, the study of biological classification in accordance with natural relationships, has undergone a rigorous scrutiny of its methodological basis. This debate has been fought largely, though not entirely, amongst zoologists and vertebrate palaeontologists and a vast literature now exists discussing the virtues and vices of phyletic, phenetic, and gradistic methods of classification. This debate has done nothing but good for the science of systematics and I feel that cladistic methodology has proved itself the most internally consistent and the most informative method of organizing data on character distribution. My interests lie in unravelling the phylogeny of echinoderms and producing a classification that reflects this. The phylogeny can be inferred from analysis of character distribution which can be presented in the form of a branching diagram (cladogram) and the most informative classification is one that follows the hierarchical pattern revealed by the cladogram. However, I shall not discuss the merits of cladistics over other methods of classification since there is more than enough written on this subject already. Those unfamiliar with the ideas of cladistics and how they compare with more traditional methods may read one of the many books that have recently appeared on the subject (e.g. Eldridge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1982).

While arguments have raged in systematic zoology, the systematics of fossil invertebrates, as reflected in the pages of this journal, has continued much as before. Of course, some articles using cladistic methodology have appeared but there is still the prevailing feeling that the fossil record holds the key to understanding relationships. But this belief has been challenged. Fossils, it is said, are irrelevant in determining biological relationships (Kitt 1974; Løvtrup 1977) or play only a minor role

(Patterson 1982). If these challenges are correct then systematic palaeontologists must not only reassess their methodology but also their aims.

This paper takes a critical look at the way in which echinoderms (particularly fossil echinoderms) have been classified, outlines what their fossil record can and cannot tell us, and suggests how they might be classified more informatively. Few, if any, of the ideas are new (although they have not been applied to fossil echinoderms before) but I feel it is important to make a clear statement of the methodology employed when recommending a fairly drastic change to the classification of echinoderms.

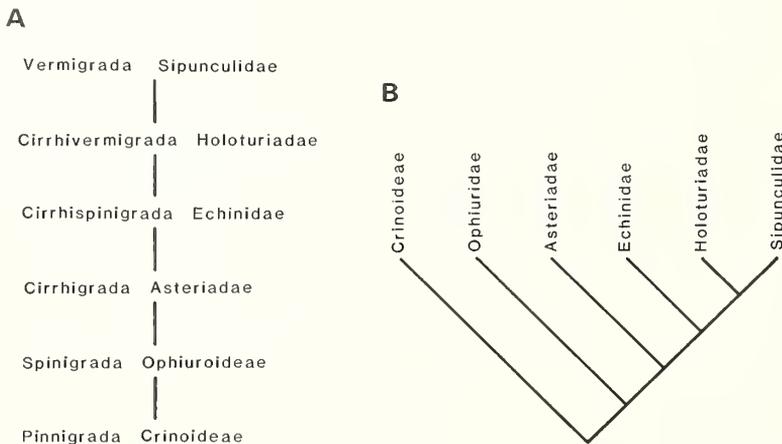
THE EVOLUTION OF ECHINODERM CLASSIFICATION

It is most instructive to follow the way in which the classification of echinoderms has altered as our knowledge of fossil echinoderms has improved. Echinoderms were not recognized as a natural group until 1791 when Bruguière subdivided Linnaeus's class Vermes in which they had previously been put. Bruguière included asteroids, ophiuroids, and echinoids in his order Echinodermata but failed to recognize holothuroids as echinoderms. In 1801 Lamarck added holothuroids to the Echinodermata but grouped them with medusoid coelenterates in the class Radiata. Twenty years later Miller (1821) formally separated a group Crinoidea for stalked echinoderms that had previously been placed with the starfish in the group Stellerides. Thus by 1821 the five classes of living echinoderm had all been recognized.

As an example of an early attempt to classify echinoderms I shall use the scheme proposed by Forbes (1841). He did not consider fossil forms and on the basis of comparative anatomy proposed the following grade classification:

- | | |
|-------------------------------|-----------------------------------|
| (i) Pinnigrada—Crinoideae | (iv) Cirrhispinigrada—Echinidae |
| (ii) Spinigrada—Ophiuroideae | (v) Cirrhivermigrada—Holoturiadae |
| (iii) Cirrhigrada—Asteroideae | (vi) Vermigrada—Sipunculidae |

Forbes based his classification on what he identified as a 'progression of organization' from polyps to vermes starting with crinoids and ending with sipunculids and he referred to it as a procession through 'forms gradually changing character'. This pre-Darwinian view of echinoderm relationships can be summarized as a gradistic tree (text-fig. 1A) and translated into a fully resolved cladogram (text-fig. 1B). Forbes then was very specific about how he thought echinoderm groups were related (though, of course, not necessarily correct) and used a classification scheme which reflected this.

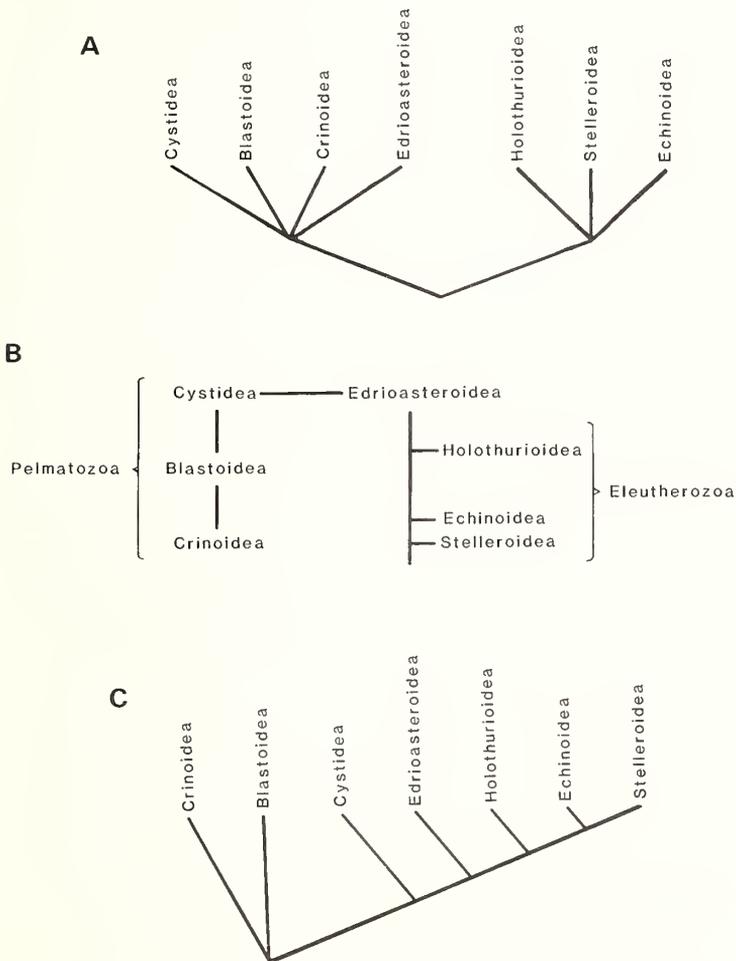


TEXT-FIG. 1. Interrelationships of echinoderm groups according to Forbes (1841). A, Forbes's gradistic classification scheme. B, the cladogram derived from the classification.

In the second half of the nineteenth century great strides were being made in both embryology and palaeontology and in 1900 Bather published a major account of Recent and fossil echinoderms in which he proposed the following classification:

- | | |
|--|--|
| Grade A Pelmatozoa
Class I Cystidea
Class II Blastoidea
Class III Crinoidea
Class IV Edrioasteroidea | Grade B Eleutherozoa
Class I Holothurioidea
Class II Stelleroidea
Subclass Asteroidea
Subclass Ophiuroidea
Class III Echinoidea |
|--|--|

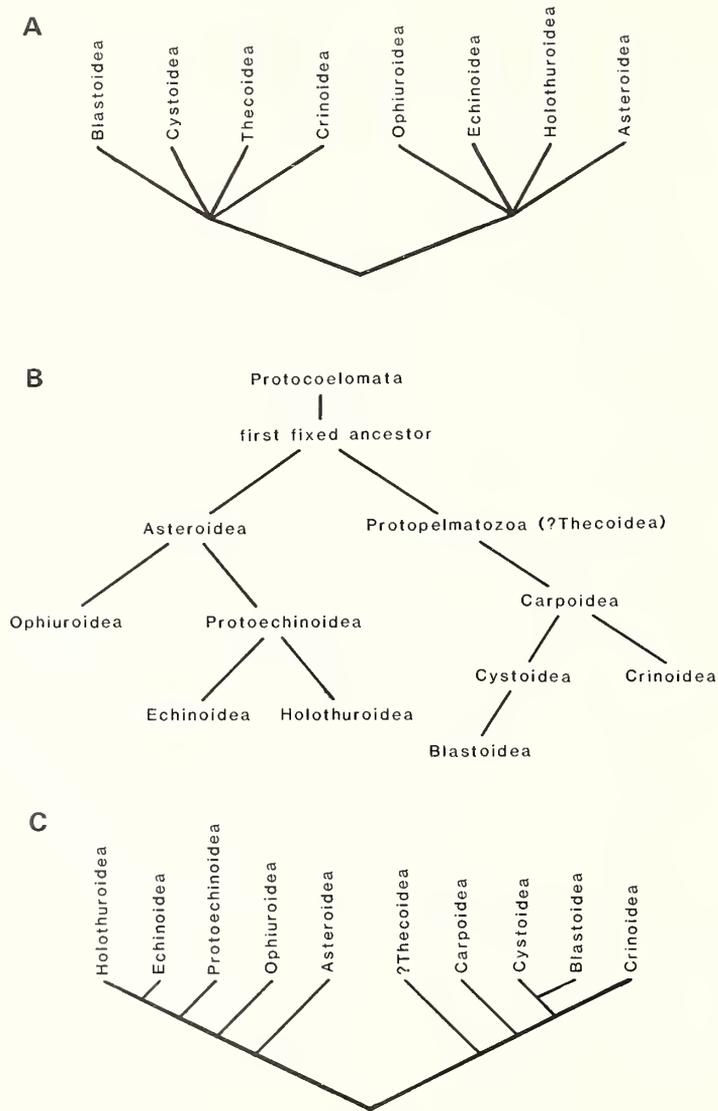
Bather's classification identifies three components within the Echinodermata (text-fig. 2A): a group Pelmatozoa, a group Eleutherozoa, and a group Stelleroidea. This is compatible with any of forty-five fully resolved statements of relationship. In addition, he presented a diagram which summarized his views on how these groups were related phylogenetically (text-fig. 2B) which can be transformed



TEXT-FIG. 2. Interrelationships of echinoderm groups according to Bather (1900). A, the information concerning relationship that is conveyed in Bather's classification. B, his diagram showing how he thought the various groups were related to one another. C, a phylogram derived from B.

into a phylogram (text-fig. 2C). Comparing the classification and phylogeny shows that Bather used a classification that conveyed some but not all of the phylogenetic information.

Bather's scheme made three changes to the previous scheme of Forbes, two of which stem from the growth in knowledge about fossil echinoderms. Palaeontology showed that living crinoids were only a small remnant of a once much larger and more diverse group of stemmed echinoderms. Bather recognized three fossil groups in addition to crinoids, placing the whole lot in the subphylum Pelmatozoa. He also realized that the other living groups were more advanced in being unattached



TEXT-FIG. 3. Interrelationships of echinoderm groups according to MacBride (1906). A, the information concerning relationship that is conveyed in MacBride's classification. B, his diagram of echinoderm phylogeny. C, a phylogram derived from B.

and grouped them together in the subphylum Eleutherozoa. Secondly, Bather chose to group asteroids and ophiuroids together because fossils existed that were intermediate in form making any distinction based on character distribution in living groups unworkable. The illogicality of this view is discussed later. Finally, he reinterpreted holothuroids as the most primitive living eleutherozoans, not the most advanced, on the basis of embryological data. Bather recognized holothuroids to be 'primitive with respect to Pelmatozoic structures, specialised as regards eleutherozoic' but chose to emphasize the symplesiomorphic aspects of holothuroid development which, in retrospect, was a misjudgement.

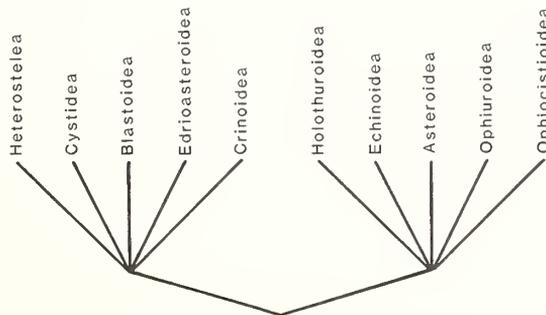
We can contrast the approach taken by Bather, who was a palaeontologist, with that of MacBride, an embryologist. MacBride (1906, 1914) considered the phylogenetic significance of echinoderm development without reference to the fossil record. He used a classification scheme that was identical to Bather's except that asteroids and ophiuroids were separated at class level. His classification then identifies just two components (text-fig. 3A). MacBride (1906) illustrated how he believed the various echinoderm groups were related in a diagram (text-fig. 3B) which can be translated into a fully resolved phylogram (text-fig. 3C). Although MacBride chose a classification whose structure contained little of the information he had gleaned from embryology, he was able to make a positive contribution by reversing the position of asteroids and ophiuroids as set out by Forbes. He did this by recognizing that embryologically ophiuroids were more advanced than asteroids.

Throughout this century palaeontologists have continued to discover and describe new fossil groups and in 1955 Hyman published her excellent review of echinoderms with the following classification:

Subphylum Pelmatozoa	Subphylum Eleutherozoa
Class Heterostelea	Class Holothuroidea
Class Cystidea	Class Echinoidea
Class Blastoidea	Class Asteroidea
Class Edrioasteroidea	Class Ophiuroidea
Class Crinoidea	Class Ophiocystioidea

Two previously known fossil groups have been elevated to class level, the carpoids (Heterostelea) and the ophiocystioids making ten classes in all. In the text Hyman seems to accept MacBride's views on echinoderm relationships yet the classification identifies just two categories higher than class level (text-fig. 4) and is consistent with over 11,000 possible fully resolved phylogenetic schemes. Thus it is relatively uninformative.

Recently, there has been a dramatic increase in the number of minor fossil groups each containing a small number of distinctive species that have been elevated to high categorial rank. In the *Treatise on*



TEXT-FIG. 4. The information concerning relationship that is conveyed in the classification of Hyman (1955).

Invertebrate Paleontology (Moore and Teichert 1978) a total of twenty-one classes, sixteen of which are extinct, are arranged into four subphyla as follows:

Subphylum Homalozoa	Subphylum Asterozoa
Class Ctenocystoidea	Class Stelleroidea
Class Stylophora	Subclass Somasteroidea
Class Homostealea	Subclass Asteroidea
Class Homoiostealea	Subclass Ophiuroidea
Subphylum Crinozoa	Subphylum Echinozoa
Class Eocrinoidea	Class Helicoplacoidea
Class Rhombifera	Class Camptostromatoidea
Class Diploporita	Class Edrioasteroidea
Class Blastoidea	Class Edrioblastoidea
Class Parablastoidea	Class Cyclocystoidea
Class Paracrinoidea	Class Ophiocystoidea
Class Crinoidea	Class Echinoidea
	Class Holothuroidea

This classification relies heavily on the work of Fell (1945, 1962, 1963, 1965, 1967) who rejected embryology as a guide to relationships and in its place attempted to use fossils as the guiding criterion. The results of this departure can be seen in the marked increase in uncertainty about relationships. The information content contained in the classification has also decreased significantly (text-fig. 5). Just four components are recognized leaving five polychotomies and this scheme is consistent with over 2×10^{11} possible statements of relationship!

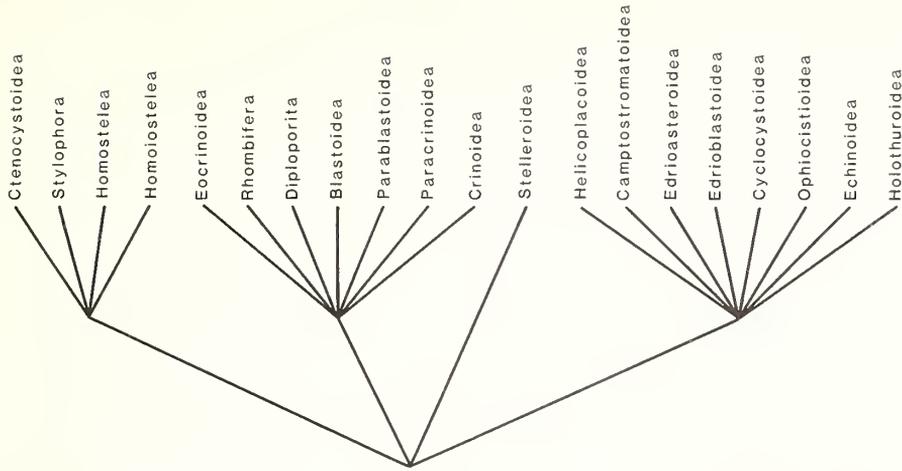
An alternative classification has been proposed by Sprinkle (1980) who recognized a fifth subphylum, as follows:

Subphylum Crinozoa	Subphylum Echinozoa
Class Crinoidea	Class Edrioasteroidea
Class Paracrinoidea	Class Edrioblastoidea
Subphylum Blastozoa	Class Cyclocystoidea
Class Eocrinoidea	Class Helicoplacoidea
Class Rhombifera	Class Ophiocystoidea
Class Diploporita	Class Echinoidea
Class Parablastoidea	Class Holothuroidea
Class Blastoidea	Subphylum Homalozoa
Subphylum Asterozoa	Class Stylopora
Class Asteroidea	Class Homoiostealea
Class Ophiuroidea	Class Homostealea
	Class Ctenocystoidea

The information content of this classification is better, but only marginally so (text-fig. 6). Five components are identified leaving four unresolved polychotomies and the classification is consistent with over 1.7×10^9 different statements of relationship.

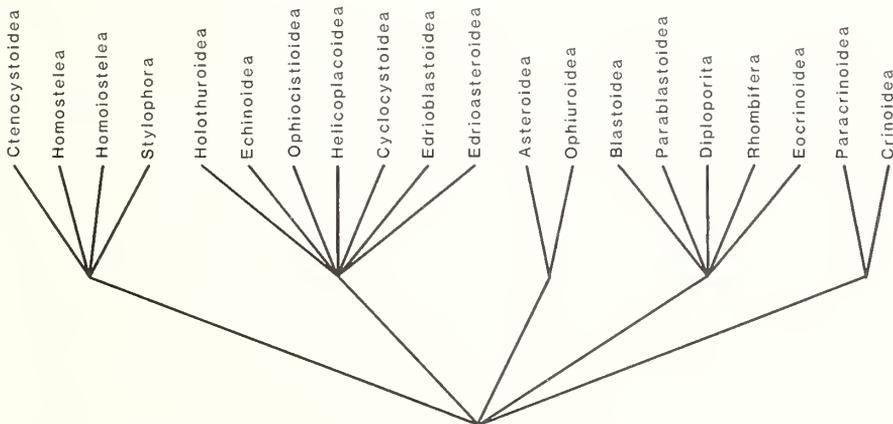
So what conclusions are to be drawn from the way in which echinoderms have been classified in the past? Forbes provided a classification in which his ideas of relationship, as revealed by morphological organization, were clearly specified. Since then there has been a progressive decrease in the information about relationships that is incorporated into classification schemes, despite an increasing understanding of embryology and palaeontology. The growth of knowledge concerning embryology led to the construction of clearly defined phylogenetic hypotheses and corroborated all but one of Forbes's findings. By showing that of the four extant classes of eleutherozoans, asteroids have the most generalized development and are therefore more primitive than ophiuroids, embryology made a positive contribution to our knowledge of relationships.

The increased knowledge of the fossil record seems to have had no such beneficial effect. The result



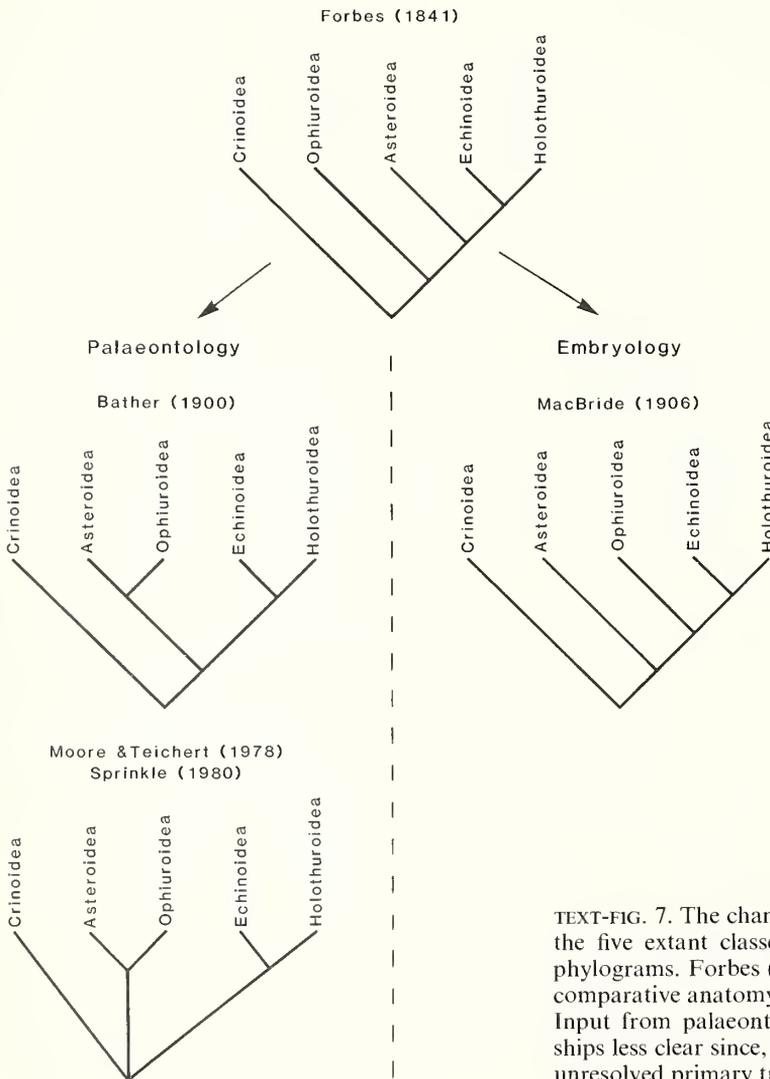
TEXT-FIG. 5. The information concerning relationship that is conveyed in the *Treatise* classification (Moore and Teichert 1978).

of discovering more and more fossil groups that have some characteristics that set them apart from living groups has been to add to the general confusion. By elevating these fossil groups to high taxonomic rank, the hierarchical arrangement of Linnaean classification has been largely destroyed and its most important attribute, its information content, greatly reduced. The most recent classifications are also the least specific about character distribution amongst the groups they recognize. The obvious question then arises—is our increasing uncertainty about relationships in echinoderms real or is it an artefact of the way in which data, particularly palaeontological data, have been handled? If the former is correct and the more fossils we continue to find the more confused our ideas of relationship become, then palaeontology can have nothing to contribute to this subject. However, the confusion that has arisen is attributable to two causes, misinterpretation of what the fossil record tells us and an inappropriate taxonomic methodology. The following two examples are given in illustration.



TEXT-FIG. 6. The information concerning relationship that is conveyed in the classification of Sprinkle (1980).

1. *The position of ophiuroids in relation to other echinoderms.* The clearest example of how the fossil record has been misinterpreted comes from the way in which ophiuroids have been linked with asteroids. Most zoologists who have considered the relationship of ophiuroids to other echinoderms have been so struck by the fact that ophiuroids and echinoids pass through very similar developmental stages that are advanced compared to those in asteroids, that they believe ophiuroids and echinoids to be more closely related (e.g. Hyman 1955). Yet amongst many palaeontologists from Bather onwards there has been a clear belief that the fossil record shows asteroids and ophiuroids to be more closely related and distinct from echinoids (text-fig. 7). This has led some palaeontologists to claim that embryology is misleading and best ignored (e.g. Fell 1967) whilst some zoologists flatly refuse to believe that the fossil record can be correct (e.g. Hyman 1955). What then does the fossil record show? Excellent work by Schondorf, Schuchert, and Spencer has shown that, in the lower Palaeozoic, asteroids and ophiuroids are much less distinct from one another (i.e. they have fewer autapomorphies) and that indeed there are some forms so generalized (primitive) in form that



TEXT-FIG. 7. The changing ideas of relationship amongst the five extant classes of echinoderm, in the form of phylograms. Forbes (1841) based his ideas primarily on comparative anatomy, MacBride (1906) on embryology. Input from palaeontology has actually made relationships less clear since, in recent classifications, there is an unresolved primary trichotomy.

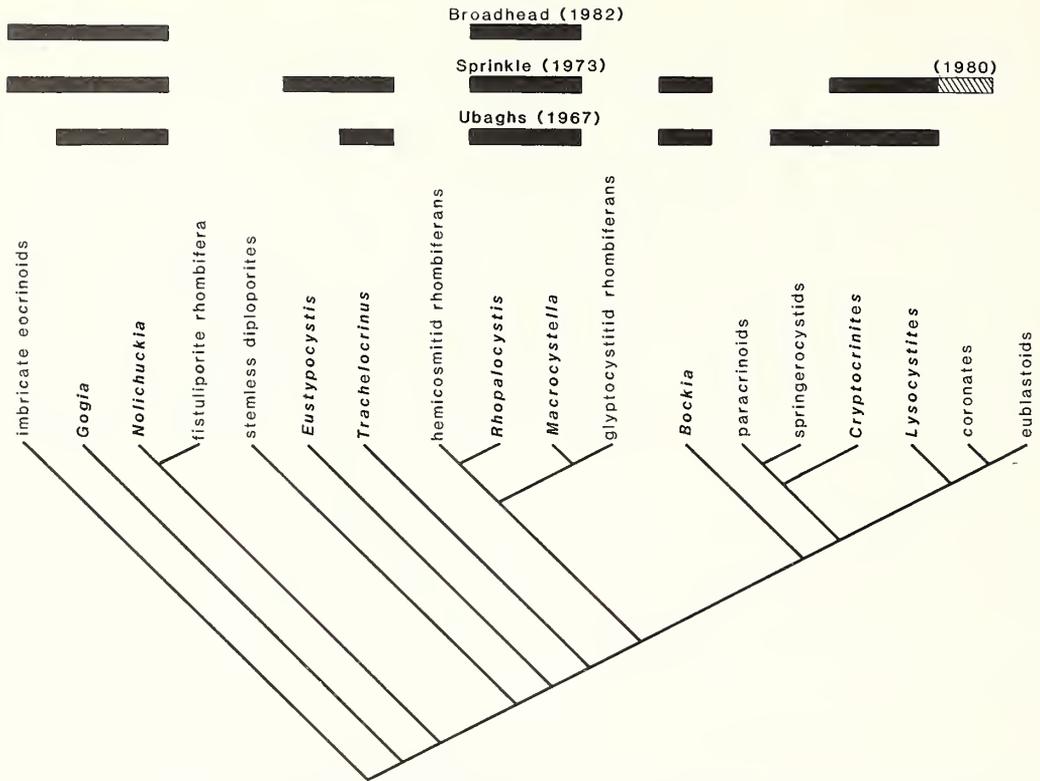
they can be interpreted as ancestors to both asteroids and ophiuroids. This led to the claim that because the fossil record proves that asteroids and ophiuroids stemmed from a common ancestor they must be more closely related compared to echinoids, whose origins are still largely unknown palaeontologically (e.g. Nichols 1968).

It may come as some surprise then to realize that the two views are not contradictory but complementary. Both embryological and palaeontological observations are in complete agreement; it is only the interpretation placed on the palaeontological data that is at fault. The fossil record shows that asteroids and ophiuroids share a common ancestry—but this is also predicted from embryological evidence (see text-fig. 7). Embryological data make a further prediction: that echinoids and ophiuroids shared a common ancestor that was not also shared with asteroids, i.e. that some of the so-called primitive ophiuroids will turn out to be generalized enough to have been ancestral to both living ophiuroids and living echinoids. Surprisingly, the implications of the embryological data have not been realized before now and the absence of obvious fossil evidence has been taken as sufficient proof for rejecting the wealth of zoological data. The question which has never before been addressed and which is only now beginning to be investigated concerns which of the 'primitive ophiuroids' are true ophiuroids and which are so generalized in morphology that they are best considered as ancestors to both living ophiuroids and living echinoids.

2. *The classification of eocrinoids.* As an example of what could be considered to be misdirected taxonomic endeavour I shall discuss the way in which eocrinoids, a primitive group of cystoids, have been classified. Eocrinoids were first recognized as a distinct group by Jaekel (1918), who believed them to be primitive crinoids. More recent work has clearly identified them as cystoids *sensu lato* (= Blastozoans), and there seems to be complete agreement amongst all workers that eocrinoids are the most primitive group of cystoids from which all the other cystoid groups evolved: the 'root stock' of other cystoid groups to use gradistic terminology. More than any other pelmatozoan group, eocrinoids have been difficult to diagnose satisfactorily. For example, one of the most thorough and detailed reviews of the eocrinoids was carried out by Sprinkle (1973), yet his diagnosis for the Class Eocrinoidea is as follows: 'Early blastozoan echinoderms having an irregularly adjacent or imbricately plated globular or flattened calyx, with or without epispires, an irregularly multiplied holdfast or a true stem as an attachment appendage [except for Lichenoididae], a primitive ambulacral system bearing normal or modified brachioles and usually little pentamerous symmetry' (Sprinkle 1973, p. 58).

The only unifying characteristic of this group of pelmatozoans seems to be 'primitiveness'. Indeed, the Eocrinoidea includes a heterogeneous assemblage of species whose only similarity is that they lack the autapomorphic characteristics of the other, less ambiguously defined, cystoid groups. As such, they are simply what remains of the Cystoidea once species with diplopores (Diploporita), rhombs (Rhombifera), hydrospires (Blastoidea), and asymmetrical thecas with uniserial ambulacra and brachioles (Paracrinoidea) have been removed, and cannot possibly represent a natural (i.e. monophyletic) grouping.

Largely because it is difficult to give any satisfactory diagnosis for the Eocrinoidea (because they are not a natural group) there has been a great deal of futile argument about precisely which species should be included in, and which rejected from, the 'Class' Eocrinoidea. Simply taking some of the changes that have been proposed since the *Treatise* (Ubahgs 1967) will show how much disagreement exists. Paul (1968), for example, removed *Macrocystella* from the eocrinoids and grouped it with glyptocystitid rhombifera, but Sprinkle (1973) rejected it as a rhombiferan and returned it to the eocrinoids; arguments about this still continue. *Springerocystis*, *Columbocystis*, and *Foerstecystis* were removed from the eocrinoids by Sprinkle (1973) who placed them with paracrinooids. Parsley and Mintz (1975), however, objected to them being paracrinooids and returned them to the eocrinoids. Recently the coronates, which were originally grouped together with blastoids (Regnéll 1945) and which were later transferred to inadunate crinoids by Fay (1978), have been added to the eocrinoids by Sprinkle (1979, 1980). Broadhead (1982) has added to the general confusion still further by rejecting all those species without epispires from the eocrinoids without making any positive contribution as to how the rejected taxa ought to be classified.



TEXT-FIG. 8. A phylogram showing the relationships of a number of cystoid groups taken from the phylogenetic tree given by Paul in Paul and Smith (1984). Three alternative views of what constitutes the 'Class Eocrinoidea' are shown. As eocrinoids are a paraphyletic grouping of primitive cystoids their boundaries are inevitably arbitrary.

The arbitrary way in which eocrinoids have been grouped becomes obvious when the various alternative schemes are plotted on a phylogram of cystoid groups (text-fig. 8). Clearly there will always be arguments as to where boundaries are to be drawn for such a subjective and paraphyletic group as the 'Eocrinoidea'. Such arguments about what constitutes a paraphyletic group are not only futile (since unnatural groups will always be arbitrary) but are a positive hindrance to discovering relationship amongst cystoids.

An understanding of how the various cystoid groups are related will become much easier if the 'Class' Eocrinoidea is abandoned and its members allocated to appropriate monophyletic groups. Although this will necessitate the creation of new taxa or the redefinition of old taxa, it will lead to a much clearer and very much more precise view of cystoid evolution. Here, then, is an example where misdirected taxonomic endeavour has actually hindered growth of knowledge concerning the relationships of cystoid groups.

CHARACTER DISTRIBUTION AND THE INFORMATION CONTENT OF CLASSIFICATIONS

Before discussing the positive contribution that the fossil record can make to phylogenetic analysis, it is worth while outlining the concept of stem and crown groups which was first developed by Hennig (1966, 1981). Identifying pattern in the distribution of morphological characters is the

essence of recognizing relationship. Derived characters shared amongst two or more species are synapomorphies that indicate phylogenetic kinship, those unique to one species or one group of species are referred to as autapomorphies. Obviously a character that is a synapomorphy uniting a group of species can also be thought of as an autapomorphy of that group as a unit.

The presence of derived characters shared amongst two or more species is usually taken as an indication of phylogenetic kinship. This is not to say that convergence does not occur. Convergence can only be recognized on the pattern of character distribution, since to suggest that a derived character found in two species is a convergent feature requires that at least two further derived characters are known that link one of those species to a group that does not include the other species. Evolutionary convergence is invoked where there is incongruence in character distribution and parsimony is used to determine which characters are true synapomorphs and which due to convergence.

Any monophyletic group with both living and fossil species can be divided into two parts—a crown group and a stem group. The crown group contains the latest ancestor common to all living members of that group together with all of its descendants. They are recognizable as crown group members because they possess all of the synapomorphies that unite the living members and form a monophyletic group. The stem group contains only fossil species and is a paraphyletic assemblage. They are identified as stem group members since they will have at least one, but not all, of the autapomorphies of the crown group. In phylogenetic terms, the stem group consists of all those species to evolve after the group had separated from its living sister group but prior to the evolution of the latest common ancestor of the crown group. The importance of differentiating between crown and stem groups will become apparent later.

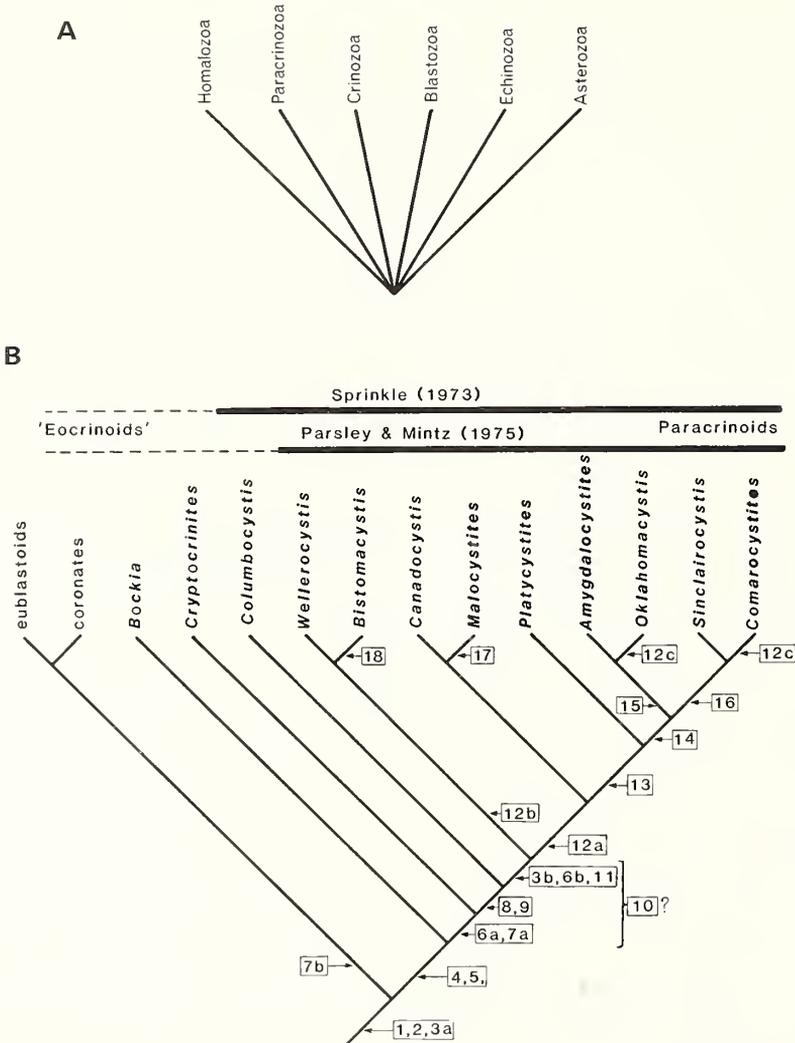
A 'natural' classification scheme is best considered as a method of conveying information about character distribution. Both character distribution and the Linnaean system of classification have the form of a nested hierarchy. Maximum information about character distribution is conveyed when the hierarchical pattern of the classification exactly matches the pattern of character distribution. Unfortunately, past classification schemes have not been as informative as they might be and the recent predilection for erecting notional class status for small problematic groups of fossil echinoderms has had a most detrimental effect on the information content of classifications by destroying the hierarchical arrangement.

In support of small fossil groups of high categorial rank Sprinkle (1975, 1980) and Paul (1979) have argued that it is a true reflection of an early diversity of form in echinoderm evolution. Even if this is so, it is no reason for elevating a large number of groups within one taxon to the same categorial rank since this is uninformative about character distribution within the higher taxon. Their preferred classifications are based not on the distribution of shared characteristics, but on the development of prominent autapomorphies (hence the necessity for a 'class' Eocrinoidea for all those cystoids left once other groups have been distinguished on autapomorphies). The presence of autapomorphies provides no information about the relationships with other groups. Unlike Breimer and Ubaghs (1974), it is not the taxonomic rank that I primarily object to but the purely subjective way in which a large number of groups are given the same rank within a large taxon. This procedure is not only arbitrary but makes no contribution to the search for pattern in character distribution and hence relationship.

The illogicality of this approach can be illustrated by the recent creation of a sixth subphylum of echinoderms, Paracrinozoa, by Parsley and Mintz (1975). There are just eight genera of paracrinozoa (seven when Parsley and Mintz erected the subphylum), all of which have a distinctively asymmetrical theca and uniserial free appendages. Prior to this paracrinozoa had always been considered cystoids, but Parsley and Mintz thought that the group had characteristics which were in part cystoid (stem and theca) and in part crinozoan (subventral system). Given that they are correct in their interpretation, then paracrinozoa, crinozoa, and cystoids must form a phylogenetically closely related group within the Echinodermata, a fact which Parsley and Mintz acknowledged. Yet by elevating the paracrinozoa to subphylum rank they are in effect stating that it is as closely related morphologically to carpoids

(Homalozoa), sea stars (Asterozoa), and Echinozoa as it is to either cystoids (Blastozoa) or crinoids (text-fig. 9A).

In my opinion Parsley and Mintz were mistaken in their identification of the free appendages as crinoid arms and pinnules. There is a great deal of confusion about the homology of pelmatozoan appendages which Paul and Smith (1984) have tried to clear up. In crinoids the entire subvective system is derived from ambulacra as a whole, whereas in cystoids many of the free appendages are brachioles derived from just cover-plate series. Paracrinozoa have free or recumbent uniserial ambulacra ('arms') which give rise to free uniserial brachioles. Similar structures are known in other



TEXT-FIG. 9. The status of paracrinozoans. A, the implied relationship of paracrinozoans to other echinoderm groups in the classification proposed by Parsley and Mintz (1975). B, a cladogram for the better-known paracrinozoans and some related 'eocrinoids' to show how analysis of character distribution leads to a clear statement about the status of paracrinozoans within the cystoids. Characters 1-18 are stated in Table 1.

cystoids: uniserial appendages are found in diploporite cystoids while free or recumbent ambulacra with brachioles are found in many cystoids such as the eocrinoid *Bockia*, glyptocystitid rhombiferans, coronates, and blastoids. Sprinkle (1973) quite correctly pointed out that springerocystid eocrinoids had an asymmetrical arrangement of 'arm' facets and a theca with stem and peristome offset as in paracrinoids. *Cryptocrinites*, another eocrinoid, has a similar asymmetric theca but has no discernible asymmetry of 'arm' facets. Thus, although paracrinoids are unusual in having brachioles arising from just one side of the ambulacrum their relationship as cystoids is to my mind unambiguous. A cladogram of character distribution (text-fig. 9B) can be constructed to suggest how paracrinoids relate to certain other cystoid groups.

FOSSIL EVIDENCE IN DETERMINING RELATIONSHIPS AMONGST LIVING GROUPS

The idea that relationship of living groups can be determined by looking at the fossil record is, at first glance, very appealing. After all, the fossil record is often thought to provide the only tangible evidence of evolution. And yet, if this is so, why has the advancement in palaeontological knowledge

TABLE 1. Character distribution for selected genera of paracrinoid and other cystoids as shown in text-fig. 9b

Primitive	Derived
1. Polyplated stalk	Holomeric stem composed of thin discoidal columnals
2. Basals undifferentiated	Three basals
3. Ambulacra forming an integral part of the thecal wall	(a) Ambulacra erect, exothecal, attached to facets close to the peristome (b) Ambulacra secondarily recumbent, overlying thecal plates
4. Periproct in C/D interray	Periproct lateral in B/C interray
5. Oral area flush with theca	Oral area a spout-like projection
6. Oral area composed of seven plates, six of which surround the peristome	(a) Oral area composed of six plates all surrounding the peristome (b) Oral area composed of four plates around the peristome
7. Thecal plates numerous, new plates added by intercalation	(a) Thecal plates relatively few, not intercalated during growth (b) Thecal plates reduced to three cycles
8. Brachioles arise from both sides of the ambulacra	Brachioles arise from only one side of each ambulacrum
9. Peristome at apex of theca, opposite the stem	Peristome offset; periproct at apex of theca, opposite the stem
10. Ambulacra and brachioles biserial	Ambulacra and brachioles uniserial
11. Ambulacra more or less straight	Ambulacra curved in a solar direction
12. Pentamer symmetry of rays	Two primary rays: (a) unbranched; (b) both branched; (c) one only branched
13. Globular or sac-like theca	Biconvex theca
14. Plates without internal pits	Internal (respiratory) pits
15. Plates smooth	Plates strongly ornamented with radially arranged and internally excavated ribs
16. Plates convex	Plates concave
17. Brachioles erect	Brachioles recumbent
18. Peristome exposed	Peristome covered by oral plates

of echinoderms not been reflected in an increased understanding about the interrelationships amongst living groups? Since 1900 many new fossil echinoderm groups have been described, yet taking just the five extant classes (text-fig. 7) we are no nearer understanding how they are interrelated than Bather (1900) was. Indeed, uncertainty has actually increased; whereas Bather accepted eleutherozoan echinoderms as a natural group, the failure of palaeontology to identify obvious intermediates between asterozoan and echinozoan eleutherozoans has resulted in less certainty about the relationship of these two groups (text-fig. 7). One can only conclude that historically, palaeontology has provided no input to the unravelling of relationship amongst living echinoderm classes. This, to some extent, may be because, until recently, there has not been the methodology to use the fossil record constructively, but it is also because the fossil record cannot by itself resolve problems of relationship.

One of the difficulties of working with fossils is that only skeletal morphology is generally preserved. In comparison with the wealth of anatomical, genetic, biochemical, and embryological data available in living echinoderms, fossils can provide only a small part of that information. It is therefore not surprising that there is an increased uncertainty about affiliation amongst fossil groups. For example, in echinoderm classification the position of the radial water vessel, whether external or internal, is a character of some importance. Embryology shows quite unequivocally that the internal position of the radial water vessel is secondary and derived during development from an originally external position (MacBride 1914). Yet, as the radial water vessel is composed entirely of soft tissue, when we look at fossils it is open to argument where the radial water vessel was situated. Bather (1915), Ubahgs (1975), and myself (in Paul and Smith 1984) have all argued that in edrioasterids the radial water vessel lay external to the flooring plates. However, Bell (1975, 1977) has argued that edrioasterids had an internal radial water vessel. Although one or other side may present more convincing arguments, there is no way in which we can be absolutely certain unless a specimen with preserved soft tissue is found. Therefore, at least some characters that are crucial in identifying relationship amongst living echinoderms are absent or unprovable in fossil groups. Fossils preserve only a small proportion of all character attributes available in living groups.

A second reason why palaeontology has had little or no impact on resolving relationships stems from the fact that fossils rarely contain a more informative pattern of character distribution than is present in extant groups. The following example will help to explain what is meant. Consider three extant groups A, B, and C each of which is quite distinct in having a number of autapomorphies. In addition, let us assume that only one synapomorphy 'j' can be discovered which identifies B and C as sister groups. Can we get more information from looking at the character distribution in fossils? As we go back in time the three groups will appear to become less distinct from one another as autapomorphic characters 'disappear'. Eventually a point will come when groups B and C no longer exist as distinguishable taxa since their members are plesiomorphic with respect to all characters save for character 'j' which distinguishes them from group A members. So, although fossils may show that extant groups were more similar due to plesiomorphy in the past, the only characters which allow us to identify sister groups (synapomorphies) are very often already known from comparative anatomy of the living members. The fossil record simplifies by removing autapomorphies but cannot generally add to the number of synapomorphies. There are, of course, exceptions where the fossil record can show characters to be more general in distribution than might be suspected from living groups or might identify structures as homologous which are highly modified in living groups, and these are discussed below. In general, however, fossils contain a no more informative pattern of character distribution than is present in extant groups.

Fossils provide information about their geological age from their stratigraphical occurrence, yet as Nelson and Platnick (1981) have argued this has no value on its own in determining relationship. Ideas on relationship are not based initially on stratigraphical occurrence but on comparative skeletal morphology. Where the stratigraphical sequence agrees with deductions based on comparative morphology then the fossil record is accepted as an adequate guide to relationships. Where comparative morphology and the stratigraphic record conflict then the fossil record is dismissed as incomplete. Clearly then, the fossil record on its own is no guide to relationship, since it

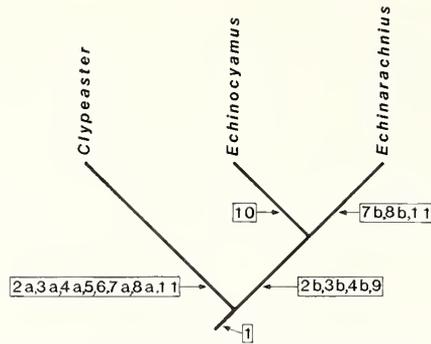
is accepted as adequate when in agreement but rejected as inadequate when in conflict with comparative anatomy. All that can be claimed is that if the fossil record agrees with a hypothesis of relationship based on morphology (and one would hope that it might) then yet another piece of evidence has been added in support. If it conflicts then the hypothesis may still be correct, since the fossil record could be incomplete.

Turning now to a practical example, clypeasteroids are believed to have evolved in the Tertiary and have an excellent fossil record. Here then is a group where one might reasonably expect the fossil record to provide additional evidence on how clypeasteroids are interrelated and from whence they originated. In order to simplify matters I shall just discuss three extant clypeasteroids, *Clypeaster*, *Echinocyamus*, and *Echinarachnius*, as representatives of the groups Clypeasterina, Fibulariina, and Scutellina respectively. Analysis of character distribution amongst these three clypeasteroids gives the cladogram in text-fig. 10. Outgroup comparison suggests that their closest living relatives are the cassiduloids (holectypoids are rejected since the character used by Durham *et al.* (1966) to unite holectypoids and clypeasteroids was the presence of a lantern, which is plesiomorphic). Morphologically, *Echinocyamus* is the least specialized of the three (i.e. it has the fewest autapomorphies) and both *Clypeaster* and *Echinarachnius* pass through a developmental stage in which they resemble fibulariids. It is therefore most parsimonious to assume that at some period in the past cassiduloids and clypeasteroids shared a common ancestor which they did not share with any other living group and that *Echinocyamus*, with its more generalized body plan, has diverged least from the latest common ancestor of living clypeasteroids. All so far has been deduced without reference to the fossil record.

If fossil clypeasteroids are examined then we find species with either clypeasterinid, fibulariinid, or scutelinid autapomorphies, a few with characters common to both fibulariinid and scutelinids but without any autapomorphies of either group, and one genus, *Togocyamus*, which has a few basic clypeasteroid features but no autapomorphies of any one group or pair of groups. *Togocyamus* is, as was predicted from character distribution amongst extant groups, rather like *Echinocyamus* in shape and was originally classified as a fibulariid. However, from the description given by Kier (1982), *Togocyamus* clearly lacks all the advanced characteristics of perignathic girdle and pore arrangement that distinguish fibulariids from other groups. So far then the fossil record has simply confirmed what was already predicted from the living groups. What about the relationship of clypeasteroids to cassiduloids—can the fossil record provide evidence of transitional forms linking these two groups? Here, however, we run into the basic problem of how to recognize a fossil as ancestral to the clypeasteroids when clypeasteroids are recognized by the presence of multiple ambulacral pores on adoral plates. All that we can be certain of is that the ancestor will have had the characteristics that are common to both cassiduloids and clypeasteroids, but none of the characteristics unique to clypeasteroids. Identifying *Togocyamus* as a primitive clypeasteroid has not made the relationship of clypeasteroids and cassiduloids any more obvious.

The conclusions that are to be drawn from this example are threefold. First, palaeontology has corroborated the hypothesis of relationship based on living groups. Secondly, it has confirmed the statement on generality of characters since *Togocyamus* conforms to the concept of a primitive clypeasteroid based on character distribution amongst living groups. Thirdly, the recognition of fossils as primitive members of an extant group does not in this case lead to any clearer understanding about their relationship to other groups. The fossil record has only been able to corroborate what was already known about character distribution and has, as yet, provided no tangible link with cassiduloids. The evidence for clypeasteroid–cassiduloid relationship comes from character analysis of the living groups.

So far I have tried to show that fossil echinoderms have done little more than corroborate hypotheses of relationship that can be deduced from the study of living groups. However, the fossil record does contain information on character distribution that is not available to neontologists and has a very positive role to play in the formulation of hypotheses of relationship as has clearly been shown by Patterson (1981). It is these positive aspects that are worth stressing since only through them will palaeontology be able to make a substantial contribution to our understanding of relationship.



TEXT-FIG. 10. A cladogram for three extant clypeasteroid genera. Characters 1–11 are given in Table 2. For discussion see text.

TABLE 2. Character distribution for three genera of clypeasteroid echinoid

Primitive	Derived	Occurrence
1. One tube foot per ambulacral plate	Multiple tube feet on ambulacral plates	<i>Clypeaster</i> , <i>Echinocyamus</i> , <i>Echinarachnius</i>
2. Lantern muscles attached to amb. and Iamb. plates	(a) Lantern muscles attached to Iamb. plates only (b) Lantern muscles attached to amb. plates only	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
3. Lantern absent in adults	(a) Clypeasterid-type lantern (b) Fibulariid-type lantern	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
4. No internal buttressing	(a) Buttressing of concentric laminae plus pillars (b) Buttressing of radial partition with or without pillars	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
5. Ambulacral plating simple	Petals with pseudo-compounding	<i>Clypeaster</i>
6. Four gonopores	Five gonopores	<i>Clypeaster</i>
7. No food groove system	(a) Simple food grooves lacking tube feet (b) Branched food grooves lined with tube feet	<i>Clypeaster</i> <i>Echinarachnius</i>
8. Tooth with fibulariid LNPS system	(a) Tooth with clypeasterid LNPS system (b) Tooth with echinarachniid LNPS system	<i>Clypeaster</i> <i>Echinarachnius</i>
9. No buccal tube feet	Buccal tube feet	<i>Echinocyamus</i> , <i>Echinarachnius</i>
10. Accessory tube feet distributed over oral plates	Accessory tube feet arranged in discrete bands	<i>Echinocyamus</i>
11. Test egg-shaped	Test discoidal to hemispherical	<i>Clypeaster</i> , <i>Echinarachnius</i>

1. Fossils can sometimes show that a character absent in a living group was present in fossil species of that group, i.e. they can show a character to be more general in distribution than is apparent from the study of living forms. For example, although echinoids, holothuroids, and asteroids all possess a madreporite, most living ophiuroids do not and show no evidence of ever having had one even during embryological development (see Hendler, 1979). Lower Palaeozoic ophiuroids do, however, possess a madreporite thus showing that the presence of a madreporite is a characteristic originally shared by all elutherozoans and that it has been secondarily lost in the great majority of crown group ophiuroids.

The fossil record is particularly helpful where synapomorphic characters have been lost completely in one branch of a monophyletic group. This can occur through developmental foreshortening. Often, fossil members of the group (those with at least one autapomorphy of the crown group) may retain synapomorphic characteristics that the group shares with its extant sister group but which have been lost in all living members. As an example of this consider the living crinoid group Holopodina. Holopodinids are a small group of minute and highly modified crinoids that live cemented to hard substrata in deep oceanic waters. They have no remnant of a stem, nor identifiable cup plating and because of their habitat nothing is known about their development. They are so modified that it is impossible to be certain about which group of articulate crinoids represents their sister group. When fossil articulate crinoids are considered we find groups that are less modified. The eudesicrinids have many of the autapomorphic characters of living holopodinids but lack fused plating. Another fossil group, the cyrtocrinoids, possess a few characteristics that are autapomorphies of living holopodinids but have not lost their stem. Because both eudesicrinids and cyrtocrinoids possess some characteristics that are unique to living holopodinids they must belong to the holopodinid stem group. The cup plating and stem morphology in fossil stem group members provide characters which have been lost from living members and which allow us to identify hyocrinids as the most likely sister group of the holopodinids.

2. The fossil record can sometimes provide the sense of direction to a morphological series which is otherwise ambiguous. For example, living echinoids have either solid or hollow spines. Solid spines are found in all cidaroids and in some euechinoids whereas hollow spines occur only in euechinoids. From generality of distribution, and as on other evidence cidaroids are the primitive sister group of euechinoids, it would be reasonable to assume that solid spines were primitive and that the evolution of hollow spines within the euechinoids might be a synapomorphy. In fact the fossil record shows that stem group echinoids, stem group cidaroids, and many early euechinoids had hollow spines. Solid spines have therefore twice evolved independently.

3. Fossils can help in the identification of homologous structures in groups that have become highly modified. Sister groups may become so different by the evolution of autapomorphies and the extinction of intermediates that it can sometimes be difficult to identify homologous structures correctly within these groups. Living crinoids are very different from their nearest living relatives, the asteroids, because a great many intermediate forms have become extinct. In the search for homologous structures the fossil record can often be useful since it is sometimes possible to trace a highly modified structure back to something more simple. By doing this we can show that the adambulacral plates in extant asteroids are probably homologous with cover-plates in crinoids, brachioles in cystoids, lateral arm plates in ophiuroids, and primary ambulacral spines in echinoids. Here the fossil record is a slightly better guide to homology than study of either development or comparative anatomy.

4. The earliest stratigraphical age at which a group is known to exist gives the latest date at which the group became split from its primitive sister group, but does not date the timing of the split more precisely since no lower limit can be fixed. However, the better the fossil record, the closer this date corresponds to the definitive time of splitting. The relative timing of the appearance of different groups should correspond to the sequence in which they appear in a cladogram of character distribution. If it does, or more or less does, then there is no problem. If it is largely incongruent then either the fossil record is poor or the cladogram is false, or both.

5. Fossils allow the sequencing of crown group autapomorphies. Every crown group is identified

by the occurrence of one or more synapomorphies which all its members share. These characters are the autapomorphies of that group. Analysis of character distribution amongst extant members of the crown group will identify a nested hierarchy which represents the pattern of character acquisition within the crown group. It will not, however, provide any method for the sequencing of crown group autapomorphies. Only by analysing character distribution within members of the wholly extinct stem group can the pattern of autapomorphy acquisition be identified. For example, living cidaroids have some characters which are common to all echinoids or to echinoderms in general (a water vascular system, a lantern, a test composed of ten ambulacral and ten interambulacral columns, articulating spines, pedicellariae, etc.) together with some unique characters. Of these unique characters, some are common to all living cidaroids (e.g. U-shaped teeth, an upright lantern with a small foramen magnum, solid spines, a perignathic girdle of apophyses) whilst others are found only in certain subgroups (e.g. perforate tubercles, conjugate pores). By analysing character distribution amongst living groups it is possible to derive a hierarchical pattern for those characters of restricted occurrence from which the sequence of character acquisition can be interpreted. But characters unique to the whole group cannot be sequenced since all living members share them. It is only by looking at the pattern of character distribution amongst members of the extinct stem group that we can identify the sequential acquisition of characters autapomorphic to the crown group. In this way it is possible to determine that in cidaroids a perignathic girdle of apophyses was acquired before an upright lantern with a shallow foramen magnum and that solid spines, a rigidly sutured test, and U-shaped teeth were all later acquisitions.

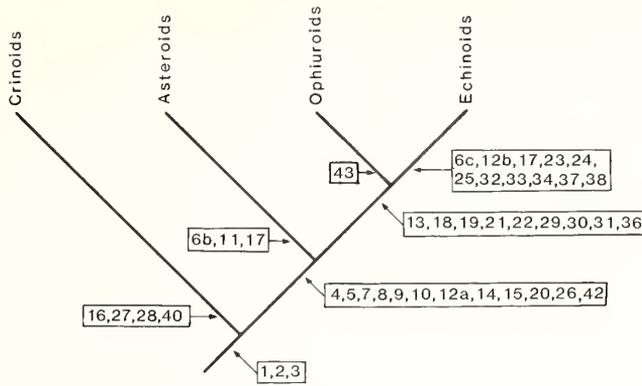
A PHYLOGENETIC APPROACH TO THE CLASSIFICATION OF ECHINODERMS

In the preceding sections I have briefly outlined the way in which fossil echinoderms have been treated in the past and have attempted to identify precisely what the fossil record can and cannot tell us about relationships. In the past, fossil echinoderms have tended to be classified in a subjective and uninformative manner. As more and more fossil groups have been raised to high taxonomic levels the hierarchical nature of classification schemes has been disrupted and its information content diminished, while no progress has been made in unravelling relationships of living echinoderms. Furthermore, reasons have been given why fossils alone cannot provide direct evidence concerning the relationship of extant groups, although they can often help in the process of discovering these relationships. It therefore seems that a fairly drastic reappraisal of how fossil echinoderms should be classified is necessary. This last section outlines how fossils can be incorporated more informatively into a classification. Again none of the ideas presented here is new. The basic methodology by which fossils could be classified was discussed by Hennig (1966) and there have been several notable contributions to this subject since then (e.g. Nelson 1972, 1974; Patterson and Rosen 1977; Wiley 1979).

Since a knowledge of fossil echinoderms has made little positive contribution to our understanding of how the principal extant groups are interrelated and indeed has often been interpreted in a misleading way, it seems sensible to construct a hypothesis of relationship on the basis of character distribution derived from comparative anatomy and developmental biology of extant species. Fossils then provide a record of character distribution in the past which can be used to check statements of homology, identify synapomorphic characters that have been lost through developmental fore-shortening, and identify the sequence of character acquisition where more than one autapomorphy identifies an extant group. The cladogram derived for living groups can then be used as a primary framework to which fossil groups can be added in their correct position.

The primary framework

Table 3 lists a variety of important characters shared amongst the five extant classes of echinoderm. These are drawn from published descriptions of embryological development and from gross comparative anatomy. The pattern of character distribution is quite unambiguous for four of the five

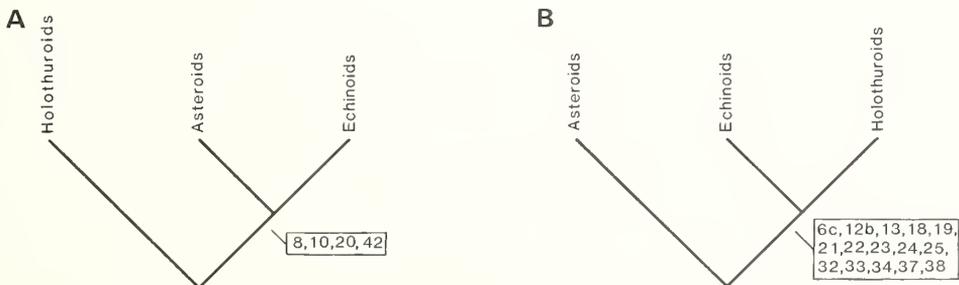


TEXT-FIG. 11. Cladogram for four of the five extant classes of echinoderm based on embryology and comparative anatomy. Characters 1-43 are given in Table 3.

classes (text-fig. 11). It identifies crinoids as a primitive sister group to the other three and asteroids as the primitive sister group to ophiuroids plus echinoids. This is in full agreement with the conclusions of MacBride (1914) and Hyman (1955).

The phylogenetic position of holothuroids is less obvious and needs careful analysis. Holothuroids share a number of derived characters with ophiuroids and echinoids and several more with only echinoids. However, there are a number of other derived characters that are common to asteroids, ophiuroids, and echinoids or only to ophiuroids and echinoids which are not found in holothuroids. To try to resolve the phylogenetic position of holothuroids the problem can be reduced to a number of three taxon problems and the alternatives compared.

First, let us ignore ophiuroids and consider whether holothuroids or asteroids are phylogenetically the more closely related to echinoids. The alternative cladograms are given in text-fig. 12. It is quite evident that there are many more derived characters that suggest that holothuroids and echinoids are sister groups than suggest that asteroids and echinoids are sister groups. It is therefore worth examining the four characters that suggest asteroids and echinoids to be more closely related and which on the grounds of parsimony alone would be rejected. The presence of a genital rachis and multiple gonads, as found in asteroids and echinoids, is undoubtedly a derived character while the single gonad and gonopore of holothuroids is primitive. However, primitive stem group echinoids have but a single gonopore and, by inference, a single gonad (Smith 1984); therefore the genital rachis

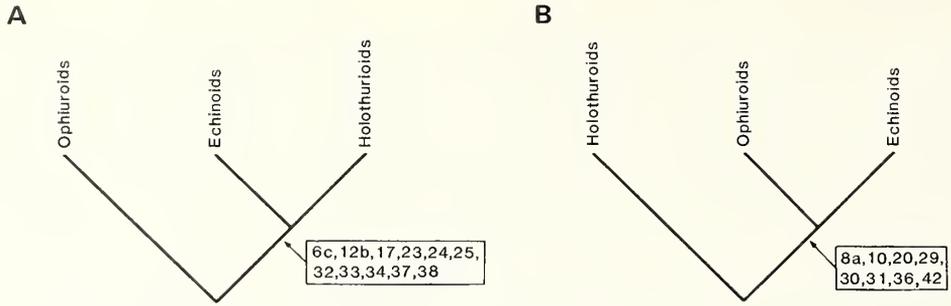


TEXT-FIG. 12. A three taxon cladogram to resolve the relationship of holothuroids to asteroids and echinoids. Characters 1-43 are listed in Table 3.

TABLE 3. Primitive and derived character states in extant echinoderm classes. The classes that possess derived character states are given in the third column

Primitive	Derived	Occurrence
1. Skeleton absent	Calcite skeleton of stereom	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
2. Larval development bilaterally symmetrical	Development of right-hand side larval coeloms suppressed	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
3. Without radial symmetry	With radial (pentamer) symmetry	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
4. Larva without processes	Larva with incipient processes (auricularia)	Asteroids, Ophiuroids, Echinoids, Holothuroids
5. Hydropore opening simple	Hydropore opening a calcified body (madreporite)	Asteroids, Ophiuroids, Echinoids, Holothuroids
6. Definitive anus opens lateroventrally	(a) No anus in adults (b) Definitive anus opens laterodorsally in B/C inter-radius (c) Definitive anus opens dorsally at site of larval anus	Ophiuroids, some Asteroids Some Asteroids Echinoids, Holothuroids
7. Adult attached	Adult free-living	Asteroids, Ophiuroids, Echinoids, Holothuroids
8. Ambulacral plates added at tip of radial water vessel	(a) Radial water vessel tip associated with terminal plate; new ambulacral plates added adorally to terminal plate (b) Ambulacral plates wanting	Asteroids, Ophiuroids, Echinoids Holothuroids
9. Tube feet arise directly from the radial water vessel	Tube feet arise from lateral branches of the radial water vessel	Asteroids, Ophiuroids, Echinoids, Holothuroids
10. No articulating spines	Articulating spines	Asteroids, Ophiuroids, Echinoids
11. Larval vestibule formed	No larval vestibule formed	Asteroids
12. Aboral surface greatly enlarged	(a) Aboral and oral surfaces equally developed (b) Aboral surface greatly reduced	Asteroids, Ophiuroids Echinoids, Holothuroids
13. Entoneural nerve plexus present	Entoneural nerve plexus absent	Ophiuroids, Echinoids, Holothuroids
14. Entoneural nerve plexus as primary motor coordination system	Ectoneural nerve plexus as primary motor coordination system	Asteroids, Ophiuroids, Echinoids, Holothuroids
15. No hyponeural sinuses	Hyponeural sinuses present	Asteroids, Ophiuroids, Echinoids, Holothuroids
16. Right hydrocoel present but vestigial in development	Right hydrocoel does not form during development	Crinoids, Holothuroids
17. Tube feet without internal ampulla	Tube feet with internal ampulla	Asteroids, Echinoids, Holothuroids
18. Larva attaches by pre-oral lobe	Larva unattached	Ophiuroids, Echinoids, Holothuroids

Primitive	Derived	Occurrence
19. Radial water vessel and nerve external	Radial water vessel and nerve enclosed by epineural folds	Ophiuroids, Echinoids, Holothuroids
20. Single internal gonad arising from genital stolon	Multiple internal gonads arising from genital rachis surrounding axial complex	Asteroids, Ophiuroids, Echinoids
21. No epineural sinuses	Epineural sinuses present	Ophiuroids, Echinoids, Holothuroids
22. Entomesoderm forms in gastrula from archenteron	Entomesoderm starts to form in blastula from one side of the wall before embolic invagination	Ophiuroids, Echinoids, Holothuroids
23. Radial water vessel grows radially	Radial water vessel grows meridionally	Echinoids, Holothuroids
24. Tube foot wall uncalcified	Tube foot wall with spicules	Echinoids, Holothuroids
25. Suckered tube feet without skeletal disc plates	Suckered tube feet with skeletal disc plates	Echinoids, Holothuroids
26. Larva lacks a mouth	Larval mouth forms	Asteroids, Ophiuroids, Echinoids, Holothuroids
27. Gonads internal	Gonads external, on arms	Crinoids
28. Ambulacra forming integral part of the theca	Ambulacra extending free of theca as arms	Crinoids
29. Larva with short processes	Larva with elongate processes	Ophiuroids, Echinoids
30. Larval processes not supported by calcite rods	Larval processes supported by calcite rods	Ophiuroids, Echinoids
31. Larval mouth retained as adult mouth but migrates to the left during development	Larval mouth lost during development; adult mouth opens to the left of the larval mouth	Ophiuroids, Echinoids
32. No peripharyngeal coelom	Peripharyngeal coelom	Echinoids, Holothuroids
33. No perianal coelom	Perianal coelom	Echinoids, Holothuroids
34. Haemal system rudimentary, an open lacuna network	Haemal system extensive and well developed, with a rete mirabile	Echinoids, Holothuroids
35. Axial complex fully developed	Axial complex absent or vestigial	Holothuroids
36. Adoralmost ambulacral ossicles forming a semi-flexible oral frame	Adoralmost ambulacral ossicles modified into a muscular jaw apparatus	Ophiuroids, Echinoids
37. Adoralmost ossicles remain an integral part of ambulacral plating	Adoralmost ossicles internal and surround oesophagus	Echinoids, Holothuroids
38. Radial ambulacral muscles interossicular and segmented	Radial ambulacral muscles internal and unsegmented	Echinoids, Holothuroids
39. Ambulacral ossicles present	Ambulacral ossicles lost	Holothuroids
40. Blastopore remains as larval anus	Blastopore closes after formation of archenteron	Crinoids
41. No polian vesicles	Polian vesicles	Asteroids, Ophiuroids, Holothuroids
42. No Tiedemann's bodies	Tiedemann's bodies	Asteroids, Ophiuroids, Echinoids
43. Vestibule sealed off from exterior during development	Vestibule remains open	Ophiuroids



TEXT-FIG. 13. A three taxon cladogram to resolve the relationship of holothuroids to echinoids and ophiuroids. Characters 1–43 are listed in Table 3.

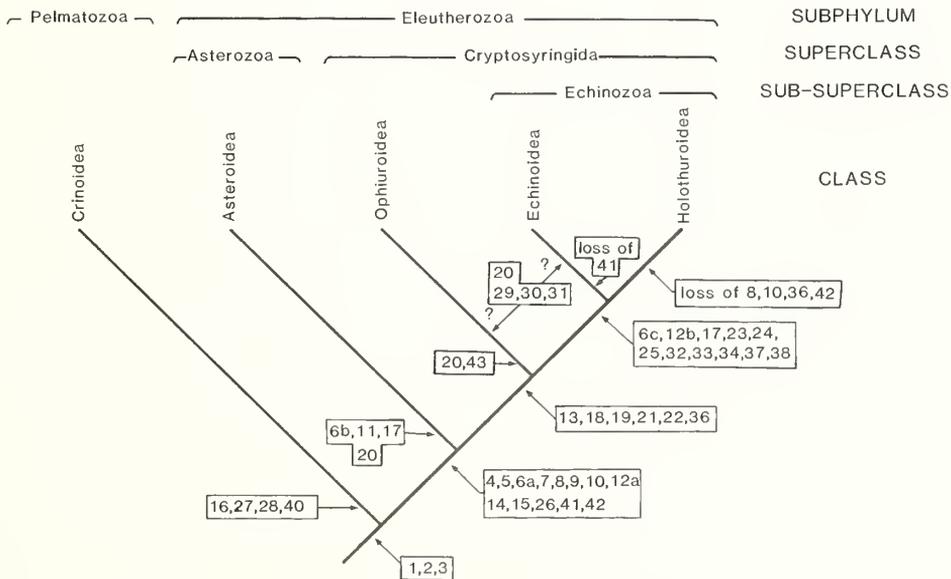
and multiple gonads must have evolved independently in echinoids and asteroids. This character can therefore be rejected as being a convergence on the basis of fossil evidence. Tiedemann's bodies are present in ophiuroids as well as in asteroids and echinoids. Their absence in holothuroids may be a secondary loss, since these bodies perform the same function as the axial complex (Bachmann and Goldschmidt 1980) which is vestigial or absent in holothuroids. The two remaining characters common to asteroids and echinoids but not to holothuroids are the presence of terminal plates (oculars), which appear early in development, and the presence of articulating spines. Neither character carries much weight as the skeleton of holothuroids has become highly modified and is usually reduced to rudimentary spicules. The development of the few living holothuroids that retain a skeleton of thin imbricate plates has never been reported and it is therefore impossible to recognize these characters in holothuroids. In view of the outstanding evidence in favour of placing asteroids as the primitive sister group of holothuroids plus echinoids, it seems reasonable to assume that living holothuroids have lost both spines and apical plates as a consequence of the profound simplification of their body wall skeleton.

The only question remaining then is, comparing ophiuroids, echinoids, and holothuroids, which pair is the more closely related? Derived characters exist that link holothuroids and echinoids and which link echinoids and ophiuroids but none exist linking ophiuroids and holothuroids. Therefore we need consider only two of the three possible cladograms (text-fig. 13). Both seem to be supported by a number of characters. However, of those identifying ophiuroids and echinoids as a group, four (the presence of a genital rachis and multiple gonads, Tiedemann's bodies, terminal (ocular) plates, and articulating spines) have already been rejected on the strength of the preceding cladogram, and cannot be used. Of the remaining four characters, one, the presence of homologous ambulacral ossicles modified into a jaw apparatus, is questionable because holothuroids have such a modified and reduced larval skeleton that such a structure might easily have been lost. The internal calcareous ring may be homologous with some plates of the jaw apparatus but there is too little evidence to be certain. This character can be rejected on fossil evidence, however, since the stem group holothuroid *Rotasaccus* has a fully developed lantern which is in all details, save for tooth structure, identical with that of echinoids (Haude and Langenstrassen 1976). Three characters remain that are incongruent: the absence of a pluteus larva with elongate processes, the absence of skeletal rods supporting the larval processes, and the retention of the larval mouth throughout development. The first two characters are interconnected since the larval skeleton forms to support processes that develop in the pluteus larva to extend the ciliated bands. Neither the processes nor the skeleton are identical in echinoids and ophiuroids. The ophiopluteus has no pre-oral processes and the main locomotory processes that develop early on are the posterolateral ones, whereas in the echinopluteus, elongate pre-oral processes are present, and the main locomotory processes are the post-oral ones. The posterolateral processes either appear much later in development and remain small or are absent

altogether. The ophiopluteus has just two centres of calcification from which calcite rods grow, one on either side, whereas the echinopluteus has five, two on the left, two on the right, and an anterior V-shaped rod for the pre-oral processes. There is therefore a distinct possibility that elongation of the small processes common to all eleutherozoan larvae occurred independently in ophiuroids and echinoids.

The evidence concerning the phylogenetic position of holothuroids, although ambiguous, definitely tends to favour echinoids and holothuroids as being sister groups. If I have identified the ophiocistioid *Rotasaccus* correctly as a stem group holothuroid then the presence of a lantern so similar to that of echinoids in *Rotasaccus* convinces me that echinoids and holothuroids are sister groups and that holothuroids have undergone fairly major change through reduction of the body skeleton since the two groups became separated. However, it must be said that the available biochemical evidence concerning sterols (Bolker 1967; Goad *et al.* 1972), phosphorus carriers (Florkin 1952), and collagen (Matsumura *et al.* 1979) do not support this and indicate that echinoids and ophiuroids share a greater similarity. As I lack expertise in this field I cannot assess these data from a cladistic standpoint and therefore cannot tell what sort of similarity it is that echinoids and ophiuroids share.

The result of analysing character distribution amongst living groups of echinoderms gives the nested hierarchy shown in text-fig. 14. If, following historical precedence, the five extant groups are given class status then the hierarchical pattern must dictate the higher classification of the Echinodermata. Names are available for all but one group. The Echinodermata can be divided into two subphyla, Pelmatozoa for the crinoids and Eleutherozoa for the asteroids, ophiuroids, echinoids, and holothuroids. (Haugh and Bell (1980) rejected the Eleutherozoa as a monophyletic taxon on the grounds that the 'absence of stem' was a non-character, an argument which comparative embryology refutes.) At superclass level we can use the name Asterozoa for the asteroids but no name has ever been proposed for the group comprising the Ophiuroidea, Echinoidea, and Holothuroidea. I therefore propose to name this group Cryptosyringida (derivation—Greek *Kryptos*, hidden;



TEXT-FIG. 14. The most parsimonious cladogram for the five extant classes of echinoderm with a suggested hierarchical classification. Characters 1–43 are given in Table 3.

Syringos, a pipe or fistula, in allusion to the fact that the radial water vessel and radial nerve becomes covered during development). Finally, the echinoids and holothuroids are grouped together in the Echinozoa at sub-superclass level.

Incorporating fossil groups into the primary classification

The concept of crown and stem groups becomes indispensable when dealing with the classification of fossil groups. Monophyletic groups of living echinoderms belong to a whole series of increasingly more generalized crown groups of which the most narrowly defined contains only members of that group and no others. Fossil echinoderms also belong to a whole series of increasingly more generalized crown groups but, with one exception, all fossils also belong to a single stem group. In systematics the pattern of character distribution is used to determine at what level a species or group of species belong. Neontologists search for the most narrowly defined crown group whereas palaeontologists attempt to discover the unique stem group that each fossil belongs to. The level of generality for stem groups is as variable as it is for crown groups. For example, the Cretaceous cidarid *Stereocidaris sceptifera* belongs to the stem group of the genus *Stereocidaris* whereas the lower Cambrian helicoplacoid *Helicoplacus gilberti* is so generalized that it is a member of the stem group of the Echinodermata.

Each stem group may contain one or many members. In some cases the stem group might be quite small, as in echinoids where there are approximately 125 known stem group species but almost 7,000 crown group species. In other cases—for example, Pelmatozoa—the stem group is enormous compared with the crown group and includes all cystoids and all crinoids except the Articulata. The members of each stem group possess at least one but not all of the autapomorphies that define the crown group. It is therefore possible to arrange fossils in the stem group according to the distribution of crown group autapomorphies (see Patterson and Rosen 1977; Wiley 1979). The most primitive will have just one autapomorphy, the most advanced will have all but one. However, a few fossils will belong not to the stem group but to the crown group. These will have all the autapomorphies that define the crown group but none of the autapomorphies of any subdivision of the crown group and will include the first member of the crown group.

Because groups can be distinguished as discrete entities only when they have evolved a new character, the maximum resolution that we can hope for is to distinguish one or a group of fossils at the appearance of each new crown group autapomorphy. Those fossils which all have the same crown group autapomorphies represent a monophyletic side branch from the stem line. The number of autapomorphies that can be identified limits the number of stem groups that can be identified, yet although this is presumably finite, there is no way of predicting how many can be recognized. Each side branch of the stem group (zwischenkategorien of Hennig 1969; plesion of Patterson and Rosen 1977) may contain only a single species or may contain a large number of species, in which case character distribution can be analysed to discover pattern and phylogenetic relationship within the side branch. Each side branch, being a monophyletic group, can be named and classified from the species level up. Their nominal categorial rank is unimportant and is best based on diversity or historical precedence. The groups which make up the stem group can then be listed in an order corresponding to the acquisition of crown group autapomorphies and incorporated into the primary classification as recommended by Wiley (1979).

As palaeontologists are concerned with pattern recognition in stem groups, it is possible that having a name for each stem group might be quite useful for communicating precisely about which group of fossils are under investigation. To avoid further proliferation of names, it is probably best if they were referred to as stem group cidaroids, stem group isocrinids, etc., but if a widely used name is available I can see no objection to its being used. For example, when I analysed the stem group echinoids (Smith 1984) the traditional group Perischoechinoidea seemed to correspond more or less to the stem group and I suggested retaining Perischoechinoidea for the paraphyletic stem group of the Echinoidea.

Some traditional fossil groups are truly monophyletic and can be incorporated into the stem group in their correct position. Others, however, turn out to be paraphyletic since they were defined on the

absence of one or more crown group autapomorphies. These will eventually have to be abandoned in favour of groups which are more informative about character distribution.

The status within this classification of the principal fossil groups of echinoderm recognized in the *Treatise* (Moore and Teichert 1978) will now be outlined:

(i) *Carpoids* ('Classes' Ctenocystoidea and Stylophora and 'Orders' Soluta and Cincta). Carpoids are all basically asymmetric, without a trace of radial symmetry and either lack ambulacra or have a single exothecal appendage. They all have a single feature, their calcite endoskeleton, which they share with crown group echinoderms. However, Jefferies (1981) believes that Stylophora show evidence of gill slits and a post-anal tail and should therefore be classified as stem chordates. If this proves to be correct then the other carpoids may be stem chordates, stem echinoderms, or stem (chordates plus echinoderms). Further work is required to resolve the phylogenetic position of these groups and I shall not consider them further.

(ii) *Helicoplacoids* ('Class' Helicoplacoidea). There are only two or possibly three genera of helicoplacoids and a handful of species. Their morphology and phylogenetic position has been discussed by Paul and Smith (1984). Helicoplacoids have a laterally positioned mouth, no oral/aboral differentiation of the skeleton and triradial ambulacra. They are stem group echinoderms and have been incorporated into the classification as a plesion with the nominal rank of family (Table 4).

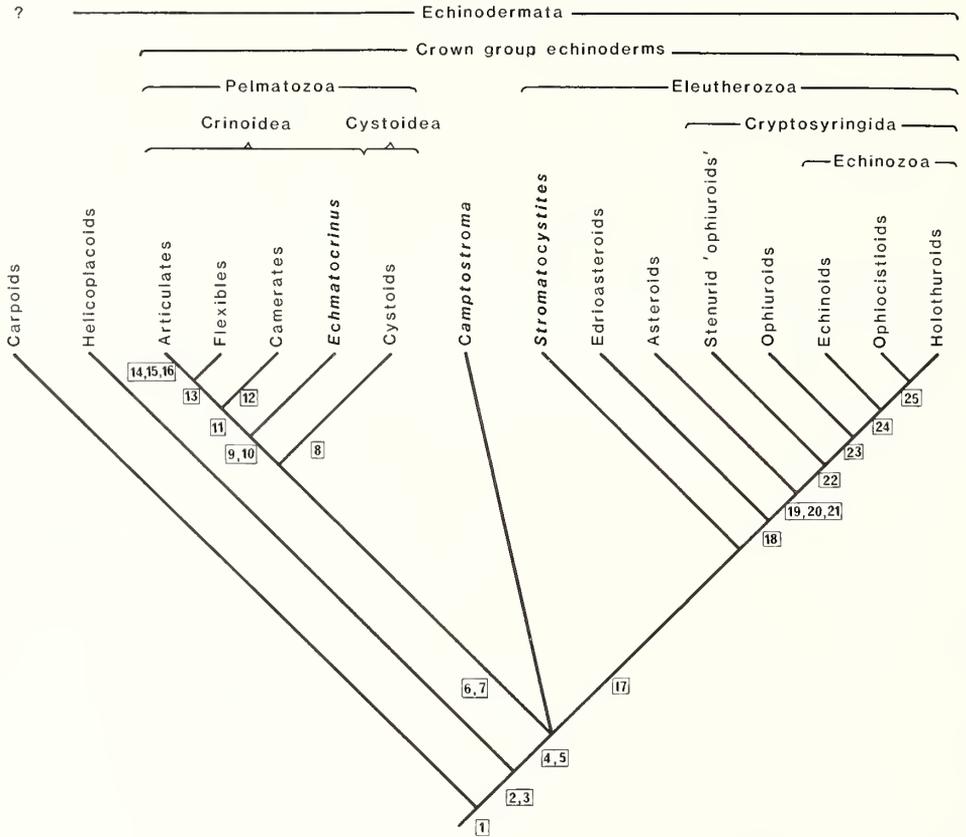
(iii) *Camptostroma* ('Class' Camptostromatoidea). The phylogenetic status of *Camptostroma* has also been discussed by Paul and Smith (1984). *Camptostroma*, represented by a single known species holds a rather important position in the cladogram (text-fig. 15) since it possesses all of the autapomorphies of crown group echinoderms but none of the autapomorphies of either Pelmatozoa or Eleutherozoa. It therefore belongs to the group in which the latest ancestor of crown group echinoderms would be placed.

(iv) Cystoids ('Superclass' Cystoidea = 'Subphylum' Blastozoa). In recent years the cystoids have been split up into a number of high categorical taxa. Some of these are undoubtedly monophyletic (blastoids, paracrinooids) whereas others are apparently paraphyletic (rhombiferans, eocrinoids—see Paul and Smith 1984) and need to be reclassified in a more informative way. Previously the presence or absence of a single character (usually a respiratory structure) has been used to identify groups. Cystoids *sensu lato* are clearly a monophyletic group and their subvective system includes brachioles which are homologues of cover-plate series. The only crown pelmatozoan autapomorphies that they share with extant crinoids are the presence of an elongate dorsal stalk and, in some, the extension of ambulacra free from the thecal wall. They are the most primitive stem group pelmatozoans known. A phylogenetic classification of cystoids should be relatively straightforward and will require a careful analysis of character distribution. Cladistic analysis of this group has never been attempted and holds considerable promise for future research. Cystoids have been incorporated into the classification as a plesion with a nominal rank of Superclass.

(v) *Echmatocrinus* ('Subclass' Echmatocrinea). The single species *E. brachiatus*, represented by some six specimens, is generally taken to be the most primitive member of the Class Crinoidea. It is more advanced than cystoids in that some at least of its ambulacra branch to produce multiple free arms, but it is primitive in comparison with other crinoids in lacking organized thecal plating or stem plating. The Class Crinoidea is monophyletic and corresponds to the crown group plus part of the stem group of the Pelmatozoa. *Echmatocrinus* is the most primitive-known crinoid and is incorporated into the classification as a plesion with generic rank.

(vi) Palaeozoic crinoids ('Subclasses' Inadunata, Camerata, and Flexibilia). The structure of this part of the stem group is the least satisfactory. This is because, although the Camerata and Flexibilia are probably monophyletic groups, the Inadunata is unquestionably a paraphyletic grouping of 'primitive' crinoids that contains the ancestors of camerates, flexibles and articulates (crown group Pelmatozoa). A paraphyletic group such as the Inadunata can only be arbitrarily defined and is undesirable since paraphyletic groupings simply mask the pattern of character acquisition within the stem group. At present only the relative positions of the Camerata and Flexibilia can be shown in a cladogram (text-fig. 15). The inadunates include stem (Camerata + Flexibilia + Articulata), stem

(Flexibilia + Articulata), and stem (Articulata). They represent one of the outstanding areas of ignorance in echinoderm phylogeny and future palaeontological research should be directed towards discovering the pattern of character distribution within inadunates and partitioning this grouping into monophyletic groups. With increasing understanding of the inadunates more plesion categories will be added to the classification in Table 4 between *Echmatocrinus* and the Articulata.



TEXT-FIG. 15. Cladogram incorporating some of the more important fossil groups to show how they fit into the classification scheme. All fossil groups can be assigned to a stem group of one of the crown groups identified in text-fig. 14. Characters 1–25 as follows: 1, calcite endoskeleton of stereom; 2, biserial ambulacra forming integral part of body wall; 3, ambulacra arranged radially, around the mouth (triradial); 4, skeleton differentiated into dorsal and ventral surfaces; 5, pentaradial symmetry; 6, free appendages developed carrying extensions of the radial water vessels; 7, dorsal surface modified to form a stalk; 8, brachioles arise from ambulacra; 9, ambulacra extend free of the theca and carry extensions of major body coeloms; 10, ambulacra uniserial and branched; 11, cup plating clearly differentiated from stem plating; 12, arm plates incorporated into tegmen; stout, rigid tegmen; pinnate arms; 13, tegmen flexible with differentiated ambulacral and interambulacral zones; 14, some arm articulations muscular; arms pinnate; 15, mouth opens through tegmen; 16, anal plates lost from cup; 17, dorsal surface generally flat; adults primitively free-living; 18, epispires lost from ventral surface; 19, mouth frame flexible, composed of ambulacral ossicles only; 20, calcified madreporite; 21, cover-plates modified to adambulacral/lateral arm ossicles; 22, adoralmost ambulacral ossicles modified to form jaw apparatus; 23, radial water vessel enclosed; 24, meridional growth pattern; 25, wheel spicules in body wall.

TABLE 4. A phylogenetic classification of the Echinodermata (conventions as in Wiley 1979)

Phylum Echinodermata
plesion (Family) <i>Helicoplacidae</i>
Subphylum Pelmatozoa
plesion (Superclass) <i>Cystoidea</i>
Class <i>Crinoidea</i> *
plesion (Genus) <i>Echmatocrinus</i>
plesion (Subclass) <i>Camerata</i>
plesion (Subclass) <i>Flexibilia</i>
Subclass <i>Articulata</i>
Subphylum Eleutherozoa
plesion (Genus) <i>Stromatocystites</i>
plesion (Class) <i>Edrioasteroidea</i>
Superclass <i>Asterozoa</i>
Class <i>Asteroidea</i>
Superclass <i>Cryptosyringida</i>
Subsuperclass <i>Ophiuroidea</i>
Subsuperclass <i>Echinozoa</i>
Class <i>Echinoidea</i>
Class <i>Holothuroidea</i>

* Phylogenetic analysis of the Inadunata will add a number of plesions between *Echmatocrinus* and *Articulata* in the future.

(vii) Edrioasteroids ('Class' *Edrioasteroidea*). Edrioasteroids are best considered as stem group Eleutherozoa. The most primitive members were unattached (e.g. *Stromatocystites*) and probably common ancestors to all Eleutherozoa. Most edrioasteroids, however, have a number of autapomorphies and represent a monophyletic side branch of the stem group. Most returned to a fixed mode of life attached via their aboral surface. Unlike pelmatozoans, those that elevated themselves above the sea floor did not develop an aboral stem but expanded their oral surface to become pedunculate. Edrioasteroids have been added to the classification as a plesion with nominal class status.

(viii) Cyclocystoids ('Class' *Cyclocystoidea*). These form a small but diverse group characterized by a number of well-defined autapomorphies. They also share a number of autapomorphies with isorophid edrioasteroids, notably uniserial ambulacral flooring plates and a marginal ring with a single layer of peripheral platelets. I therefore now prefer to place them within the edrioasteroids as the sister group of the *Isorophida* and with a nominal rank of Order.

(ix) Ophiocistioids ('Class' *Ophiocistioidea*). Ophiocistioids share a number of synapomorphies with the *Echinozoa*. The discovery of the Devonian ophiocistioid *Rotasaccus* by Haude and Langenstrassen (1976) was a most important find, since *Rotasaccus* has the body wall skeleton of a holothuroid but possesses an echinoid-type lantern. This provides evidence that stem group holothuroids possessed a lantern even though it has been lost in all living holothuroids. Ophiocistioids are undoubtedly a paraphyletic group and an analysis of character distribution within this group will lead to a better understanding of the early history of the *Echinozoa*.

A simplified cladogram that incorporates the more important fossil groups is shown in text-fig. 15 and a scheme of classification derived from this cladogram is given in Table 4. I have followed the recommendation of Patterson and Rosen (1977) in giving plesion categories only nominal rank and the order in which plesions are listed is dictated by the pattern in the cladogram, as formally recommended by Wiley (1979).

Finally, I should like to point out some of the major gaps in our knowledge about the phylogeny of echinoderms. There remains a basic ignorance about the phylogenetic relationships of cystoid groups which a cladistic approach could help to dispel. More seriously, the classification of Palaeozoic crinoids is most unsatisfactory and a careful and searching look at the Inadunata is needed so that this grouping can be abandoned in favour of monophyletic (and therefore more informative) groups. Thirdly, the phylogeny of primitive 'starfish' has yet to be unravelled satisfactorily and promises to be a most rewarding task. The development of cladistic methodology, which is now such a powerful tool in determining relationships, has opened up new and exciting possibilities for making a real advance in our understanding of echinoderm phylogeny.

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A MUSCLE ATTACHMENT PROPOSAL FOR SEPTAL FUNCTION IN MESOZOIC AMMONITES

by R. A. HENDERSON

ABSTRACT. The unusual septal surface typical of lytoceratid ammonites is described from unique Western Australian specimens of the late Cretaceous Indopacific species *Pseudophyllites indra* (Forbes). Median dorsal septal recesses and inner septa combine to form a septate tunnel lying within the phragmocone; their free margins are complexly fluted like that of the septal periphery in contact with the outer shell wall. Functional analysis of the fluted septal recesses and inner septa suggest that they were not related to phragmocone strength but facilitated the attachment of adductor muscles. By analogy, a muscle attachment function is argued for the fluted septal periphery of *P. indra* and for the septal periphery of Mesozoic ammonites in general. The role of septal design in contributing necessary strength to phragmocone construction is re-evaluated and considered subordinate.

Muscle attachment translocation during growth, a special problem for ectocochleate cephalopods, was accomplished by the release of muscle attachment and rapid forward movement of the ammonite animal in its shell. Muscles were re-attached along a narrow zone at the free margin of a newly formed septum, convolution of which enlarged the attachment surface. It is argued that connecting rings of the siphuncle were preformed in the body chamber prior to movement of the animal; location of the siphuncle, details of its construction, and the nature of associated structures are consistent with this proposal. The muscle-attachment hypothesis is further supported by shell microfabrics known for Mesozoic ammonites, including new data for *Sciponoceras*. Gross differences in shell form and ornamentation which separate Mesozoic ammonites and nautiloids are thought to be due to differences in growth style, necessitated by the manner in which muscle attachments were translocated in members of the two groups.

AMMONITES were one of the most common shelled-invertebrate groups in Mesozoic seas and their shells, characterized by completely fluted septa and a ventral siphuncle, have attracted functional comment throughout the history of invertebrate palaeontology. Raup (1966, 1967) has demonstrated that the outer shell form of planispiral ammonites can be generalized to a mere three parameters. No such simplicity is apparent for septa which show a bewildering array of morphologies among Mesozoic members of the subclass yet are taxonomically specific, showing no more variation at the species level than any other test attribute. Clearly their morphology was under close genetic control, seemingly at considerable expense relative to the genetic investment in other elements of shell morphology. By implication the septa, or the body surface they replicated, must have fulfilled an important functional role for the living animal. Further, the clear phyletic changes of septal design shown by discrete lineages of Mesozoic ammonites (Wiedmann and Kullman 1981) suggest the constant operation of selection pressures tuning septal morphology to its functional role.

As reviewed by Westermann (1971) and Kennedy and Cobban (1976) a number of functions have been attributed to the fluting of ammonite septa since Owen (1843) suggested that they were designed in such a way as to impart necessary additional strength to the shell. Owen's view has been frequently endorsed in the literature (Zittel 1884; Pfaff 1911; Ruzhentsev 1946; Arkell 1949; Kennedy and Cobban 1976) and according to Westermann (1975) is the consensus of present-day opinion.

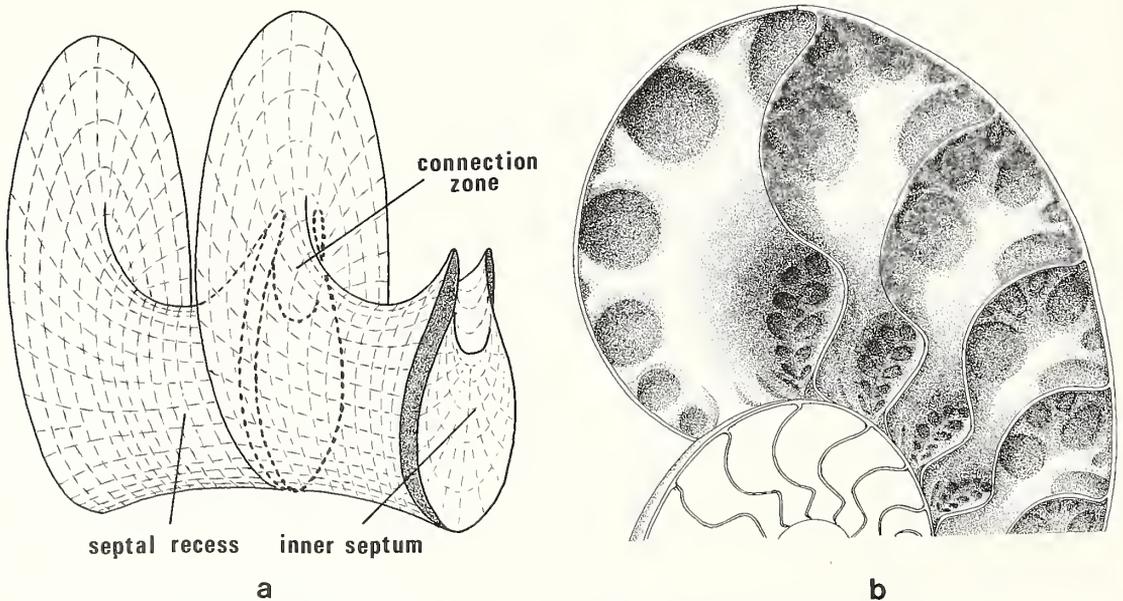
Maastrichtian specimens of *P. indra* (Forbes) from the Miria Marl, Carnarvon Basin, Western Australia show with exceptional clarity the extraordinary septal surface that typifies the Jurassic and Cretaceous suborder Lytoceratina. Its septal morphology is incompatible with the strength paradigm of function which is thereby brought into question. It is here re-evaluated for Mesozoic ammonites generally. An alternative proposal, that the complex morphology of the septal periphery was required for muscle attachment, is argued for *P. indra* and its general applicability to Mesozoic ammonites is examined.

Location of specimens. The following abbreviations are used to denote the repositories of figured specimens: WAM—Western Australian Museum, Perth; NMV—National Museum of Victoria, Melbourne; BM(NH)—British Museum (Natural History), London; OUM—Oxford University Museum, Oxford.

SEPTAL SURFACE OF *PSEUDOPHYLLITES INDRA*

Description

The periphery of the septal surface in contact with the outer shell is complexly fluted to the fourth order. Convex flutes, corresponding to saddles of the suture, widen towards the periphery and arch forward in an adapertural sense. Concave flutes, corresponding to lobes of the suture, arch backwards towards the shell apex and narrow towards the periphery so that they form conical vaults below the outer shell. Minor flutes die out rapidly away from the periphery and at approximately the mid-line between the periphery and centre of the septum, first-order flutes disappear. The septal surface is then essentially planar across a narrow zone which is horseshoe-shaped in plan view. Inside this zone the septal surface is curved uniformly backwards to form a pronounced depression, here termed the septal recess, occupying the mid-dorsal septal field (Pl. 48, figs. 2, 5; text-fig. 1). The



TEXT-FIG. 1. Septal architecture of *Pseudophyllites indra* (Forbes). *a*, schematic representation of two successive septal surfaces (fluting omitted). Note the zone of connection, provided by the neck of the inner septum, between each septal recess and the main chamber which succeeds it. *b*, phragmocone cut in the median plane; note the two chamber systems and the interconnection between them provided by the necks of the inner septa which do not close on to the preceding septal recesses.

EXPLANATION OF PLATE 48

Figs. 1–5. *Pseudophyllites indra* (Forbes) showing details of the septal surface. 1, 2, lateral and apertural view of phragmocone, WAM 60.44, $\times 1$. 3, latex cast from internal mould of septal recess, WAM 81.2500, $\times 1$. 4, latex cast from internal mould showing the fluted free margin of a septal recess and fluted inner septum. Note that the line of suture is continuous from the septal recess to the inner septum, both being part of a single septal surface, WAM 81.2433, $\times 4$. 5, internal mould of septal surface showing septal recess and inner septum, WAM 60.130, $\times 1$.



1



2



3



4



5

septal recess is in effect a short tube, terminating at the mouth of its equivalent on the preceding septum. Thus successive septal recesses link one septum to the next, forming a tunnel which extends throughout the phragmocone (Pl. 49, fig. 1).

The tunnel is, however, itself septate. A large limb subtended from the median ventral wall of each septal recess, here termed the inner septum, plugs the mouth of the septal recess formed by the previous septum (Pl. 48, figs. 4, 5). In concert the septal recesses and inner septa combine to form an inner phragmocone analogous to the phragmocone proper which surrounds it. Chambers of the two phragmocone systems are linked, a zone of interconnection being provided in the necks of the inner septa which do not close against the mid-ventral sector of the subjacent septal recesses. Text-figure 1 provides a diagrammatic summary of the septal architecture.

The free margin of the septal recess is complexly fluted (Pl. 48, figs. 3, 4). Its third-order subdivisions splay out to form a fringe which reaches beyond the mouth of the previous septal recess, extending across the subjacent planar septal surface to the base of the first-order flutes of the outer perimeter (Pl. 48, fig. 4). Fluting of the inner septum is also complex and represents a smaller scale equivalent to the structure of the outer septal periphery. Margins of the septal recess and inner septum are confluent and comprise the septal lobe of sutural nomenclature (Arkell 1957; Kullmann and Wiedmann 1970). The suture of the inner septum thus comprises a very large median saddle within the septal lobe proper which is formed by the free margin of the septal recess. The septal lobe is confluent with, and may be considered as an extension of, the internal lobe.

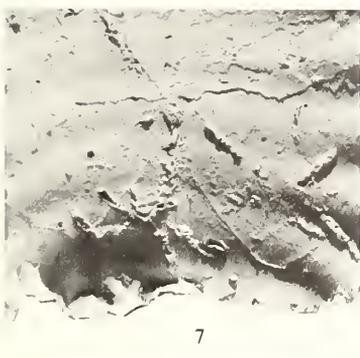
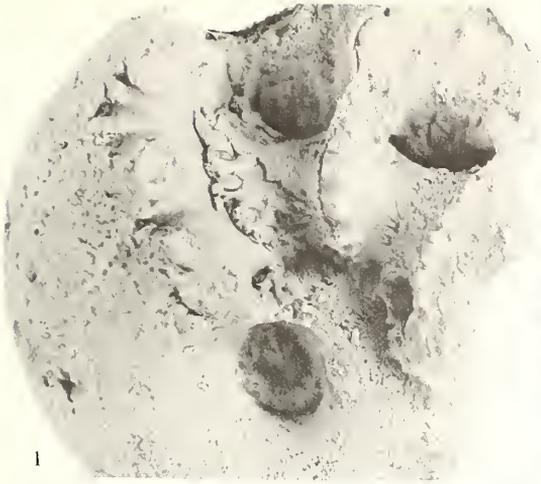
A septal lobe is already present at a shell diameter of 8 mm, the smallest growth stage in the collection displaying a septal surface. Subsequent growth trends are isometric across the size range of septal surfaces available for measurement (text-fig. 2) The pattern of fluting associated with the septal recess and inner septum, like that of the septal periphery, was stabilized early in ontogeny. A detailed comparison of fluting represented at shell diameters of 44 mm and 162 mm shows it to be identical in all respects other than scale. Flutes associated with minor lobes within the septal lobe are more intricately divided and more elongate than those associated with the minor saddles so that the suture shows a marked polarity (Pl. 48, fig. 4).

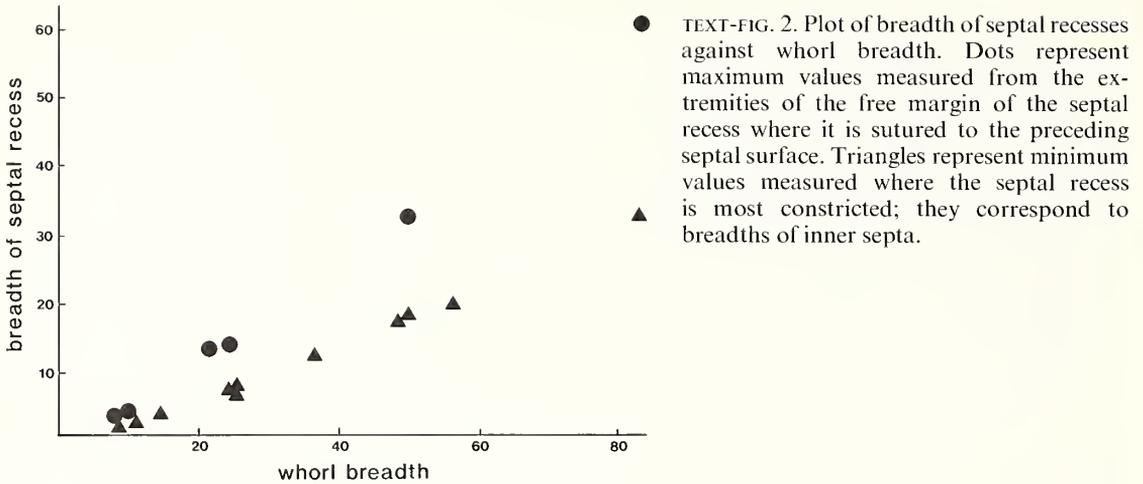
Interpretation

Structures associated with the septal lobe are striking features of *Pseudophyllites* phragmocones and represent a considerable genetic investment in shell architecture and in organization of the posterior

EXPLANATION OF PLATE 49

- Fig. 1. Internal mould of *Pseudophyllites indra* (Forbes) showing two linked septal recesses, one showing the sutural trace of an internal septum. WAM 80.976, $\times 1.2$.
- Figs. 2, 3. Two halves of a juvenile shell of *Nautilus pompilius* (Linneus) in which the last septum is incomplete and represented by a rim of shell only. 2, uncoated and showing the mural zones of the two last septa. 3, coated with ammonium chloride and showing that the last septum is widely separated from the mural ridge which bounds the mural zone of the previous septum. OUM 14475, $\times 2$.
- Figs. 4–10. Latex peels of internal moulds of ammonites showing structures of the inner shell surface. 4, *Kitchinites* sp. nov. showing midventral ridge on inner shell, NMV P31013, $\times 3$. 5, *Lytoceras cornucopia* (Young and Bird) showing the posterior of the body chamber on the midventral line. Note the ridges extending a short distance into the body chamber and showing an indistinct lobate termination, BMNH 43902, $\times 3$. 6, *Phylloceras heterophyllum* (J. Sowerby), showing midventral ridge with minor ridges converging on to it, OUM J20360, $\times 3$. 7, *Hamites maximus* J. Sowerby showing faint ridges of shell forming a pair of rings straddling the mid-dorsal line of the body chamber immediately anterior to the last septum. Figured by Crick (1898, pl. 17, figs. 6, 7) who regarded them as muscle scars, BMNH C6802, $\times 3$. 8, *Gunnarites kalika* (Stoliczka), showing midventral ridge, WAM 80.845, $\times 3$. 9, *Maorites densicostatus* (Kilian and Reboul), showing midventral ridge, NMV P31023, $\times 3$. 10, *Gaudryceras kayei* (Forbes), showing midventral ridge and subordinate ridges parallel to it, WAM 80.839, $\times 3$.





body of the *Pseudophyllites* animal. Their retention as enduring features in the *Tetragonites-Pseudophyllites* stock, and in the *Lytoceratina* in general, indicates that they served some specific functional role. Given the comparability of fluting associated with the septal lobe with that of the external septal periphery, an integrated function or functions may be adduced for the septal surface *in toto*.

Strength. Since phragmocone strength is the generally accepted functional role attributed to septal design, it is instructive to examine the septal lobe and its associated structures in this context. Fluting related to the septal lobe is entirely internal and therefore cannot have contributed to support of the outer shell. It might be argued that fluting associated with the inner septum contributed strength, and consequent economy in shell thickness, to the median dorsal part of the septal surface *in toto*. As discussed more fully below, each septal surface must, at some stage of phragmocone growth, have carried the hydrostatic load and it has been argued that septal architecture in ammonites reflects a response to this requirement. The internal septum might thus merely represent a somewhat bizarre elaboration of this theme.

However, design of the flared and fluted base of the septal recess intersecting the preceding septal surface at a low angle along a deeply embayed line of suture which displays marked polarity, cannot be readily reconciled with shell strength as its functional role.

Phyletic context. The septal lobe is a structure of considerable phyletic longevity. It is characteristic of the morphologically conservative suborder *Lytoceratina* whose range extends from early Jurassic to late Cretaceous (Kullmann and Wiedmann 1970). The earliest *Pseudophyllites* are of Santonian age and the genus is best known from the Campanian and Maastrichtian. Origins of the genus are clearly to be found in *Tetragonites* (see Kennedy and Klinger 1977), which also shows a well-developed septal lobe and which first appears in late Aptian times. The septal lobe was therefore a stable morphological feature of the *Tetragonites-Pseudophyllites* stock for some 40 m.y. and was likely to have been stable over a much longer period, probably having appeared in an ancestral lytoceratid stock during the early Jurassic.

The peculiarities of lytoceratid septal architecture cannot be considered as unique among ammonites but, as has long been recognized, merely represent an extreme development of the dorsal flute of the septum corresponding to the internal lobe of the suture. The septal lobe of sutural terminology represents an extension of the internal lobe onto the preceding septum (Wiedmann and Kullmann 1981). Thus the septal recess is homologous with the flute corresponding to the internal lobe which is ubiquitous among ammonites except for a few Devonian forms. The inner septum is

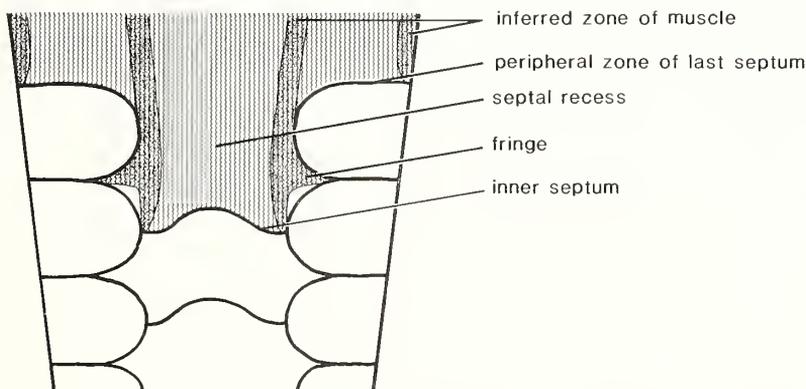
homologous with a minor flute corresponding to a small median saddle contained within the internal lobe of most Mesozoic ammonites.

Organization of associated soft-tissue. Disposition of soft-tissue associated with the formation of each septal recess and associated internal septum is replicated by the shell itself and is complex. The suture line at the free margin of the septal recess marks the intricate termination of a fringe of tissue which followed the shape shown by the distal portion of a septal recess, curving away from the main body of tissue (Pl. 48, fig. 2; text-fig. 3). A space, presumably fluid-filled in life, must have lain between this fringe and the main body of the animal. The inner septum replicates the posterior termination of the animal's soft parts which plugged the narrowest part of the preceding septal recess. Its complex suture represents branching arms of tissue that extended along the walls of the preceding septal recess (Pl. 49, fig. 1).

In moving forward during growth to the site of a new septum, all tissues were withdrawn from the septal recess. To accomplish this, considerable constriction of the fringe would have been necessary as the smallest cross-section of the septal recess is as little as 60% of the area displayed by the associated fringe (Pl. 48, fig. 3; text-figs. 2, 3). The space between the fringe and the main body of tissue would have assisted in accommodating the constriction. The fringe itself must have consisted of tissue with exceptional elastic properties for, having been compressed and distorted, the fringe recovered its original shape, fitting exactly to the mouth of the previously formed septal recess with the fine divisions of its delicately serrated margin reaching across the previously formed septal surface towards its periphery. Collagenous connective tissue organized as a pliant composite, or tissue capable of hydrostatic self-support, would possess the appropriate mechanical attributes (Wainwright *et al.* 1975). Soft tissue lying adjacent to the septal periphery adopted a complex shape of identical type to that of the fringe and was laterally continuous with it. The same type of tissue must therefore have been located along the frilled periphery of the *Pseudophyllites* septum.

The episodic, growth-required stress imposed on the fringe of soft tissue lining the septal recess and producing marked changes in its shape suggests that forward movement of the animal within the shell itself was episodic. It seems likely that short periods of rapid forward movement and distortion of the fringe were followed by long resting periods when the fringe adopted its unstressed shape.

Certain authors (Seilacher 1975; Bayer 1977a) have contended that the posterior of the ammonite animal's soft tissue functioned as a membrane surface prior to septal fabrication. In this model the membranal precursor of the septum is thought to have approximated initially to a planar surface



TEXT-FIG. 3. Transverse longitudinal section drawn in the plane of maximum whorl breadth for the last two camerae and posterior body chamber of *Pseudophyllites indra* (Forbes) showing the relationship of tissue to shell.

occupying the whorl cross-section and attached at a number of point locations on its periphery. Hydrostatic or muscular stress acting perpendicular to the initial planar membrane resulted in its deformation and the production of the complex, fluted surface later replicated in shell by secretion of the septum. Deformation was maximized at the periphery of the subsequent septum, with its free segments stretched between the point attachments. Orientation of the major folds in the suture line is thereby controlled by the direction of stress imposed on the membrane.

Fluting of the fringe, of which the free margin of the septal recess is a replica, has a different orientation and cannot have resulted from the same mechanism. Here the sutural folds are orientated perpendicular to the inferred stress direction and are unrelated to it (see Pl. 48, figs. 3, 4).

Fluting shown by the septal recess is identical to, and laterally continuous with, that shown by the outer septal periphery and the inner septum. Furthermore, the entire septal surface was almost certainly the result of a single secretional episode. Clearly the type of tissue, its episodic movement and the secretory processes responsible for formation of the septal recess were general to the entire septal surface.

STRENGTH PARADIGM OF AMMONITE SEPTAL FUNCTION RE-EVALUATED

Accepting that ammonite phragmocones functioned like that of living *Nautilus* and were filled with gas of about one atmospheric pressure which imparted buoyancy to the shell, they may be regarded as sealed vessels required to withstand hydrostatic pressure. Three aspects of phragmocone strength need to be considered: the strength of the outer shell which is supported by the septa, the strength of the septa themselves and the strength of the junctions between the outer shell and the septa on the line of suture. An initial concern, however, is the palaeobathymetry of ammonites and thereby the hydrostatic pressures to which their phragmocones were likely to have been subjected.

Palaeobathymetry

The depth habitat of ammonites is not easily evaluated because shells which are buoyant in life may be easily transported in death to a completely different environment (Reyment 1958). Post-mortem cessation of siphuncular osmotic pumping may have caused flooding of the phragmocone and sinking of the shell to a site of fossilization at much greater depth than that inhabited by the living animal. Alternatively post-mortem separation of body from shell may have caused the latter to float to the surface and drift inshore to a shallow water, even littoral, environment as is common for *Nautilus* (House 1973; Reyment 1973).

The broad palaeoecological context of ammonites is best assessed from the types of sediment in which their remains occur and the nature of fossil assemblages of which they are part. More recent data support the conclusion of Miller and Furnish (1957) that ammonites are predominantly associated with sedimentary rocks of shallow-water origin. McKerrow (1978), in a comprehensive review of British fossil assemblages, many of which are also widely represented in Europe and elsewhere, recorded ammonites as essentially of neritic palaeoecology throughout their history. Casey and Rawson (1973) drew similar environmental conclusions for ammonite-bearing strata of the Jurassic and Cretaceous boreal realm, whilst Kauffman (1977) concluded that the vast epeiric sea which invaded the Western Interior of North America and sponsored an abundance of ammonites had a maximum depth of perhaps 300 m. Cretaceous sediments containing spectacularly diverse ammonite assemblages accumulated in passive continental margin, neritic settings on the borderlands of the Indian Ocean following the fragmentation of eastern Gondwana in Madagascar and southeastern Africa (Blant 1973; Kennedy and Klinger 1975; Basairie and Collignon 1956), Western Australia (Veevers and Johnstone 1974; Henderson and McNamara unpublished) and southern India (Kossmat 1898; Sastri *et al.* 1973).

In comparison, records of ammonites from deep-water sedimentary environments are few. In addition to neritic assemblages, Scott (1940), Ziegler (1967), and Tanabe *et al.* (1978) have recorded distinctive assemblages typified by Phylloceratina and Lytoceratina from deeper water environments

where they were considered to have had benthic or bathypelagic life habits. Phylloceratids and lycoceratids are however best known from shelf sediments and may have been shallow-water nectopelagic organisms whose range extended beyond the continental shelves (Birkelund 1965) and their deep-water associations could well be a post-mortem artefact (Kennedy and Cobban 1976; Tanabe 1979). Ammonites, like all macrofossils, are very rare in Mesozoic eugeosynclinal flysch (continental rise and trench) sediments such as those of the Franciscan assemblage in California (Irwin 1957) and the Torlesse Supergroup in New Zealand (Stevens and Speden 1978) whereas they are much more common in subjacent broadly coeval sedimentary rocks of the northern part of the Great Valley sequence (see also Ojakangas 1968; Matsumoto 1960) and Mirihiku Supergroups respectively where shallower water depositional environments prevailed.

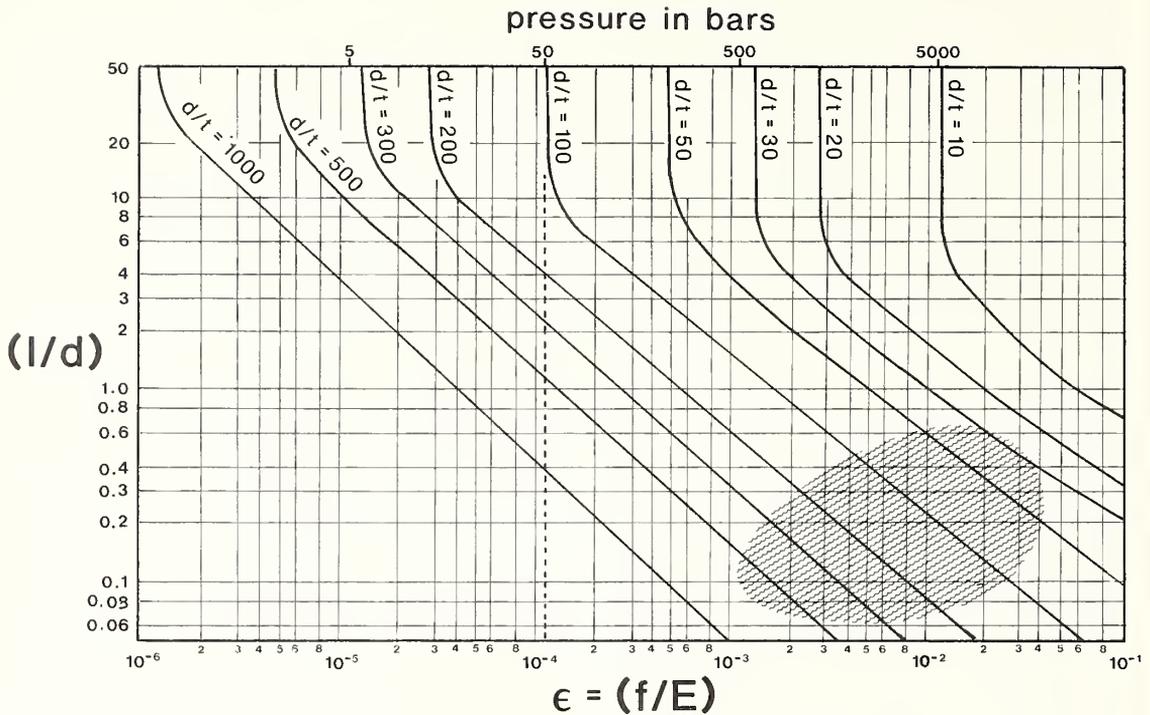
The record of ammonites in deep-sea, pelagic sediments is sparse but its interpretation is rendered equivocal by the dissolution of aragonite shells at depth as shown so clearly by pteropods in the deep-sea Cenozoic record (Kennett 1982). As reviewed by Bernoulli and Jenkyns (1974), Mesozoic ammonite and aptychus-bearing pelagic lithofacies are well known from onshore exposures in the Alpine-Mediterranean region where they are considered to be continental margin deposits which accumulated partly under neritic conditions within the photic zone and partially in deep-water environments. Many of the records of ammonite phragmocones and lamellaptychi from deep-sea drilling and dredging represent neritic deposits of Mesozoic continental margins (Renz *et al.* 1975; Wiedmann and Neugebauer 1978) or deep-water pelagic deposits which are not greatly distant from Mesozoic continental margins (Renz 1972, 1978, 1979a, 1979c, Wiedmann 1979). However, reports of lamellaptychi from the central Pacific (Renz 1973) and Atlantic sites distant from any continental mass (Renz 1977, 1979b) show that some ammonites were fully oceanic. Lamellaptychi are characteristic of the Opelellidae (Arkell *et al.* 1957), a cosmopolitan family which is well known from shallow-water sediments. All ammonite genera known to occur in deep-sea, pelagic sediments as phragmocones are also known from shallow water occurrences.

Overall the lithofacies and associational data for ammonites support the view of Lehmann (1975) that they were predominantly of neritic palaeoecology and lived in water depths ranging to perhaps 300 m corresponding to a hydrostatic pressure of 30 bars. The contention of Mutvei (1975), based largely on considerations of functional morphology, that ammonites were predominantly denizens of the open oceans where they ranged into deep-water environments, finds no support in the fossil record.

Strength of outer shell

Ammonite phragmocone strength in this context can be assessed in an approximate way by reference to the engineering of thin-walled pressure vessels for which there is a sound theoretical design basis to contend with failure by buckling. As shown by Brownell and Young (1959) the strength of cylindrical vessels subjected to external pressure is governed by the diameter of the cylinder, the thickness of its wall, the spacing of internal strengthening rings or septa, and the elastic properties of the wall material as determined by Young's Modulus. Segments of ammonite phragmocone may be considered as approximations to such vessels. Wall thickness and septal spacing can be measured directly. Young's Modulus has been measured for *Nautilus* nacre (Wainwright *et al.* 1975) and the nacre which comprises the principal shell layer of ammonite phragmocones (Birkelund 1981) may be expected to have shown comparable elasticity. Very few ammonite phragmocones conform to a circular cross-section; a diameter which matches the widest arc of cross-sectional curvature and represents minimum strength seems an appropriate approximation to adopt in the analysis.

Text-figure 4, which is adapted from Brownell and Young (1959, text-fig. 8.4), charts the relationship between cylindrical pressure vessel specifications and strain at failure. By employing Young's Modulus for *Nautilus* nacre, the abscissa may be rescaled for stress. Also shown is the field to which ammonite phragmocones approximate and the stress imposed by a hydrostatic pressure of 50 bars. The strength indicated for ammonite phragmocones assuming planar septa departs from the stress field to which they were probably subjected (up to 30 bars), plus an appropriate safety margin, by an order of magnitude. Whilst it is admitted that the analogy between ammonite phragmocones



TEXT-FIG. 4. General chart showing relationship between diameter (d), thickness (t), distance between internal septa (l), and strain (ϵ) at the point of failure by buckling for cylindrical thin-walled vessels subjected to external hydrostatic pressure (from Brownell and Young 1959). The field to which Mesozoic ammonites approximate, based on shell measurements for seventy-five taxa, is shaded. A value of Young's Modulus (E), adopted as 44 G Nm^{-2} determined for *Nautilus* nacre by Wainwright *et al.* (1976), allows calculation of a scale in terms of pressure. Even with simple septa, Mesozoic ammonite phragmocones appear to have been immune to failure by buckling at the maximum pressure (50 bars) to which they were probably subjected in life.

and cylindrical pressure vessels is a gross approximation, the disparity between indicated strength and expected stress is so marked that septal fluting, as a design to enhance strength by reducing the effective spacing between septa, seems to be completely unwarranted.

Further, the plan of septal fluting shown by ordinary planispiral phragmocones seems inappropriate if support for the outer shell was the only design consideration. The presence of a convolute internal suture is commonplace in Jurassic and Cretaceous ammonites (see Wiedmann and Kullman 1981) and represents septal fluting which buttresses directly to the venter of the previous whorl, abutting a shell surface that is already fully supported. The internal lobe straddling the dorsal mid-line is especially noteworthy; it represents a major septal flute in almost all ammonites yet in the vast majority of phragmocones the dorsum is not part of the outer shell and can have carried no hydrostatic load.

There are many ammonites for which fine divisions of the suture, reflecting fine fluting of the septal periphery, cannot have added any appreciable strength to the outer wall. This is true for most ceratitic and pseudoceratitic ammonites in which second-order sutural divisions at the base of the lobes are very fine. The same general argument applies to many Jurassic and Cretaceous ammonites with highly frilled sutures. Often in such forms the finest divisions, or more properly the flutes they represent, contribute little or nothing to minimizing the size of unsupported spans of outer shell. In

addition, the distinctive shape of certain sutural elements is difficult to reconcile with the strength paradigm. A convenient example is provided by the distinctive, phyletically enduring phylloid terminations to saddles of the *Phylloceratina*.

As shown by Bayer (1977b), the fluctuation in septal distance during growth displayed by several ammonites and the generally poor relationship between the septal spacing and shell form are anomalous in the context of strength. Many authors, most recently Wiedmann and Kullman (1981), have emphasized the conservatism of suture lines, and by implication, septal fluting. Patterns displayed by suture lines often allow stocks of common ancestry to be recognized whereas other aspects of shell morphology, including whorl profile, show wide variation within stocks and repeated convergence between stocks. Given that whorl profile is an important mechanical factor in strength of the outer shell, a close relationship between suture lines and whorl profiles would be predicted by the strength paradigm. Such is patently not the case.

Strength of septum itself

As noted by Raup and Stanley (1971, p. 179) hydrostatic pressure would have affected both the outer shell and the last septum to form part of an evacuated chamber. Body fluids of the living animal would have been at the hydrostatic pressure and the living tissue would have had little strength or at least much greater elasticity than the enclosing shell. At some stage of ontogeny, therefore, each septum would have been obliged to accept the full hydrostatic load. Several authors, for example Westermann (1975) and Wainwright *et al.* (1976), have noted that the convex form of ammonite septa is generally favourable to withstanding hydrostatic stress.

Septa are too complex to permit any rigorous strength analysis but some general observations are pertinent. The strengths of curved shells is inversely proportional to their radii of curvature and proportional to their thickness. Tensional and compressional strengths of the constructional material are additional factors; for *Nautilus* nacre compressional strength is approximately twice that of the tensional strength (Wainwright *et al.* 1976) and a similar contrast may be expected for the nacre of which ammonite septa are constructed. To conform to the strength paradigm, each subzone of a septum should be of equal strength. Since shell thickness does not vary between convex flutes and concave flutes, though these would have experienced compressional stress and tensional stress respectively, the two types of flute should show marked differences in radii of curvature. However, suture lines show that this is not the case; in almost all ammonites lobes and saddles are invariably of comparable widths.

Proliferation of fluting towards the septal periphery resulted in shell economy, reduction in radii of curvature of the flutes being reciprocated by a reduction in septal thickness. Enhancement of the weight/strength relationship, however, was not required to maintain buoyancy. Calculations by Mutvei and Reyment (1973) and Heptonstall (1970) have shown that ammonite phragmocones possessed a buoyancy potential beyond the requirements of the living animal, so much so that several chambers must have remained flooded.

Shell economy would have been desirable from a metabolic standpoint. If proliferation of fluting represented such a strategy, then it was not fully exploited. As well known to ammonite specialists, even slight abrasion of phragmocone moulds or steinkerns results in a considerable reduction in sutural complexity. In other words, fine-scale fluting is restricted to a very narrow zone at the periphery of septa. Radial lengthening of fine-scale flutes into a broader zone would seem desirable if shell economy was a matter of vital concern.

Strength of suture

Pfaff (1911) considered the suture between the septum and the outer shell to have been a zone of structural weakness and that linear elongation of the suture imparted necessary strength to the junction. He cited as evidence the allometric relationship between septal diameter and length of suture which he regarded as typical of ammonites. Since septal area, and therefore total hydrostatic load, increases in proportion to the square of its diameter whereas the circumference increases in

linear proportion to the diameter, such a relationship may be interpreted as necessary to maintain sutural strength.

However, shear strength of the interface between septal nacre and the interior surface of the outer shell at the line of suture has never been mechanically evaluated and there is no *a priori* reason for assuming it to be a zone of special weakness. Further, as noted by Westermann (1975) if the junction was a zone of mechanical weakness the septum could be wedged out against the outer shell over a broad zone of contact. This would seem a more expedient solution to the problem rather than maximizing the length of contact by sutural frilling.

Conclusion

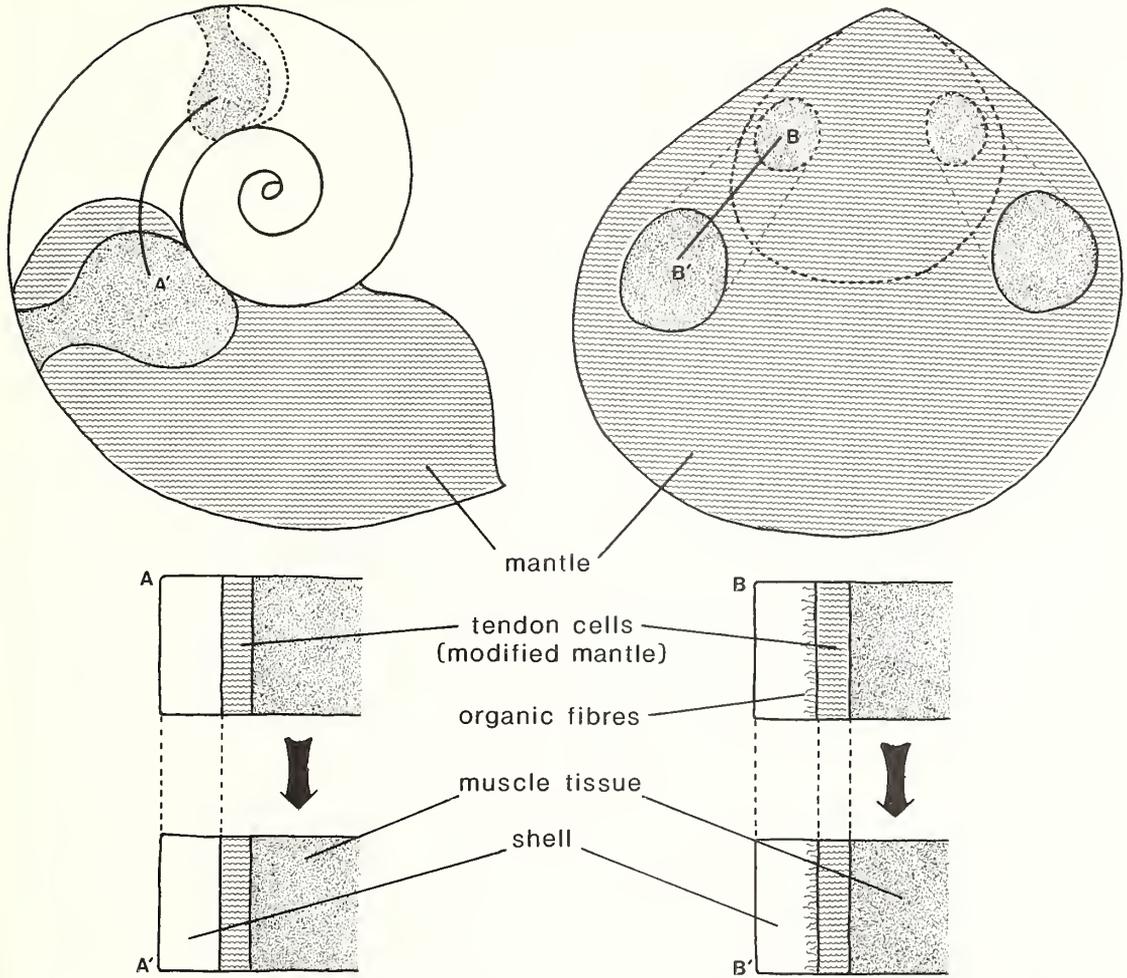
It would be in error wholly to deny the strength as a consideration in the design of ammonite septa; clearly there are several aspects of septal morphology that are consistent with such a function. Equally, it is evident that strength is not the only, nor probably the major, consideration. Septal elaboration in ammonites generally, as in *Pseudophyllites* and lycoceratids of similar shell architecture, must have served some other function.

MUSCLE ATTACHMENT PARADIGM OF SEPTAL FUNCTION

The idea that fluted margins of septa may have assisted in attaching the body of an ammonite to its shell was first noted last century and reintroduced by Spath (1919). It has subsequently been listed among alternatives for septal function in a number of reviews (for example, Raup and Stanley 1971; Westermann 1971; Kennedy and Cobban 1976) but the case has never been argued in detail.

Accepting that the attachment of body to shell in the Mollusca is intimately related to muscle attachment, it is instructive to consider the interface between muscle and shell. The general mechanism which applies in molluscs has been described by Hubendick (1957) with important emendations from Nakahara and Bevelander (1970) and Tompa and Watabe (1976). The muscle base is attached to a layer of specialized mantle epithelium, the tendon layer, from which extracellular fibres extend into the adjacent shell surface. Organic extensions from the living tissue are thereby physically embedded in the shell. During growth-required translocation of muscle attachment it is thought that mantle cells adjacent to the leading edge of the muscle base become transformed into tendon cells and extend the tendon layer. New muscle tissue is added above the tendon layer addition and concomitantly part of the tendon layer and associated muscle is atrophied at the trailing edge of the muscle base. In this way muscle bases track across pre-existing mantle in steady, progressive movement as documented for the oyster *Crassostrea* by Galtsoff (1964).

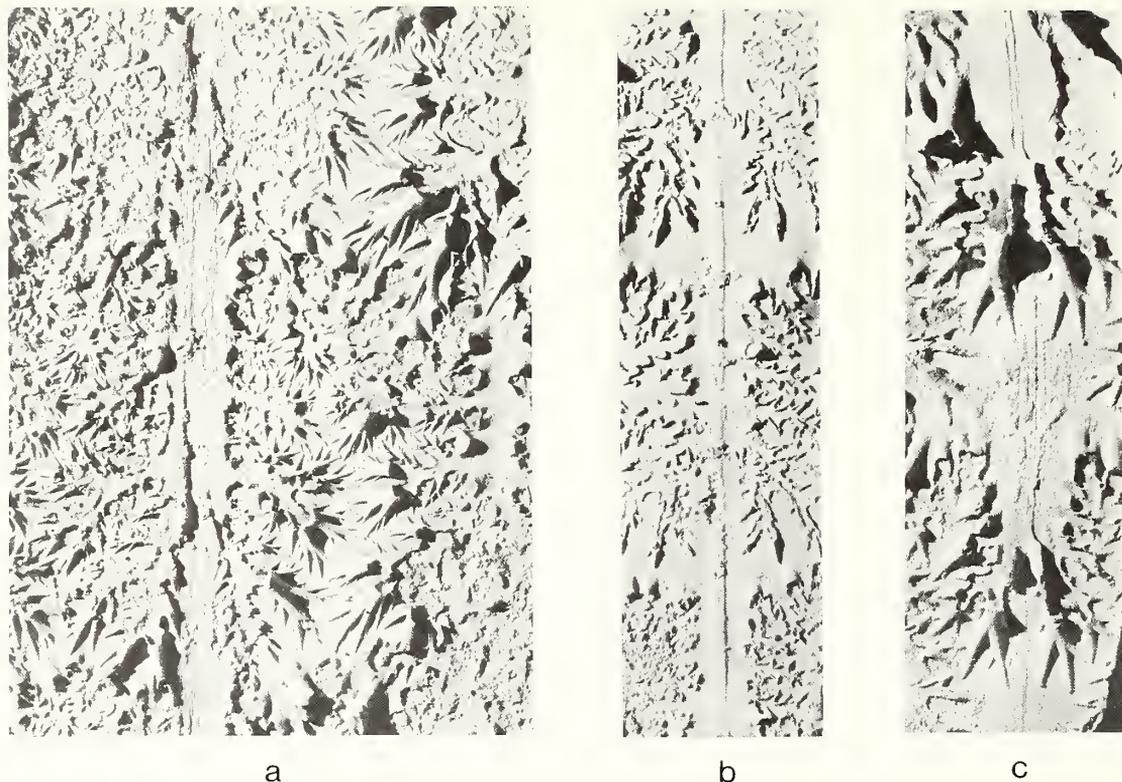
However, this mechanism cannot apply to ectocochleates in which the shell is much larger than the body. Here the entire mantle must move forward in the shell during growth because the shell is growing much faster than the body. The style of growth is more like an ecdysis with older portions of the shell progressively evacuated by the body rather than the steady, matched growth of body, mantle, and enclosing shell seen in most molluscs (text-fig. 5). It follows that muscle attachment cannot have been permanent with extracellular extensions embedded in the adjacent shell. If this were the case the mantle would have been rendered immobile, always pinned to the shell at the zone of muscle attachment. Rather, a temporary means of attachment must have applied, allowing the tendon layer to detach from the shell, move forward to a new site, and reattach. This type of muscle translocation is unique to ectocochleate cephalopods and is unstudied. Perhaps a cement, similar to that demonstrated by Bonar (1978) for muscle attachment of the nudibranch *Phestilla* to its larval shell and destroyed during metamorphosis to a shell-less adult, provided the attachment mechanism. The presence of a thin 'chitinous' layer covering the shell on areas of muscle insertion (Griffin 1900) supports this view. However, the ease with which dead *Nautilus* are slipped from their shells suggests an organic means of attachment, maintained by living tissue, was also involved.



TEXT-FIG. 5. Diagram contrasting mechanisms of muscle translocation shown by ectocochleate cephalopods, typified by *Nautilus*, and most other molluscs, typified by a bivalve. In *Nautilus* the shell is much larger than the body and enveloping mantle which must be moved forward in the shell, complementary with muscle translocation during growth. In the bivalve, mantle underlying the muscle bases is permanently bonded to the shell by extracellular organic fibres. Muscle translocation is achieved by growing new muscle tissue over pre-existing mantle at the advancing edge of the muscle base and complimentary wasting of muscle tissue at the trailing edge.

Proposal for muscle attachment in Pseudophyllites indra

The suture of *Pseudophyllites* is complex to the degree where its convolutions occupy all the available surface area of the outer shell save for a narrow zone adjacent to the mid-ventral line where the sides of the vental lobe do not quite meet (text-fig. 6a). Fine-scale fluting of the septa had reached its ultimate expression and was so from the early stages of shell growth as sutures are fully differentiated at shell diameters as small as 2 cm. Development of the septal recess and inner septum might be regarded as morphological strategies designed to extend the free septal margin and fine-scale fluting associated with it.



TEXT-FIG. 6. Latex casts taken from natural internal moulds of ammonite phragmocones to show details of the inner shell surface. *a*, *Pseudophyllites indra* (Forbes) showing fine-scale ridges and grooves along the ventral mid-line and the intricate fluting of the septal periphery; WAM 60.130, $\times 2$. *b*, *Pachydiscus* sp. showing a broad median ventral ridge; WAM 81.2693, $\times 3$. *c*, *Phylloceras* (*Neophylloceras*) *meridianum* Spath showing narrow median ventral ridge with indistinct ridges and grooves lateral to it; holotype BM(NH) C41320, $\times 2$.

As already discussed, inferences concerning the fringe of soft tissue associated with the septal recess in life suggest it was resilient in nature, capable of accepting stress by distortion followed by elastic recovery to its original shape. If the tissue possessed any appreciable strength, as might be expected from its elastic properties, it must have acted to hold the animal in its shell. A similar case can be argued for the tissue once associated with the fluted vaults lying beneath the outer shell at the septal periphery and at the margin of the inner septum. Fluted terminations of the vaults are widely splayed so that soft tissue contained in them must have been deformed when drawn forth during growth (Pl. 48, fig. 3; text-fig. 3). Accepting that attachment of body to shell is typically associated with the musculature in molluscs, it may be that the fine-scale flutes represent sites of muscle attachment.

Soft-part organization in ammonites is very poorly known and the nature of musculature can only be surmised from analogy with extant *Nautilus*. Mutvei (1957) has reviewed *Nautilus* musculature which is inserted on the annular elevation, a broad zone on the inner wall of the shell immediately in front of the last septum. Three distinct zones of muscle insertion are represented: the subepithelial muscle which originates from a narrow band at the posterior edge of the annular elevation and abutting the last septum; retractor muscles which originate from the lateral sectors of the annular

elevation and contribute the bulk of the muscle attachment area; and the mantle musculature which originates from a narrow band at the anterior margin of the annular elevation. Although insertion of the retractor muscles is lateral, the muscles themselves lie in the dorsal part of the viscera each having a reniform cross section and terminating in the cephalic cartilage (see Mutvei 1964*b*, text-fig. 2; Kennedy and Cobban 1976, text-fig. 5).

If the free septal margins represented the location of muscle attachment in *Pseudophyllites*, two subzones are apparent. The free margin of the septal recess and periphery of the inner septum would have contributed a pair of muscles located dorsally in the visceral mass and each with a reniform cross-section. The septal periphery would have contributed a sheet of muscle to the outer body wall. Such a system of musculature is strikingly similar to that displayed by *Nautilus*, the paired muscles representing retractors and the peripheral muscular sheet representing the mantle and subepithelial muscles.

The process by which the muscle attachment sites are translocated in *Nautilus* prior to the accretion of a new septum is poorly understood. Fine growth-lines on the retractor muscle scars show that these muscles were moved forward along the wall of the body chamber in very small increments, each one marked at the leading edge by a minute rim of prismatic myostracum. X-ray radiography by Ward *et al.* (1981) has shown that movement of the animal forward in its shell is episodic and rapid, taking place in less than 6 days in a cycle of chamber formation of over 70 days. In contrast, shell growth at the aperture proceeds at a slow and constant rate.

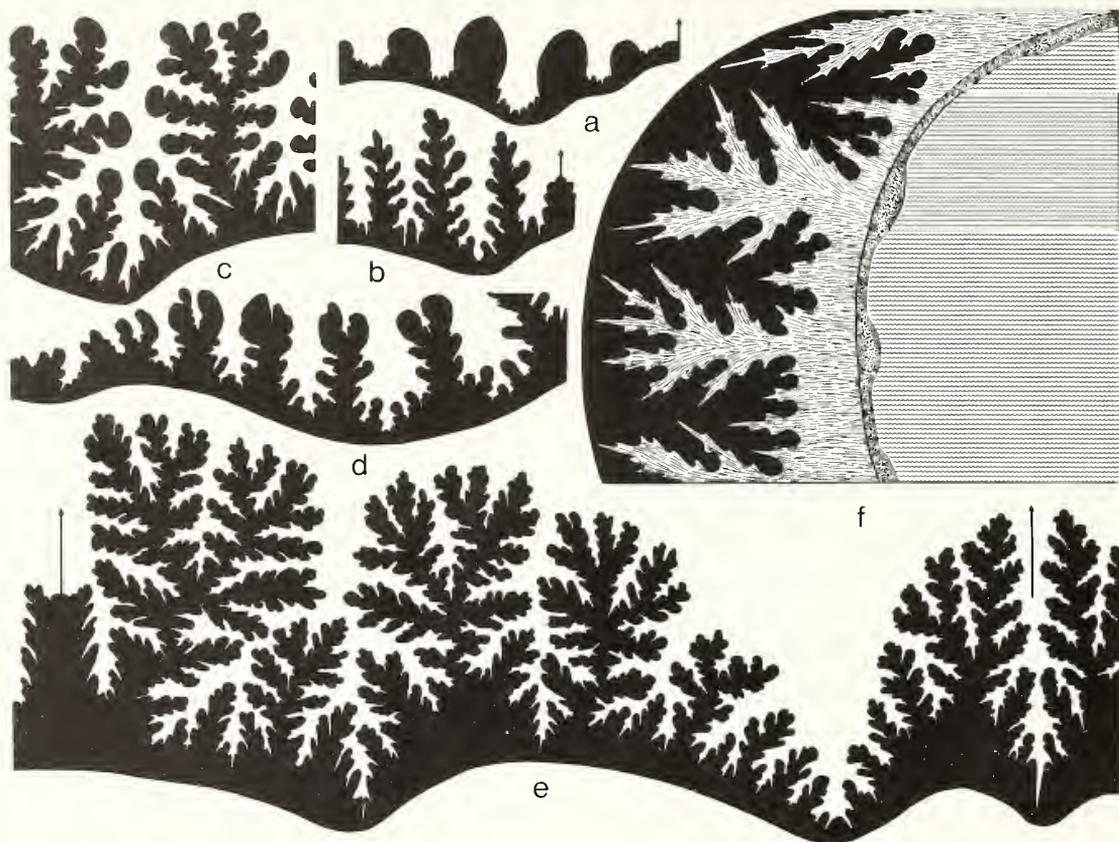
Growth-required movement of the *Pseudophyllites* animal is also thought to have been rapid because it necessitated distortion of the soft-tissue at the posterior margin of the visceral mass. Disposition of tissue responsible for secreting the septal recess (text-fig. 3) may be cited in evidence; with initiation of forward movement of the animal in its shell the fringe must have suffered distortion in shape, increasingly so as it was drawn past the central constriction of the septal recess. It would not have recovered its original shape until the forward movement had stopped. Tissue filling the fluted vaults at the septal periphery would have experienced a similar pattern of distortion and recovery.

It is suggested that muscle translocation was accomplished in a more dramatic way in *Pseudophyllites* where the muscles were inserted on the septal periphery, compared to *Nautilus* where the muscles are inserted on the wall of the body chamber. At the onset of movement, the muscles detached completely and were refastened to a newly accreted septum at the cessation of movement. This scenario suggests very rapid movement, perhaps only of a few hours, when body functions dependent on longitudinal musculature would have been suspended.

Septal surface periphery as a template for muscle organization

Accepting a need for temporary muscle attachment on the septum of a tubular, subepithelial muscle sheet as general for ammonites, the complex fluting at the septal periphery may be seen as a strategy for increasing the surface area of muscle attachment. This may have been required simply for bonding muscle to shell or, alternatively, as facilitating rapid secretion of the septal periphery prior to muscle insertion. The pattern of suture can therefore be regarded as expressing organization of the musculature; its complexity and diversity among ammonites reflects evolution of the longitudinal muscle system.

Fluting associated with major sutural lobes in Mesozoic ammonites is invariably dendritic in form with larger flutes subdividing to smaller ones; in taxa with complex sutures, four orders of fluting are represented on the septa. Muscle fibres within the fine-scale flutes, and inserted near their junction with the outer shell, would thereby have been aggregated in dendritic fashion forming thick bands of muscle tissue extending forward from the major lobes with thinner bands of muscle tissue extending from the major saddles where the dendritic pattern is less well developed (text-fig. 7). Seen in this way, unusual shapes of saddle termination, characteristic of Phylloceratina and various stocks of pseudoceratitic ammonites find a ready explanation. They are merely by-products of the particular dendritic form adopted by the lobes. The progressive, overall elaboration of sutures, from goniatic to ammonitic grade, may be considered as complementing a general advance in organization of the



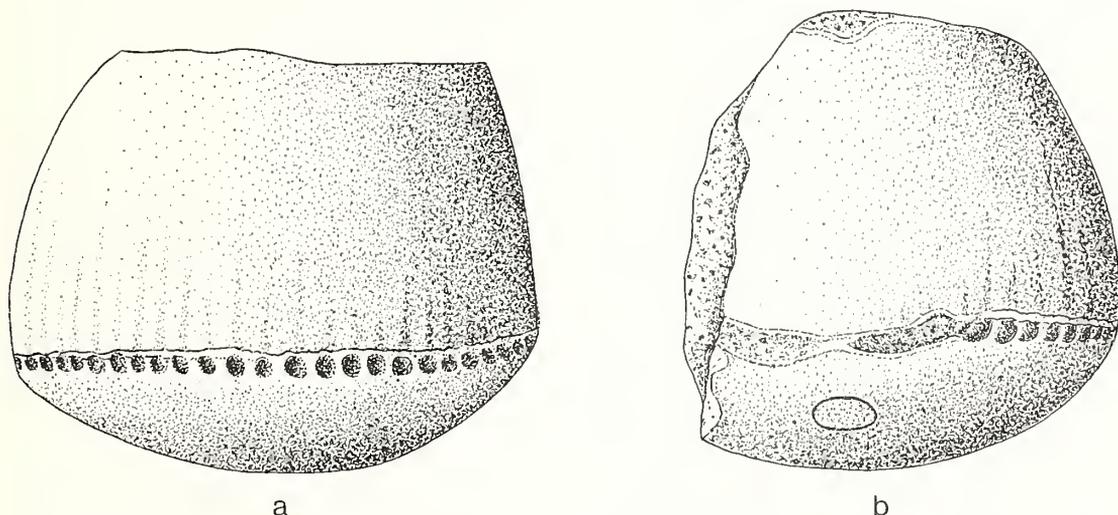
TEXT-FIG. 7. *a-e*, typical Mesozoic ammonite suture lines illustrating their dendritic nature, all $\times 1$. Ceratitina: *a*, *Hedestroemia hedestroemi* (Keyserling) (redrawn from Spath 1934); *b*, *Psilosturia mongolica* (Diener) (redrawn from Diener 1895). Phylloceratina: *c*, *Phylloceras* (*Hypophylloceras*) *onoense* (Stanton) (redrawn from Matsumoto 1959). Ammonitina: *d*, *Hypenoceras warthi* (Kossmat) (redrawn from Kossmat 1895); *e*, *Puzosia planulata* (Sowerby) (redrawn from Kossmat 1898). *f*, hypothetical reconstruction of body wall in relation to the last septum. Longitudinal muscle fibres originate at the margin of the septum resulting in a continuous muscular sheath which thickens adjacent to lobes of the suture where investment in muscle attachment is greatest.

musculature. The appearance of fine subdivisions of the primary lobes in sutures of the intermediate ceratitic grade is readily explained as part of this trend.

If the septal recess and inner septum anchored the retractor muscle in the Lytoceratina then its morphological equivalent in other suborders, the internal lobe, would also have served this function. The investment in retractor musculature in ammonites other than the Lytoceratina would seemingly have been very limited and the musculature would have comprised little more than a subepithelial sheet enveloping the body. Body-chamber shape suggests that many ammonites had elongate, worm-like bodies (Mutvei and Reymont 1973; Kennedy and Cobban 1976) curved through more than one revolution of the shell in some forms. In the heteromorphs the body was often elongate and was required to adopt different shapes as determined by changes in shell coiling that occurred during ontogeny. Body shape in all such forms is compatible with a tubular muscle sheath, less so with a pair of powerful retractors. For retractors to be efficient, their curvature needs to be limited, as in *Nautilus*

(see Mutvei 1964*b*; Kennedy and Cobban 1976). It might therefore be expected that the *Lytoceratina* should display short bodies accommodated in inflated, rapidly expanding shells of evolute form, as indeed is typical of the group (see Arkell *et al.* 1957).

It is of interest to note that shell fluting in response to organization of the musculature was independently developed, in an incipient way, by members of the 'nautiloid' orders *Oncoceratoida* and *Discoceratoida* during Ordovician time. In these groups the annular zone of muscle insertion at the base of the body chamber is ornamented with short ridges and intervening hollows. A larger paired muscle platform, thought to have been the site of retractor insertion, lies on the midline and is generally regarded as ventral (Sweet 1959; Teichert 1964). On some shells the ridges buttress the septum (text-fig. 8) and although they originate from the shell wall, they may be likened to the small septal flutes which buttress the shell wall in ammonites of the Triassic family *Sageceratidae* or the Cretaceous family *Sphenodiscidae*.



TEXT-FIG. 8. Internal mould of the Upper Ordovician *Oncoceratid* nautiloid *Diestoceras* sp. drawn from Sweet 1959, p. 42, figs. 6, 7. *a*, lateral view. *b*, ventral view; $\times 1$. The muscle attachment zone (annulus) lies on the posterior surface of the body chamber immediately adaperatural of the last septum and carries nodes which increased the surface area for muscle attachment.

Shell structure in Sciponoceras

If the septal periphery represents a zone of muscle insertion, it should carry prismatic shell which is the characteristic myostracum of molluscs. The septal periphery, because of its convoluted nature, is often difficult to examine for micro-fabrics. Juvenile *S. glaessneri* Wright from Bathurst Island, northern Australia are ideal for this purpose, displaying both simple sutures and empty phragmocones in which the original shell fabrics are perfectly preserved. As shown in text-figure 9 the junction between septum and shell wall is complex. A band of prismatic shell, here termed the preseptal prismatic zone, precedes the septum and is clearly distinct from the inner prismatic layer of the shell wall. It is narrow and sharply defined in the saddles, becoming broader and more diffuse in the lobes (text-fig. 9*a*). A second layer, of nacre, comprises the septum proper and wedges out against the inner prismatic layer of the shell wall (text-fig. 9*c*). A third band of shell with prismatic microstructure and

here termed the post-septal prismatic zone lies on the apron of the septal nacreous layer lapping on to the adjacent inner prismatic layer of the shell wall (text-fig 9*b, c*). In the saddles, where the angle between septum and outer shell is obtuse, its development is unconstrained and it forms a ridge. In the lobes, however, it lies in an acute angle between septum and outer wall and no such ridge is developed.

The postseptal prismatic zone of *S. glaessneri* is regarded as the location of subepithelial muscle insertion. Related structures have been identified in a number of studies of ammonite shell microstructure. Howarth (1975) observed that septal nacre in the Dactyloceratidae is replaced by prismatic shell, thickened to form a ridge, at the junction of septum and outer shell. According to Kuliki (1979, pl. 44, fig. 2), a similar transition marks the margin of septa in *Quenstedtoceras*. Birkelund and Hansen (1974, 1975) described a prismatic layer on the adapertural face of septa in *Hypophylloceras*. It appears to thicken at the septal periphery (Birkelund and Hansen 1974, pl. 9, fig. 2) gradually replacing nacre at the confluence of septum with shell wall (Birkelund and Hansen 1975, pl. 1). Well-preserved internal moulds of Cretaceous ammonites often show a faint gutter immediately adapertural of each septum in the crests of saddles (text-fig. 9*d*; see also Kennedy and Cobban 1976, pl. 2, fig. 3*a*). The gutter reflects a ridge of shell similar to that of *S. glaessneri* and probably represents the postseptal prismatic zone.

The preseptal prismatic zone is represented in *Nautilus* as a ridge of shell lying in the angle each septum makes with the shell wall. Mutvei (1964*a*) recorded it as the suprasedal ridge but, as his interpretation of ectocochleate orientation has not been widely accepted, this term is not used here. In addition to *Nautilus*, Blind (1975, 1976, 1980) recognized it in some Palaeozoic nautiloids and in a few taxa of ammonites. According to Blind, the preseptal prismatic layer corresponds to the mural ridge, an annular band of prismatic shell deposited as myostracum to a band of subepithelial muscle attachment which abuts the adapertural edge of the septum where it finally wedges out against the shell wall. Blind supposed that the mural ridge served a double function: first, as a zone of muscle attachment and secondly as a precursor elevation of shell to which the posterior of the animal's body is fitted prior to the secretion of a new septum. This suggestion was also adopted by Ward *et al.* (1981) who documented chamber formation in living *Nautilus* by X-ray radiography.

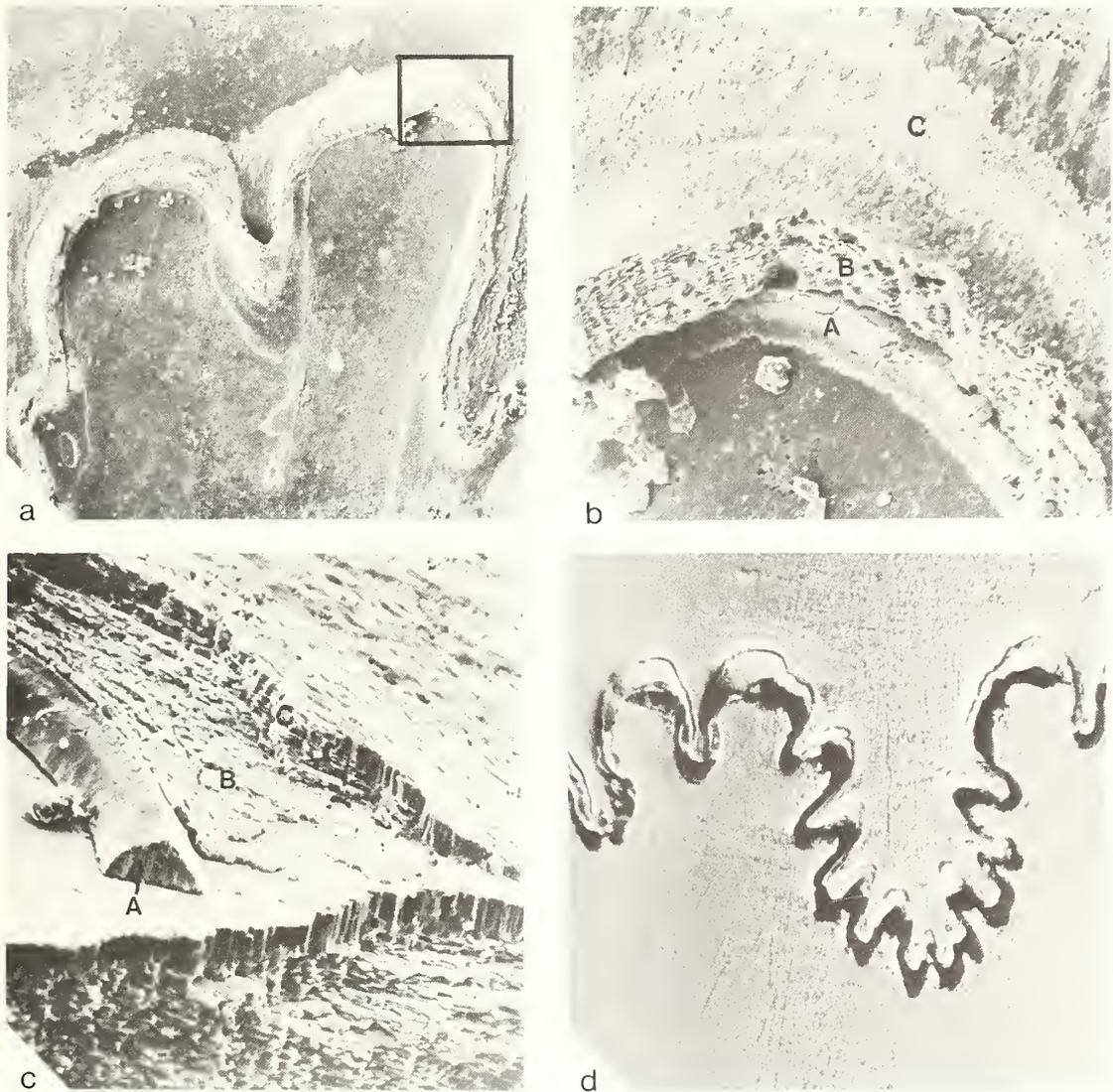
Contrary to these views, however, the preseptal prismatic zone and the mural ridge of *Nautilus* are quite separate, unrelated structures (Pl. 49, figs. 2, 3). The preseptal prismatic zone is here considered to represent an immediate precursor to secretion of the septum proper. It is thought that when the animal had moved forward to the position of a new septum, the band of myoadhesive epithelium at the posterior margin of its body established adhesion by secreting the preseptal prismatic zone. With the body thus stabilized in position, a new septum was secreted beginning at the periphery as reported by Willey (1902, p. 749).

The preseptal prismatic zone of *Sciponoceras* is thought to have served a similar role. A portion of the myoadhesive epithelium at the perimeter of the posterior, septa-forming part of the mantle adhered to the shell wall and secreted prismatic shell. The nacreous layer of the septum proper was then rapidly added, followed by a second zone of prismatic shell, the preseptal zone, which marked the stable location of muscle insertion until such time as a new septum needed to be formed.

Shell wall markings interpreted as muscle scars

If the septal periphery is to be regarded as the principal site of muscle attachment, consideration must be given to various markings on internal moulds of ammonite body chambers that have been interpreted as muscle scar impressions by a number of workers (see Kennedy and Cobban 1976, p. 10).

The best-known structures consist of two narrow gutters enclosing a pair of matched shapes on the mould, symmetrically disposed on its dorsal surface. In planispiral ammonites each gutter encloses a semi-elliptical area abutting the last septum whereas in the heteromorphs each gutter typically forms a ring, completely enclosing an oval or bean-shaped area which lies some distance in front of the last septum (Pl. 49, fig. 7). The areas so defined have generally been interpreted as the sites of retractor muscle insertion, comparable to those of *Nautilus* (Kennedy and Cobban 1976). In *Nautilus* the retractor scars are bounded adaperturally by an annular ridge of shell to which subepithelial muscles



TEXT-FIG. 9. *a-c*, microstructure at the septal periphery of juvenile *Sciponoceras glaessneri* Wright. *a*, plan view of septal junction with outer shell adjacent to a saddle of the suture; $\times 30$. *b*, detail of (*a*) as indicated showing the preseptal prismatic zone (A), the nacreous septal periphery (B) and the post-septal prismatic zone (C); $\times 180$. *c*, broken shell surface in the saddle of a suture showing the shell wall (thin inner prismatic layer and thick nacreous layer), the preseptal prismatic layer (A), the nacreous septal periphery (B) and the postseptal prismatic zone (C); note the superpositional relationships of the preseptal zone, septum proper and postseptal zone; $\times 225$. *d*, dorsal lobe of *Baculites ovatus* Say on an internal mould showing a well-developed gutter immediately adapertural of the suture proper, interpreted as a mould of the postseptal prismatic zone.

were attached (Mutvei 1957). The gutter on ammonite body chamber moulds, or rather the ridge of shell it replicated, is not homologous with the annular ridge of *Nautilus*. As clearly shown by the heteromorphs, in which it forms a complete ring, it cannot represent the site of subepithelial muscle insertion. The retractor scars in *Nautilus* carry a layer of prismatic myostracum and are clearly marked by growth lines, neither of which have been identified on their supposed counterparts in ammonites. Perhaps the markings represent the imprint of internal organs which pressed against the mantle and had their outlines recorded on the shell.

A variety of other structures have been described from internal moulds as representing zones of muscle attachment on the outer shell, most recently by Jordan (1968). They include lobate markings lying immediately adapertural to the ventral saddle of the last suture (sometimes showing as a continuous track along the siphuncular line), large tongue-shaped markings on the flanks of body chambers, and annular markings encircling the posterior of the body chamber. They are much less common than the paired dorsal structures and are commonly defined by staining or by slight differences in texture of mould surfaces. Their interpretation is considered here to be conjectural. Some of the ventral structures may record growth of the siphuncle according to the proposals outlined below.

It should be noted that acceptance of such structures as muscle scars does not wholly invalidate the model of septal muscle attachment argued here. They could be viewed as additional sites of muscle attachment, separate from those of the subepithelial sheath.

Growth model for siphuncle

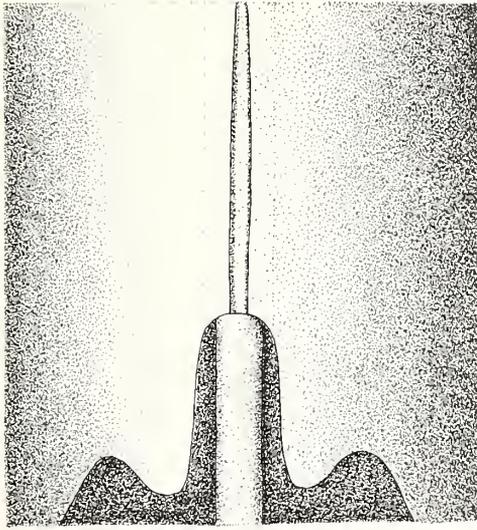
The model of septal muscle insertion, in which the animal episodically detached its muscles and moved rapidly forward in its shell to a new site of septal fabrication and muscle insertion, has implications for the siphuncle. New siphuncle could not have grown at such a rapid rate and a length of siphuncle, sufficient for the increment of forward movement, would need to have been performed. This problem does not apply to *Nautilus* where forward movement of the body, although episodic, is thought to take several days (Ward *et al.* 1981).

Only the hard sheath of ammonite siphuncles is preserved, consisting of connecting rings (horny organic tissue perhaps mineralized in some taxa) and calcareous funnels at the ventral margins of septa formed by an extension of the septal nacre (septal necks) or by independent structural elements (false septal necks and auxiliary deposits). The disposition of these various elements shows considerable variety among different ammonite stocks (Birkelund 1981).

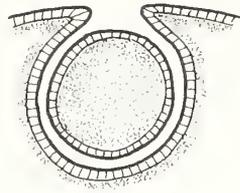
Any proposal for the growth of the siphuncle and fabrication of its protective coating must account for the following features shown by the sheath and the midventral line of the inner shell wall:

1. The range of geometries and relationships of its structural components.
2. Location of the connecting rings on the ventral midline in contact with the shell wall. In some taxa the septal necks are also in contact with the shell wall but in many others they lie free.
3. The prochoanitic projection of septal necks.
4. Projection of the connecting rings into the living chamber in some phylloceratid taxa as reported by Drushchits and Doguzhayeva (1974), Kuliki (1979), and Westermann (1982).

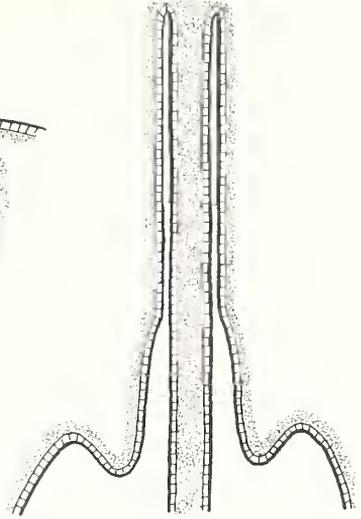
TEXT-FIG. 10. Morphology of the siphuncular sheath and tissue inferred to have been responsible for its formation. *a-c*, inferred disposition of tissue at the posteroventral margin of the ammonite animal. *a*, soft parts adjacent to the tip of the ventral saddle of the last septum showing the siphuncle and the parting in the mantle above the siphuncle. *b* and *c*, cross-section and longitudinal section of (*a*) showing invagination of the mantle to form a sleeve. *d, e*, diagrams showing components of the siphuncular sheath comprising septal necks (dashed) connecting rings (black) and false septal necks and auxiliary deposits (blank); adapted from Birkelund (1981) and orientated with the adapertural portions uppermost. *d*, *Saghalinites*. *e*, *Tetragonites*. *f*, *Phylloceras* (*Hypophylloceras*). *g, h*, decoupling of mantle sleeve and secretion of hard parts as the ammonite animal moves forward in its shell during growth, shown in longitudinal section. Mantle of the sleeve secretes the septal neck while mantle of the siphuncle itself secretes the connecting ring.



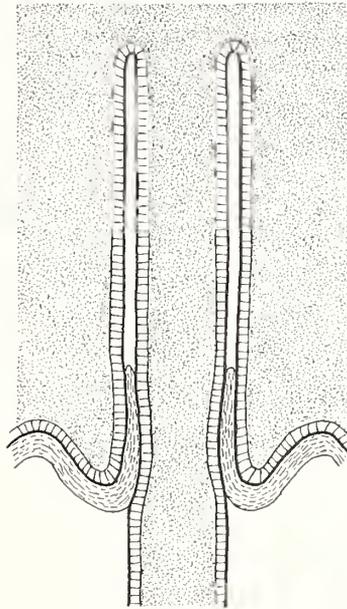
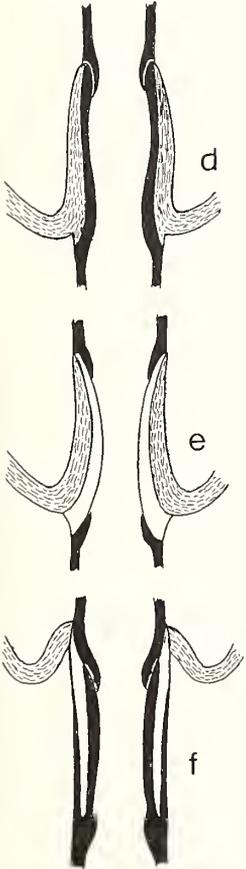
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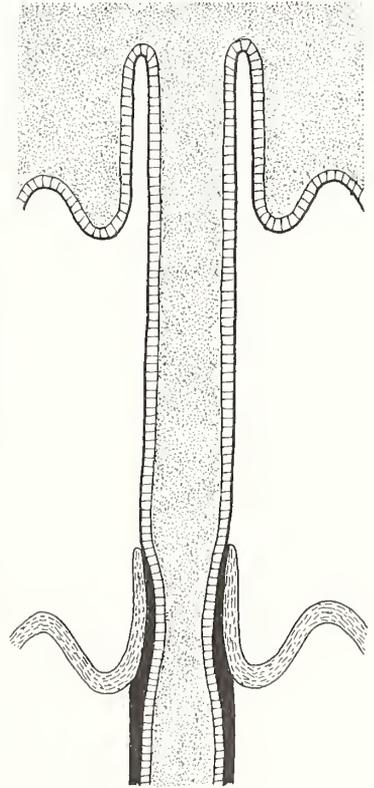
b



c



g



h

5. The existence of horny membranes which connect the siphuncular sheath to the shell wall and to the septa in a variety of taxa (Grandjean 1910; Westermann 1971; Erben and Reid 1971; Kuliki 1979).

6. The presence of fine longitudinal grooves and ridges which show on the inner shell surface along the midventral line on many phragmocones and is doubtless related to the formation of the siphuncle (Pl. 49, figs. 3–5, 7–9, text-fig. 7). On other phragmocones this zone of the inner shell is smooth.

Given such specifications, the mode of growth of the siphuncle is severely constrained. A siphuncular growth model involving the preformation necessary for rapid forward movement of the animal proposed here is consistent with the observed morphology of the sheath. It is thought that the siphuncular mantle extended along the ventral midline at the posterior of the body and invaginated itself to form an outer sleeve which opened along the midline as a slit (text-fig. 10). At its posterior margin, the sleeve was continuous with the septal-secreting part of the mantle. Growth of the siphuncle and its sleeve is envisaged to have been slow and constant with their zone of formation migrating forward with respect to the remainder of the body. Prior to forward advance of the body at the initiation of an episode of chamber formation, the new length of preformed siphuncle was detached from the outer sleeve via the slit and adpressed to the shell wall by contraction of the musculature of the body wall. In some taxa, horny membranes that accreted on the mantle of the sleeve braced the siphuncle to the shell wall and to adjacent parts of the septum (Kuliki 1979; Birkelund 1981). They have been most commonly described from close proximity to septa in those taxa where the septal neck is not in contact with the shell wall and a small part of the adjacent connecting ring is suspended within the chamber. A more general means of attachment of the siphuncle was provided when its mantle began secreting the connecting ring, thereby cementing it to the shell wall. The midventral markings on the inner shell wall represent shell secretion at the lip of the slit in the sleeve. A median ridge is its common expression (Pl. 49, figs. 4–6, 8–10; text-fig. 6*b, c*) and the adjacent set of fine markings may represent shell secretion by folds in the mantle which formed as tissue near the slit was compressed by enlargement of the siphuncle beneath. The faint lobate markings lying on the midventral line and some distance in front of a septum (Pl. 49, fig. 3) which shows on rare specimens may mark the zone where the siphuncular mantle invaginated to form the sleeve rather than a site of muscle insertion as some authors would have it.

Secretion of a new septum followed movement of the body, slipping past the newly emplaced segment of siphuncle (text-fig. 10*g, h*). The posterior part of the siphuncular sleeve secreted the septal neck which was structurally continuous with the septum. False septal necks and auxiliary deposits (text-fig. 10*e, f*) are considered to be mineralized parts of the connecting ring proximal to the new septum and to have been secreted by the mantle of the siphuncle rather than that of the sleeve. The connecting ring inclusive of its mineralized parts is invariably constricted in the septal neck (text-fig. 10*d–f*) indicating that the final part of each segment of connecting ring formed later than the septal neck to which it relates. The segmented nature of the connecting ring, with individual segments joined together within the septal neck or at its termination (text-fig. 10*d–f*), show that its secretion was episodic, with a hiatus following the completion of each new septum.

Mesozoic ammonites show marked changes in siphuncular organization during growth. Very early growth stages commonly display a morphology like that of *Nautilus*, with retrochoanitic septal necks and connecting rings suspended free within the chambers (Spath 1950; Kuliki 1979). The siphuncular organization of adults proposed here could easily have been developed from such a precursor by gradually moving the position of the siphuncle and by progressively developing an evagination of its mantle.

Shell shape and ornament

The type of growth experienced by the ectocochleate animal influences the gross nature of its shell. In nautiloids the body movement is gradual and the muscle insertions track across the inner shell wall. Here the body can expand its girth by gradual growth to fit a shell form in which there is a rapid increase in expansion rate. Ornate shells with corrugated inner shell surfaces are not conducive to the translocation of muscles by this mechanism.

The converse is held to be true for ammonites. Here the animal moves rapidly forward in the shell and is therefore required to expand its girth rapidly to fit the new whorl dimensions. It might be expected that ammonite shells should generally show more gradual whorl expansion rates than nautiloids. A comparison of shell shape in Mesozoic ammonites and nautiloids provided by Ward (1980) shows that this is indeed the case. Transposition of the ammonite body would have been unconstrained by irregularities in the shell wall because muscle tracking was not involved. The striking contrast between Mesozoic ammonites and nautiloids in the general development of ornament thereby finds a ready explanation.

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PRINCIPAL FLORAS OF PALAEOZOIC MARINE CALCAREOUS ALGAE

by BORIS CHUVASHOV and ROBERT RIDING

ABSTRACT. The stratigraphic distribution of eighteen groups of fossils commonly assigned to the calcareous algae reveals three major floras in shallow marine carbonate deposits of Palaeozoic age: (1) Cambrian flora, (2) Ordovician flora, (3) Carboniferous flora. The Cambrian flora appears abruptly near the Precambrian–Cambrian boundary and is dominated by cyanophytes. The Ordovician flora appears quickly during the lower and middle Ordovician and is dominated by chlorophytes, rhodophytes, and problematic groups. The Carboniferous flora appears gradually, mainly during the Carboniferous, and is dominated by rhodophytes, chlorophytes, and problematic groups. Important extinctions occurred near the ends of the Devonian, Carboniferous, and Permian.

The succession of floras is reflected in the changing sedimentological roles of Palaeozoic calcareous algae. Cambrian reefs are dominated by *Epiphyton–Renalcis* assemblages which reappear briefly in the Devonian. During most of the middle Palaeozoic algae are subordinate to metazoan reef-builders, but Solenoporaceae, *Rothpletzella*, and *Wetheredella* are nevertheless important locally. Following a hiatus during the lower Carboniferous, *Donezella*, *Ungdarella*, phylloid algae, and *Tubiphytes* were important reef-builders. Skeletal oncoids built by *Girvanella*, *Hedstroemia*, *Ortonella*, and *Rothpletzella*, together with *Solenopora* rhodoliths, are common at many levels in the Palaeozoic, but skeletal stromatolites are generally rare. Nodules formed by *Archaeolithophyllum* and *Cuneiphyucus* occur in the upper Palaeozoic. Sand- and gravel-size fragments, mainly of chlorophytes and rhodophytes, increase in abundance from the Ordovician onwards.

По особенностям стратиграфического распространения восемнадцати групп окаменелостей, обычно относимых к известковым водорослям, различаются три основных комплекса в мелководных морских карбонатных отложениях палеозоя: (1) кембрийский комплекс; (2) ордовикский комплекс; (3) каменноугольный комплекс.

Кембрийский комплекс водорослей появляется видимо вблизи нижней границы кембрия; в его составе доминируют цианобактерии. Ордовикский комплекс появился быстро в среднем ордовике и представлен преимущественно хлорофитами, родофитами (?) и проблематичными группами. Каменноугольная флора формируется постепенно, главным образом, в течении карбона. В ее составе доминировали родофиты, хлорофиты и проблематичные группы. Важные изменения происходили в конце девона, карбона и перми.

Установленная последовательность в развитии водорослей отражается в изменении седиментологического значения палеозойских известковых водорослей.

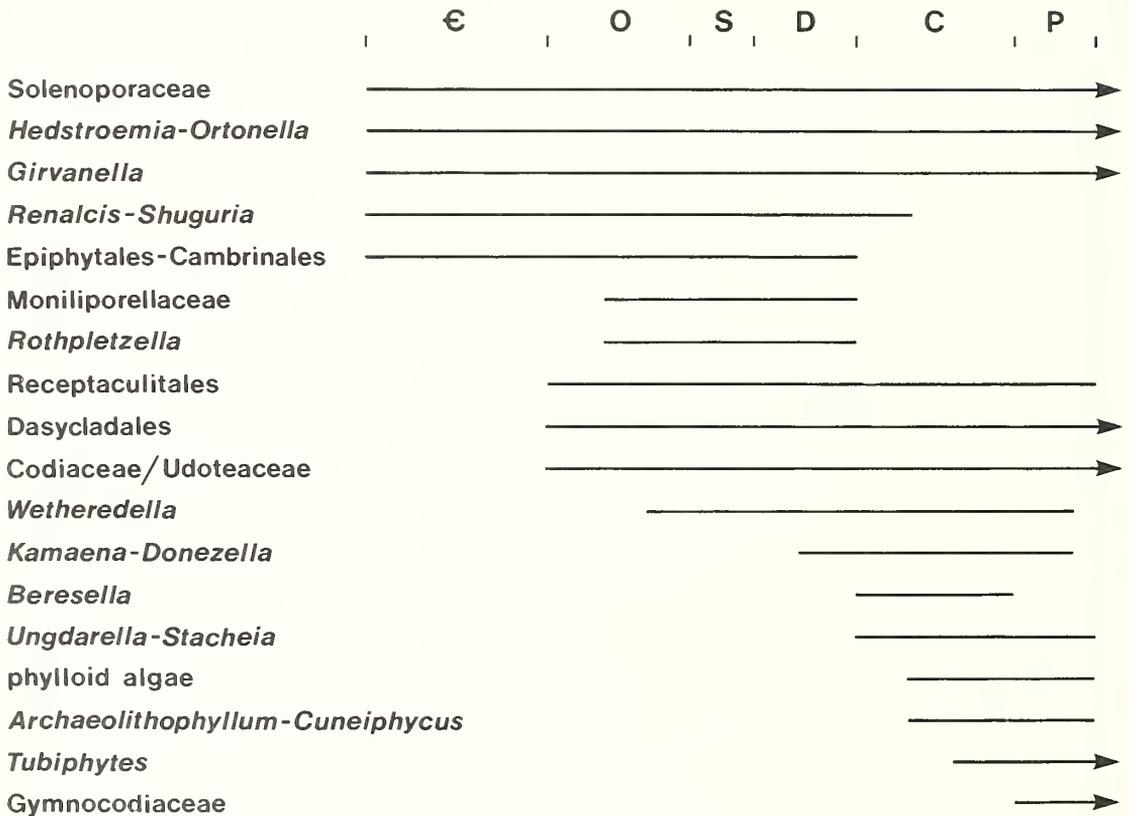
Среди кембрийских рифов доминировало сообщество родов *Epiphyton–Renalcis*, которое затем на короткое время появляется вновь в девоне. В течение среднего палеозоя водоросли, как рифообразователи, были подчинены метазою, но Solenoporaceae, *Rothpletzella* и *Wetheredella* играли местами важную роль в создании осадков.

После нижнего карбона, в течение которого пороодообразующее значение известковых водорослей заметно падает, *Donezella*, *Ungdarella*, филлоидные водоросли, а также *Tubiphytes* были важными рифообразователями.

Скелетные онкоиды, построенные *Girvanella*, *Hedstroemia*, *Ortonella* и *Rothpletzella* совместно с *Solenopora*-родолитами являются обычными на многих уровнях палеозоя, но скелетные строматолиты обычно редки. Желваки, образованные с участием *Archaeolithophyllum* и *Cuneiphyucus* встречаются в верхнем палеозое. Зерна песчаной и гравийной размерности образованы, главным образом, за счет зеленых и красных водорослей, увеличиваются количественно в осадках с позднего ордовика.

WE present a general overview of the stratigraphic distribution of calcareous algae during the Palaeozoic. Our aims are to discern broad patterns of calcareous algal evolution and to evaluate briefly how these are reflected in the sedimentological importance of these fossils. We have

incorporated available data from North America and one or two other areas, but most of our information is derived from work in Europe and the USSR. In order to present this we have divided the many genera involved into a number of groups which have a broad base within current systematic schemes. The problems of affinity in Palaeozoic calcareous algae are well known (Riding 1977a), but remain largely unresolved. They are mainly responsible for uncertainty concerning the systematics of these fossils. We have selected groups which have some degree of morphological similarity. In some cases their affinities are clear, in others doubtful. Some groups include members which are possibly not algae. In this paper we attempt to encompass all groups which are commonly regarded as algae, even if we personally have doubts concerning such an attribution. However, we have neglected some small groups represented by only a few genera. It would be a major undertaking to plot accurately and comprehensively the distribution of the large number of genera involved, and such a compilation would necessitate substantial taxonomic revision. Our aim here is to review the changing composition of these floras during the Palaeozoic in a very broad way in order to assess general patterns. Thus, these results are preliminary and doubtless imperfect with respect both to the groups selected and their ranges. In particular we have recognized the fewest possible number of major groups, and this has involved a degree of 'lumping' which will be open to criticism. Nevertheless, we believe that this procedure enhances, rather than detracts from, the validity of the patterns elucidated here.



TEXT-FIG. 1. Stratigraphic ranges of eighteen major calcareous algal groups during the Palaeozoic. Generic names indicate groups, not individual genera (see Table 1), except in the case of *Tubiphytes*. Ranges are drawn from the base of the sub-period (early, middle, late) in which the first member of a group appears, to the top of the sub-period in which the last member occurs. Arrow indicates that group continues into the Mesozoic. Length of periods is based upon Harland *et al.* (1982).

TABLE 1. Eighteen major groups of Palaeozoic calcareous algae and possible calcareous algae, showing their main characters and the affinities confidently or currently attributed to them. The references give sources of further information but in many cases do not cite the authors of the groups or of the named genera themselves.

Group	Contents	Characters	Affinities	References
1. Solenoporaceae	<i>Solenopora</i> Dybowski, <i>Parachaetetes</i> Deninger, etc.	Massive, tabular, hemispherical or nodular skeleton composed of closely packed cellular filaments, sometimes possibly containing sporangia	Probable rhodophytes; possibly related to the Corallinaceae	Johnson (1960); Maslov (1962)
2. <i>Hedstroemia</i> - <i>Ortonella</i> group	<i>Botomaella</i> Korde, <i>Bevocastria</i> , Garwood, <i>Garwoodia</i> Wood, <i>Hestroemia</i> Rothpletz, <i>Ortonella</i> Garwood, etc.	Fan-like bundles of branched tubes of varying cross-sectional shape. In some genera the tubes are closely packed and share walls, in others the tubes are separate. Branching ranges from dichotomous, to irregular and multiple	Several of the genera resemble extant calcareous cyanophytes	Wray (1977, pp. 38-39)
3. <i>Girvanella</i> group	<i>Batenevia</i> Korde, <i>Botominella</i> Reitlinger, <i>Cladogirvanella</i> Ott, <i>Girvanella</i> Nicholson and Etheridge, <i>Obruchevella</i> Reitlinger, etc.	Narrow simple tubes of constant diameter and without cross-partitions. Tubes may be straight, sinuous, irregularly tangled, or spiral, and may be arranged in tightly woven, cable-like bundles or loose masses	Probably filamentous cyanophytes	Wray (1977, pp. 36-37)
4. <i>Renalcis</i> - <i>Shugaria</i> group	<i>Gemma</i> Luchina, <i>Izhella</i> Antropov, <i>Renalcis</i> Vologdin, <i>Shuguria</i> Antropov, <i>Tarthinia</i> Drosdova, etc.	Cloud-like forms consisting of clusters of a few or many hollow, bubble-like compartments, sometimes arranged in short branched series	Possibly cyanophytes	Drosdova (1980, pp. 14-19); Wray (1977, p. 40)
5. Epiphytales- Cambrinales	<i>Cambrina</i> Korde, <i>Epiphyton</i> Bornemann, <i>Gordonophyton</i> Korde, <i>Potentillina</i> Korde, <i>Tubomorphophyton</i> Korde, etc.	Dendritic solid micritic, tubiform or chambered thalli. Branches narrow; branching dichotomous or irregular	Possibly cyanophytes or rhodophytes	Korde (1973, pp. 125-212); Luchinina (1975)
6. Codiaceae/ Udoteaceae	<i>Dimorphosiphon</i> Hoeg <i>Lancicula</i> Maslov, <i>Litanaia</i> Maslov, <i>Palacoporella</i> Stolley, etc.	Entire or segmented thallus, may be branched, internally divided into cortex and medulla consisting of numerous branched tubes	Chlorophytes	Gnilovskaya (1972, pp. 79-100); Shuysky (1973, pp. 61-80)
7. <i>Rothpletzella</i> group	<i>Flabellia</i> Shuysky, <i>Halysis</i> Hoeg, <i>Rothpletzella</i> Wood	Flat, curved, or encrusting sheets of juxtaposed tubes which branch dichotomously in one plane	Microproblematica, often regarded as cyanophytes or chlorophytes	Flügel and Wolf (1969)

Group	Contents	Characters	Affinities	References
8. <i>Wetheredella</i> group	<i>Aphralysia</i> Garwood, <i>Asphaltina</i> Mamet, <i>Sphaeroporella</i> Antropov, <i>Wetheredella</i> Wood, etc.	Short tubes, possibly branched, with blister-like or rounded cross-sections; fibrous wall structure sometimes with additional micritic layer	Microproblematica sometimes regarded as chlorophytes, foraminifers, or worms	Ischenko and Radionova (1981); Mamet and Roux (1975, pp. 156-166)
9. Receptaculitales	<i>Calathium</i> Billings, <i>Ischadites</i> Murchison, <i>Receptaculites</i> Deshayes, etc.	Large, hollow, pear- or sack-like bodies, usually open at one end, with double-walls and faceted outer surfaces	Problematica, often referred to the Chlorophyta	Nitecki (1972); Rietschel (1969); Zhuravleva and Myagkova (1981)
10. Dasycladales	I. <i>Dasyoporella</i> Stolley, <i>Rhabdoporella</i> Stolley, <i>Vermiporella</i> Stolley, etc. in middle Palaeozoic; II. <i>Diplopora</i> Schafhäütl, <i>Epimastopora</i> Pia, <i>Globiferoporella</i> Tchuvashev, <i>Macroporella</i> Pia, <i>Mizzia</i> Schubert, etc. in upper Palaeozoic	Hollow sack- or stick-like algae, usually large and erect, sometimes segmented; relatively thick walls pierced by simple or branched pores Palaeozoic forms show clear separation into middle Palaeozoic and upper Palaeozoic assemblages (I and II)	Chlorophyta	Pia (1920); Elliott (1972); Shuysky (1973, pp. 80-87), Chuvashov (1974)
11. <i>Kamaena</i> - <i>Donezella</i> group	<i>Donezella</i> Maslov, <i>Jansaella</i> Mamet and Roux, <i>Kamaena</i> Antropov, <i>Palaeoberesella</i> Mamet and Roux, etc.	Branched, mainly dichotomously, septate tubes with finely porous or fibrous wall-structure. Septa may be entire or incomplete	Microproblematica, often regarded as chlorophytes or rhodophytes, sometimes as foraminifers	Maslov (1956); Antropov (1967); Mamet and Roux (1974)
12. <i>Beresella</i> group	<i>Beresella</i> Machaev, <i>Dvinella</i> Khvorova, <i>Uraloporella</i> Korde, etc.	Moderately large, straight to sinuous, branched tubes; sometimes septate; wall relatively thick with pores which may be simple or branched	Microproblematica, but commonly regarded as dasycladaleans	Korde <i>et al.</i> (1963, p. 211, p. 217)
13. Phylloid algae	<i>Anchicodium</i> Johnson, <i>Eugonophyllum</i> Konishi and Wray, <i>Ivanovia</i> Khvorova, <i>Neoanchicodium</i> Endo, etc.	Large, thin, wavy, leaf-like thallus; cortex thick, usually porous, sometimes containing 'sporangia'; medulla filamentous, usually poorly preserved	Commonly regarded as codiaceans/udoteaceans; some genera are comparable with Squamariaceae (Peyssoneliaceae, Rhodophyta)	Wray (1968; 1977, pp. 52-54)
14. <i>Archaeolithophyllum</i> - <i>Cuneiphyucus</i> group	<i>Archaeolithophyllum</i> Johnson, <i>Cuneiphyucus</i> Johnson, <i>Eftugelia</i> .	Encrusting or hemispherical masses; coarse cellular construction, occasionally bearing conceptacles	Rhodophyta (<i>Archaeolithophyllum</i>) and Microproblematica	Wray (1977, pp. 71-72)

Group	Contents	Characters	Affinities	References
15. <i>Ungdarella</i> – <i>Stacheia</i> group	<i>Aoujgalia</i> Termier and Termier, <i>Epistacheoides</i> Petryk and Mamet, <i>Fourstonella</i> Cummings, <i>Komia</i> Korde, <i>Stacheia</i> Brady, <i>Stacheoides</i> Cummings, <i>Ungdarella</i> Maslov, etc.	Encrusting or erect, rod-like, branched fossils with cellular construction; cells sometimes aligned in coarse rope-like strands	Microproblematica, often regarded as rhodophytes	Maslov (1962); Petryk and Mamet (1972); Massa and Vachard (1979)
16. Gymnodiaceae	<i>Gymnodiaceum</i> Pia, <i>Permocalculus</i> Elliott, etc.	Cylindrical or sack-like fossils, sometimes segmented; cortex thin, with external pores; medulla filamentous. Sporangia may be present	Chlorophytes or rhodophytes	Elliott (1955); Korde (1965)
17. <i>Tubiphytes</i> group	<i>Tubiphytes</i> Maslov	Large erect, irregular, or encrusting skeletons with a dense, dark, pseudo-cellular construction showing concentric bands; irregular internal tubes often present	Microproblematicum, sometimes regarded as a cyanophyte; possibly a sponge (E. Ott, pers. comm. 1982)	Maslov (1956); Flügel (1977, pp. 324–325, p. 339)
18. Moniliporellaceae	<i>Ansoporella</i> Gnilovskaya, <i>Contexta</i> Gnilovskaya, <i>Moniliporella</i> Gnilovskaya, etc.	Cylindrical, nodular, or irregular fossils with hollow interior; sometimes segmented; thick wall consisting of cellular filaments	Rhodophytes or chlorophytes	Gnilovskaya (1972, pp. 100–126)

GROUPS OF CALCAREOUS ALGAE

In Table 1 we list the certain and the equivocal algal groups whose stratigraphic distribution we have plotted in text-fig. 1. Each group is distinguished by either a supra-generic name or by one or two genera representing typical or well-known elements of the group. We list a few additional generic examples which normally represent only a small fraction of the total for each group. In addition we indicate the likely affinities (or doubts concerning affinities) for each group. Pertinent references are also given.

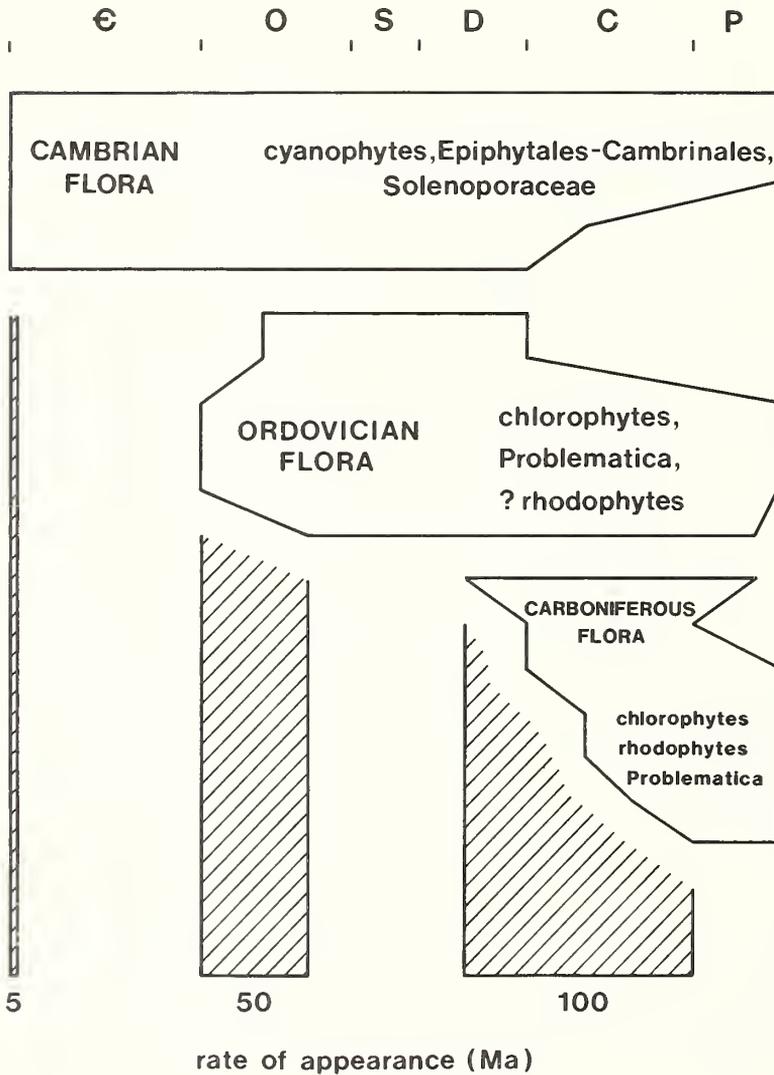
STRATIGRAPHIC DISTRIBUTION

The distribution chart of major calcareous algal groups (text-fig. 1) has been compiled from the literature cited in the table and from our personal experience of working with these fossils. It shows the first and last occurrences of each group as a whole, and not of the named genera alone. For example, *Hedstroemia* and *Ortonella* are principally Silurian and Carboniferous fossils respectively, but other members of the *Hedstroemia*–*Ortonella* group, as it is defined here, such as *Botomaella*, occur in the Cambrian and related types like *Cayeuxia* Frollo occur in the Mesozoic.

The pattern of stratigraphic distribution of the major groups (text-fig. 1) allows three distinct floras to be recognized (table 1; text-fig. 2): (1) Cambrian flora, (2) Ordovician flora, (3) Carboniferous flora.

The Cambrian flora is dominated by cyanophytes (*Hedstroemia-Ortonella* group, *Girvanella* group) and possible cyanophytes (Epiphytales-Cambrinales, *Renalcis-Shuguria* group); the possible rhodophyte group, Solenoporaceae, is present but rare. This flora ranges intact into the upper Devonian but then loses the Epiphytales-Cambrinales and *Renalcis-Shuguria* groups. The remaining elements continue beyond the Permian-Triassic boundary.

The Ordovician flora is dominated by Codiaceae/Udoteaceae, Dasycladales, the possible rhodophyte Monilioporellaceae, the possible chlorophyte Receptaculitales, the problematic *Rothpletzella* and



TEXT-FIG. 2. Three principal floras of Palaeozoic marine calcareous algae (from text-fig. 1) showing ranges, general composition, and rates of appearance. The Cambrian, Ordovician, and Carboniferous floras appeared over periods of 5, 50, and 100 Ma respectively. Length of periods is based upon Harland *et al.* (1982).

Wetheredella groups, together with the major elements of the Cambrian flora. Its new, characteristic, elements originated mainly in the lower and middle Ordovician and persist to the upper Devonian or beyond.

The Carboniferous flora is dominated by the problematic *Kamaena-Donzella* group, the possible chlorophyte *Beresella* group, a new assemblage of dasycladaleans, the possible rhodophyte *Ungdarella-Stacheia* group, the chlorophyte or rhodophyte phylloid algae and Gymnocodiaceae, the partly rhodophyte *Archaeolithophyllum-Cuneiphycens* group, and the doubtfully algal *Tubiphytes* group, together with elements of the Cambrian and Ordovician-Devonian floras which survived an important phase of extinction near the Devonian-Carboniferous boundary. The Carboniferous flora was introduced episodically, mainly during the lower and middle Carboniferous, with the *Kamaena-Donzella* group appearing earlier (in the middle Devonian) and the *Tubiphytes* group and Gymnocodiaceae later (in the upper Carboniferous and early Permian respectively). Most of these new upper Palaeozoic groups did not survive into the Mesozoic.

SEDIMENTOLOGICAL ROLES

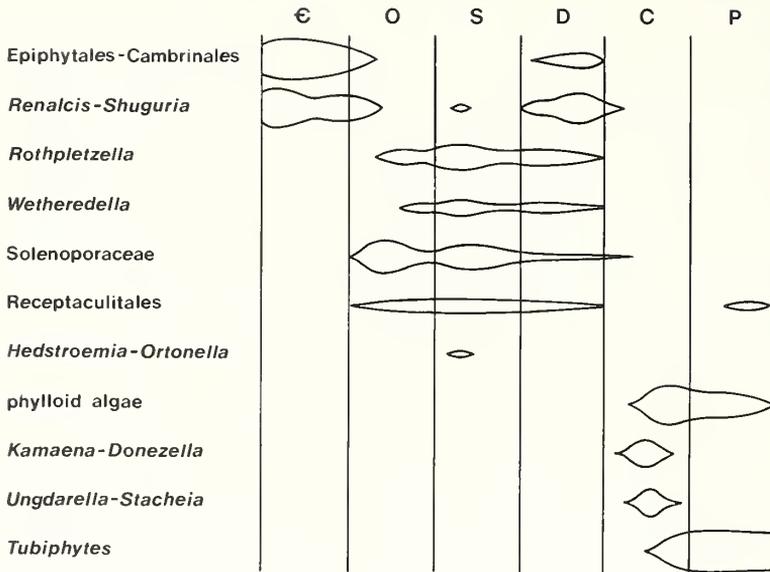
The importance of calcareous algae as producers of loose and *in situ* sediment is clear in Recent carbonate environments. It is equally recognizable in its effects upon limestone deposition from the first appearance of calcareous algae near the base of the Cambrian. The sedimentological roles of particular algal groups depend essentially upon the morphology and mode of growth of the algae, and the succession of algal floras has in turn imprinted a stratigraphic pattern upon their sedimentary products. The reef-building algae of the Cambrian differ in size, shape, and effects from those of the Carboniferous, the abundance of algal skeletal fragments changes through time, and the types of nodule-forming algae also change. The broad patterns of these variations are controlled by evolution and extinctions more than by sedimentary processes and palaeogeography.

In order to show these changes we have plotted qualitative assessments of the relative importance of Palaeozoic algal groups in the following roles: reef-building; stromatolite, oncoid, and rhodolith formation; and the production of recognizable, usually sand- to gravel-size, fragmentary (broken or disaggregated) material (text-figs. 3-7).

Reef-building

The three floras recognized here are clearly reflected in Palaeozoic reef-building (text-fig. 3). The Cambrian algal reef-builders belong mainly to two groups: the Epiphytales-Cambrinales and *Renalcis-Shuguria*. *Angulocellularia* Vologdin, omitted from these distribution charts because it constitutes a taxonomically small group, is also locally an important reef-builder (see Riding and Voronova 1982). These are all small but abundant fossils and commonly exceed archaeocyathans in volumetric importance in the early lower Cambrian (James and Debrenne 1980).

Ordovician-Devonian algal reef-builders are more diverse and, in general, none has the individual importance of those in the Cambrian. Receptaculitaleans are rather rare fossils, and *Hedstroemia* is at present only known to be important in reefs in the Silurian (Riding and Watts 1981). *Rothpletzella* and *Wetheredella* form thick crusts (Copper 1976), but usually on large metazoan reef builders such as stromatoporoids, corals, and bryozoans. Solenoporaceans form the largest individual skeletons but are, nevertheless, usually subordinate to metazoans (Harland 1981). On the whole, a variety of algal groups is locally conspicuous in middle Palaeozoic reefs, but they are usually only accessory to larger and more abundant metazoans. A curious feature of middle Palaeozoic algal history is the reappearance of 'Cambrian' reef-building genera in the Devonian, especially the upper Devonian. These are members of the Epiphytales and *Renalcis-Shuguria* groups and their return to prominence at this level, after insignificance from the middle Ordovician to early Devonian, has so far defied satisfactory explanation.

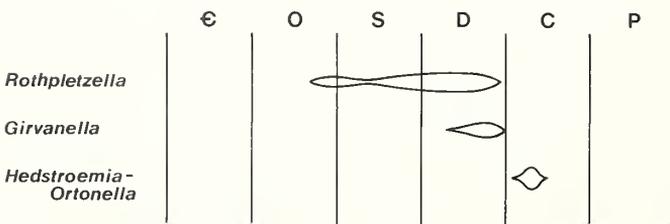


TEXT-FIG. 3. Reef-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

There is a hiatus in the early Carboniferous with few algal reef-builders following the demise of some of the Cambrian-Devonian groups. Only members of the *Renalcis-Shuguria* group have been reported as common reef constituents at this level. However, the phase of algal evolution which took place in the lower to middle Carboniferous yielded several important groups which filled this gap. In particular *Donzella* (Rich 1967, Riding 1979) and *Ungdarella-Komia* (Freeman 1964) are important mound-builders or, at least, mound-associates in the middle Carboniferous and Pennsylvanian. Phylloid algae also created bioherms from the middle Carboniferous to early Permian (Wilson 1975) and *Tubiphytes* is important from the upper Carboniferous until the Triassic (Flügel 1977).

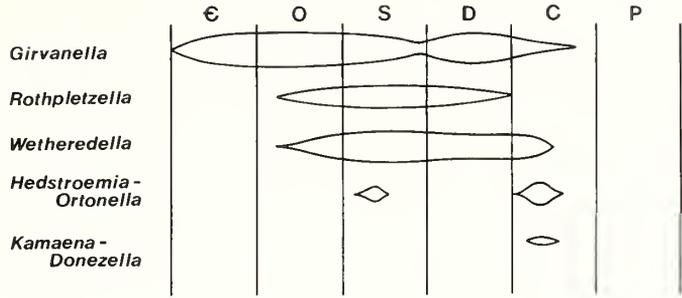
Stromatolites

Skeletal stromatolites, i.e. stromatolites formed by calcareous algae rather than by algae which merely trap and bind sediment (Riding 1977b) are, so far, only known to be common in parts of the Ordovician, Devonian, and Carboniferous (text-fig. 4). *Rothpletzella* and *Wetheredella* form stromatolitic crusts on metazoan skeletons in upper Ordovician reefs (Copper 1976). *Rothpletzella* forms stromatolitic caps on stabilized oncoids on the fore-reef slope of the upper Devonian Canning Basin reefs in Western Australia (Playford, Cockburn, Druce and Wray 1976). *Girvanella* builds stromatolites in the Devonian of the Ural Mountains, USSR, and *Ortonella* and *Bevocastria* build stromatolites in the lower Carboniferous of the Scottish border country, Great Britain (Garwood 1931).



TEXT-FIG. 4. Stromatolite-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

TEXT-FIG. 5. Oncoid-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.



Oncoids

Skeletal oncooids are much more widespread than skeletal stromatolites in the Palaeozoic (text-fig. 5). *Girvanella* forms oncooids from the Cambrian to Carboniferous, and in association with *Nubecularia* it was responsible for *Osagia* nodules in the Pennsylvanian (Johnson 1946). *Rothpletzella* and *Wetheredella* are often mutually associated in oncooids from the Ordovician to Devonian. *Hedstroemia* forms oncooids in the Silurian of Gotland and *Bevocastria*, *Ortonella* and *Garwoodia* are involved in oncooid formation, as well as stromatolite formation in the Lower Carboniferous of Britain. In addition, *Donzella* forms encrusted nodules in the middle Carboniferous.

Rhodoliths

Solenoporacean nodules are common during the Ordovician and Silurian (Johnson 1960) and are also locally abundant in the Upper Palaeozoic (Belka 1979). *Archaeolithophyllum* and *Cuneiphyucus* form nodules in the upper Carboniferous (text-fig. 6).

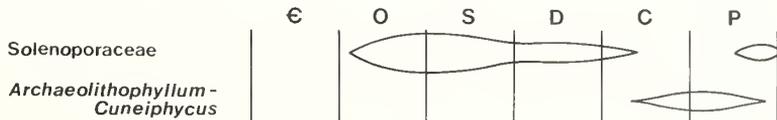
Fragments

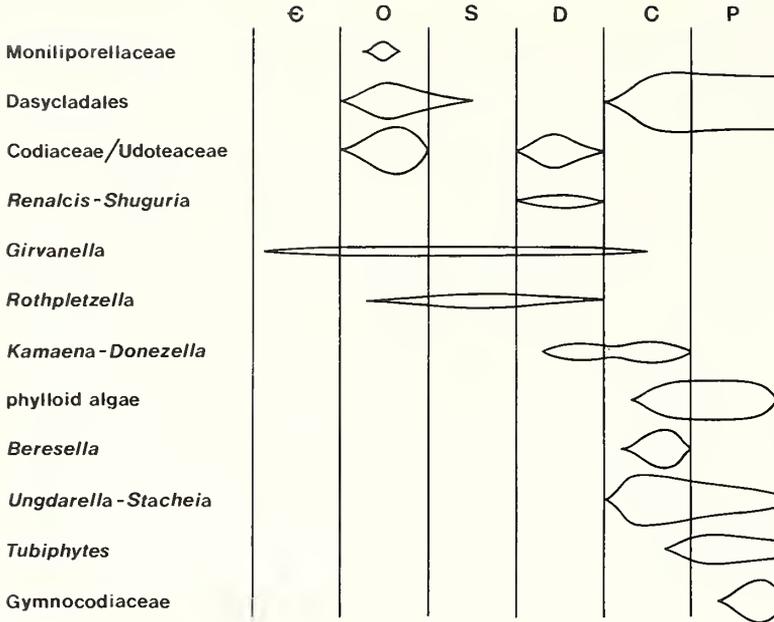
The presence of algal skeletal debris in shallow marine Palaeozoic limestones reflects the history of fragile or jointed specimens which were readily broken or disaggregated into sand- or gravel-size pieces (text-fig. 7). Algae, like the modern codiacean/udoteacean *Penicillus*, which may have disaggregated after death into mud- and silt-size particles leave no readily recognizable trace because the resulting particles are too small for their origin to be recognized.

At times during the Palaeozoic, as in subsequent geological eras, chlorophytes produced large quantities of calcareous debris. This sedimentological role commenced in the Ordovician when codiaceans/udoteaceans and dasycladalean fragments are also associated with those of moniliporellaceans. Codiacean/udoteacean debris is also locally common in the Devonian, but is more rare in the Carboniferous when this role was mainly occupied by dasycladaleans.

In the Cambrian, algal fragments are rare. This is a result both of the absence of calcareous chlorophytes and the fact that the common cyanophytes were generally firmly attached reef-builders. If the latter were broken from their substrates they produced small, micritic fragments difficult to distinguish from peloids. Nevertheless, in the Devonian, members of the *Renalcis-Shugaria* group are locally common as transported grains, as are *Girvanella* and *Rothpletzella*. The latter are also minor components of near-reef sediments in the Ordovician and Silurian. *Kamaena-Donzella* group fragments are common at various levels from middle Devonian to upper Carboniferous, but the

TEXT-FIG. 6. Rhodolith-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.





TEXT-FIG. 7. Debris-producing calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

principal increase in algal debris in the upper Palaeozoic took place in the middle Carboniferous when fragments of phylloid algae, plus the *Beresella*, *Ungdarella-Stacheia*, and *Tubiphytes* groups, combined with those of the new assemblage of dasycladaleans to produce loose material which often dominated shallow marine carbonate microfacies. The Gymnocodiaceae added to this, especially in the upper Permian.

DISCUSSION

Floras

The Cambrian calcareous algal flora was dominated by cyanophytes and possible cyanophytes: Solenoporaceae were relatively rare. The Ordovician and Carboniferous floras are both more mixed. If groups whose affinities are unclear are not considered, then the resulting picture of algal evolution is that calcareous cyanophytes appeared in the Cambrian, chlorophytes (codiaceans/udoteaceans and dasycladaleans) in the Ordovician, and rhodophytes (*Archaeolithophyllum*) in the Carboniferous. If we take *possible* affinity into consideration, this time-distribution does not change for cyanophytes and chlorophytes but calcareous rhodophytes may be present from the early Cambrian (Solenoporaceae, Epiphytales). It is clearly a matter of current importance for research to attempt to clarify the affinities of these and other possible algal groups in the Palaeozoic.

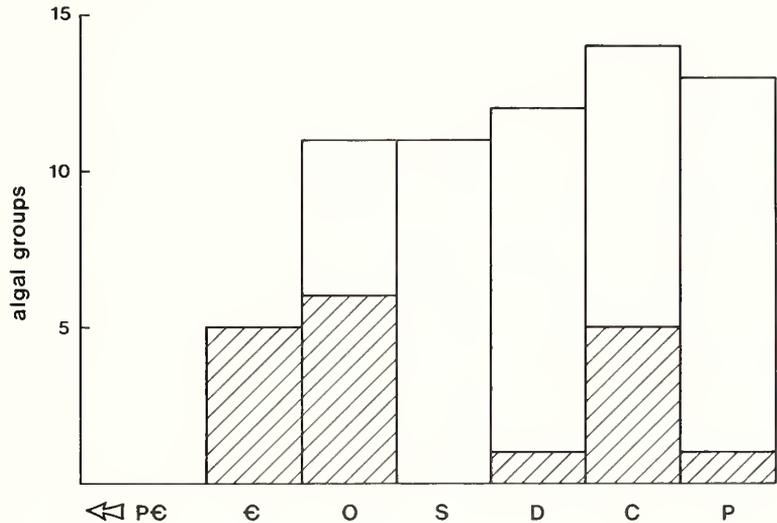
Diversity of major algal groups increases from the Cambrian (five groups) to the Ordovician (eleven groups). Subsequent increase is slight, rising to twelve groups in the Devonian, fourteen in the Carboniferous, and falling slightly to thirteen in the Permian (text-fig. 8). The resulting sigmoidal curve resembles the pattern of exponential diversification followed by equilibrium derived for marine metazoan orders during the Phanerozoic (Sepkoski 1978, fig. 9).

Evolutionary events, extinctions, ranges

The three principal algal floras recognized here were introduced in the earliest Cambrian, Ordovician, and Devonian-Carboniferous respectively. Of these, the first event near the Precambrian-Cambrian

boundary was abrupt, the Ordovician event more gradual, and that in the Devonian–Carboniferous slow (text-fig. 2). In the Nemakit Daldyn Formation of late Precambrian or early Cambrian age in northern Siberia members of the *Hedstroemia–Ortonella*, *Girvanella*, Epiphytales–Cambrinales, and *Renalcis–Sluguria* groups appear together virtually synchronously (Riding and Voronova, in prep.) and are joined, probably within 5 Ma, by solenoporaceans. The Ordovician event spanned approximately 50 Ma from early to late Ordovician, and the third phase of evolution was a slow episodic appearance of groups over a period approaching 100 Ma between the middle Devonian and early Permian (text-fig. 2). Nevertheless, both the last two events show some concentration, first in the lower–middle Ordovician and secondly in the lower–middle Carboniferous.

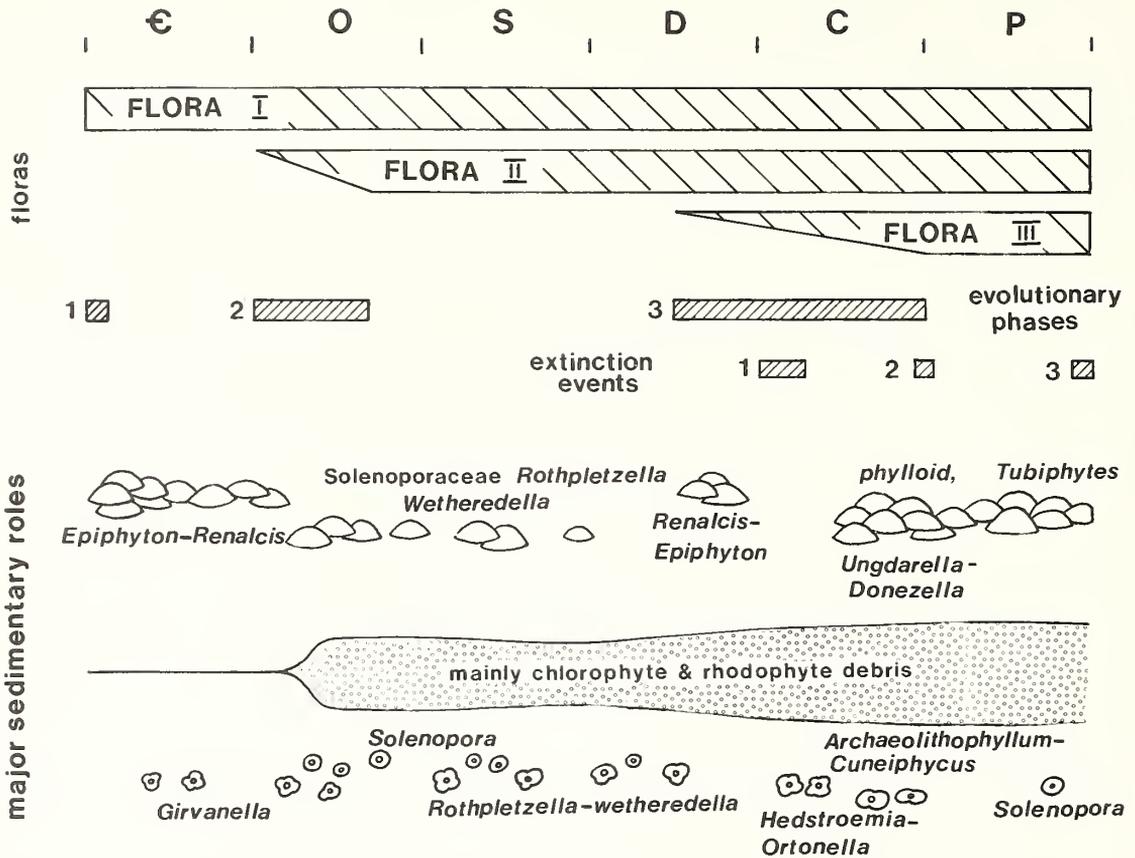
TEXT-FIG. 8. Number of major algal groups present in each Palaeozoic period. Data from text-fig. 1. Shading indicates first appearances.



Extinctions, at group-level, were concentrated near the Devonian–Carboniferous boundary, in the early Permian, and at the Permian–Triassic boundary (text-fig. 9). It is noteworthy that each flora has nearly similar numbers of groups persisting into the Mesozoic: three in the case of the Cambrian flora, two each for the other two floras (text-fig. 1). In fact, most of the groups appearing during the Cambrian and Ordovician are very long-ranging, five out of the eleven continuing not only into the Mesozoic but also into the Cenozoic. The groups appearing during the Devonian to Permian are relatively short-ranging, only *Tubiptytes* (which is also of doubtfully algal affinity) surviving into the Triassic.

Sedimentology

Cyanophytes locally dominated Cambrian reefs. In comparison Ordovician–Devonian algae were nearly always subordinate to metazoan reef-builders, although *Solenopora*, *Rothpletzella*, and *Wetheredella* can be important in the Ordovician and Silurian, and the ‘Cambrian’ *Epiphyton–Renalcis* association reappears in upper Devonian bioherms. However, nodules, including oncoids and *Solenopora* rhodoliths, are more common in the middle Palaeozoic than in either the Cambrian or Permian. The poor algal contribution to reef-building in the lower Carboniferous could be due to the scarcity of bioherms generally at this level, other than waulsortian mounds. It was middle Carboniferous expansion of the groups containing *Donezella*, *Ungdarella–Komia*, phylloid algae, and *Tubiptytes* which provided the new algal reef-builders for the upper Palaeozoic. Stromatolites built by calcareous algae are generally uncommon in the Palaeozoic.



TEXT-FIG. 9. Summary of calcareous algal floras during the Palaeozoic, showing phases of development and extinction, and sedimentological roles.

Although the patterns of reef-, nodule-, and stromatolite-formation by calcareous algae show sharp variations during the Palaeozoic, that of debris production is a relatively simple trend of increase throughout the era (text-fig. 9). Essentially this reflects the history of various fragile chlorophyte and rhodophyte groups.

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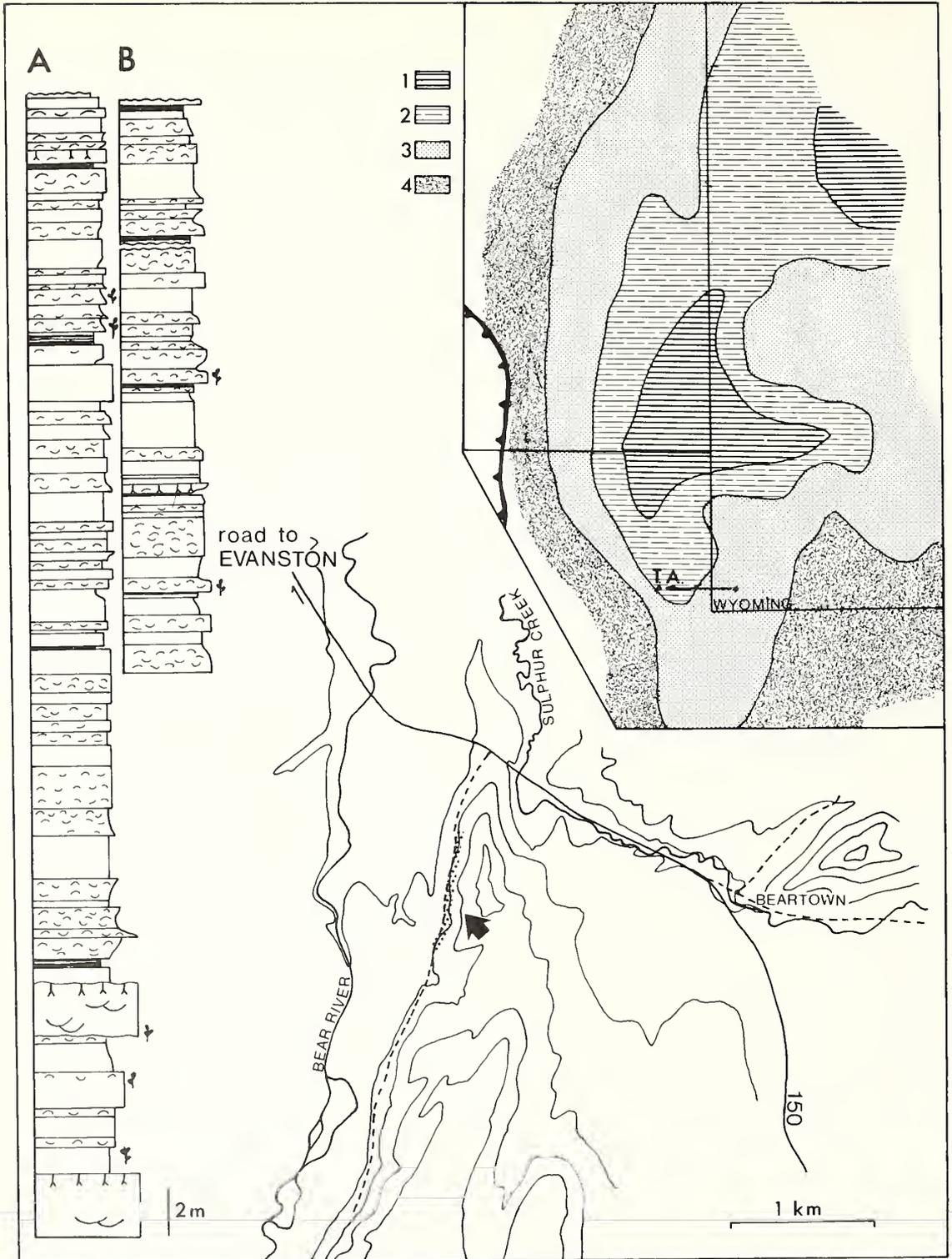
PALAEOECOLOGY OF MARGINAL MARINE SEDIMENTARY CYCLES IN THE ALBIAN BEAR RIVER FORMATION OF SOUTH-WESTERN WYOMING

by FRANZ T. FÜRSICH *and* ERLE G. KAUFFMAN

ABSTRACT. The Middle to Late Albian Bear River Formation of south-western Wyoming includes a cyclic sequence of fine-grained sediments with numerous shell beds comprised of abundant, low diversity fresh- and brackish-water faunas. These record the initial marine transgression of the Cretaceous in this region (Skull Creek-Kiowa tectono-eustatic cycle) and are interpreted as part of an extensive embayment with limited marine influence. Biostratigraphic data suggest low rates of sedimentation, frequently shifting environments, and, in the coquinas, reworking by storms to account for mixing of meso- to oligohaline and freshwater faunas. Five discrete, repetitive benthic associations are documented for the freshwater and two associations with four subsets for the brackish-water facies. They were controlled in their distribution largely by substrate, temperature, and oxygen levels in freshwater and by substrate and salinity in brackish water. Size/frequency curves of brackish species document seasonal fluctuations in salinity (tertiary cycles). Repetitive successions of facies and faunas record regressive sequences (secondary cycles), whilst fluctuations in the relative dominance of fresh- or brackish-water conditions within bundles of regressive sequences reveal a still higher order of cyclicity (primary cycles) within the Bear River Formation. These cycles are partly of climatic origin, partly autocyclic.

DURING the early Cretaceous (middle Late Albian), a narrow seaway which extended from the Proto-Gulf of Mexico to the Circum-Boreal Sea was first established in the Western Interior Basin of North America (Eicher 1960), and has been named the Skull Creek Seaway by McGookey *et al.* (1972, p. 200). Near its centre, grey to black, finely laminated, commonly organic-rich shale facies (e.g. Thermopolis Shale, Mowry Shale) characterize the seaway. Toward the west, these offshore marine facies grade into a zone of marginal facies representing deposition in estuaries, lagoons, and bays. These in turn grade further west into deposits of low-lying flood plains (text-fig. 1). Isotopic studies suggest that even in the centre of the seaway subnormal salinity existed during Skull Creek time. The Middle to Late Albian Bear River Formation represents the western marginal marine facies deposited early in transgression of the northern arm of the Skull Creek Sea (e.g. Young 1969) before a connection was established across Colorado with the warm-water incursion of the Interior Seaway from the Gulf of Mexico. The Bear River Formation comprises fluvial channel and overbank sandstones and, in its centre, lagoon or bay fill sequences of shales, siltstones, and silty carbonates. They contain, in places, low-diversity but highly abundant molluscan-dominated faunas indicative of fresh- and brackish-water conditions. The depositional environments of these fine-grained facies, and especially of the numerous small-scale sedimentary cycles within them, are poorly understood.

The Bear River Formation overlies the non-marine Smoot Formation of the Gannett Group and is in turn overlain by marine shales of the Aspen Formation. Towards the south-east, along the depositional strike, rocks of the Bear River Formation grade into those of the Dakota Formation (e.g. Horstman 1966). Due to widespread thrusting, which commonly cuts the Bear River, the thickness of the formation is difficult to evaluate. It is usually given as 175 to 1750 m, depending on the region (e.g. Stanton 1892; Veatch 1907; Wilmarth 1938). The type section (Stanton 1892, fig. 1) is near the site of the former Bear River City, about 12 miles south-east of Evanston in south-western Wyoming. This section, first described by Meek (1873) and interpreted in more detail by Stanton



TEXT-FIG. 1. Locality map, palinspastic palaeogeography, and section of part of the Bear River Formation at the Bear River Locality in south-western Wyoming. T.A.: type area; (1) offshore marine shale; (2) near-shore mud, sand, and shale; (3) marginal mud and sand; (4) non-marine sand and mud. The thrust symbol denotes position of the Willard-Paris thrust. Section B is stratigraphically higher than section A. For key of symbols, see text-fig. 2. Palinspastic reconstruction after Royse *et al.* (1975).

(1892), is now very poorly and incompletely exposed. A largely complete, freshly exposed section exists along a gravel road leading south past Myers Reservoir (text-fig. 1) 1.5 miles to the west of the type section and about 0.5 miles east of Bear River. This section, subsequently referred to as the Bear River Reference Section, displays in its middle to upper part thin coals, carbonaceous shales, siltstones, thin sandstones, and thin, resistant beds of silty limestone which contain well-preserved fossils representing the characteristic 'Bear River fauna' (Stanton 1892). Cyclic sedimentation and palaeoenvironments are reflected at three different levels of magnitude by both facies and faunas in this part of the section. Second-level cycles are most obvious. Within each secondary cycle the facies change up-section from shelly silts and silty limestones, to silty and carbonaceous shales, to coals, and finally to silty or marly freshwater limestones. The benthic fauna changes accordingly in composition from brackish-water-dominated associations to freshwater-dominated associations. It is the purpose of this paper to analyse the fauna ecologically, to describe in detail the cyclic changes of the facies and faunas, and to speculate on the origin of these cycles at all levels of development.

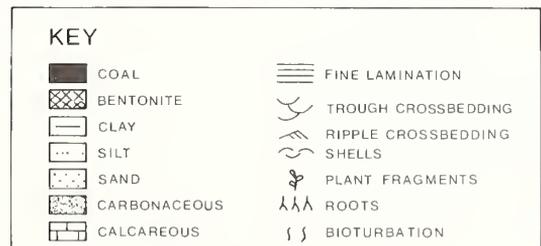
HISTORY OF RESEARCH

Although frequently discussed in the second half of the last century, little modern work has been done on the Bear River Formation. The rocks were discovered by Engelmann in 1859 near the mouth of the Sulphur Creek (type area), and first mentioned by Meek and Engelmann (1860). In 1869 Hayden gave them the name Bear River Group, after the nearby Bear River. In the following twenty-five years, there was a lively debate about the age of the rocks. Originally thought to be Eocene in age (Meek and Engelmann 1860; Meek 1860), their Cretaceous age was only gradually recognized (e.g. Engelmann 1876; White 1891). Stanton (1892) established beyond doubt the Cretaceous age of the rocks and their position below the Colorado Formation. White (1895) reviewed earlier literature, in particular the age controversy, described in detail the faunas, discussed aspects of their ecology, and concluded that the Bear River Formation was 'deposited in a brackish water lake or sea which was more or less completely cut off from open marine waters' (pp. 68-69).

Stanton (1892) had already recognized the occurrence of the Bear River fauna at other localities in south-western Wyoming (e.g. Twin Creek, Ham's Fork, Cokeville) (see also Veatch 1907). Later on rocks with similar faunas were discovered as far as northern Wyoming (e.g. LaRocque and Edwards 1954; Wanless *et al.* 1955) and, in part, described as westward equivalents of the Bear River Formation (Rubey 1973). Due to the lack of index fossils the age question was not yet settled and, in the middle of this century, the discussion was continued by Yen (1952, 1954) who, noting the similarity of the Bear River *Pyrgulifera* to those from Cenomanian localities in Europe, assumed a Cenomanian age for the rock unit, while Cobban and Reeside (1952) assigned the Bear River Formation to the Middle Albian *Inoceramus comancheanus* zone. Today, a Middle to Late Albian age is generally accepted on grounds of facies relationships, and the Bear River Formation is thought to correspond in parts to the Thermopolis Shale (e.g. Eicher 1960; Haun and Barlow 1962; Young 1969; Kauffman *et al.* 1976).

THE BEAR RIVER REFERENCE SECTION

Along the dirt road leading from U.S. 150 toward Myers Reservoir, a large part of the Bear River Formation is exposed. The rocks are overturned and faulted several times so that it was not possible to measure one continuous section. The lower part of the exposure consists of greenish to reddish clays and silts with lenticular intercalations of silt- and sandstones and rare layers of silty limestone. Fossils are very rare and consist of poorly preserved freshwater gastropods. The environment is most likely a low-lying coastal or flood plain dotted with lakes and small streams. This sequence is overlain by a series of silts, shell beds, highly carbonaceous shales with thin coal-seams, and impure limestones (text-fig. 1). Fossils are abundant at numerous horizons, often forming



TEXT-FIG. 2. Key to symbols used in text-figs. 1, 12-17, 19.

shell beds or beds of shell hash. Only the lower portion (42 m) and part of the upper half (20 m) of the fossil-rich strata were measured in detail, the remaining part being identical. The fossiliferous beds are finally overlain by unfossiliferous silty shales.

Facies types. Fine-grained sandstones occur near the base of the measured section only. They have an erosive base and exhibit, in places, large-scale trough cross-bedding and small-scale ripple cross-bedding. Occasionally, levels with rip-up clasts are present near the base. The tops of the sandstones are rooted and occasionally bioturbated (small vertical tubes and *Chondrites*-like traces).

Siltstones do not exhibit any sedimentary structures, but are sometimes bioturbated. They are usually rich in plant debris and occasionally contain scattered shells or thin shell bands.

Silty clays and clayey silts are widespread and can be subdivided into the following types: (a) laminated shales indicative of little or no disturbance of the sediment/water interface. Rarely, thin shell bands are intercalated. (b) Carbonaceous silty clays and clayey silts with a high percentage of plant debris. (c) Blocky silty clay and clayey silt, unfossiliferous or with scattered shells only. All three types may contain thin bands of jarosite.

Shell beds are very common and represent the following three types: (a) beds of shells and shell hash; the matrix is silty clay or clayey silt. Carbonized plant fragments are common in some beds. Shells are usually of brackish-water origin and largely disarticulated. (b) Beds of shelly silty limestone or calcareous siltstone. Most shells are of brackish-water origin. Disarticulated shells dominate, although sometimes individuals are found in life position. Beds of type a and b may have an erosive base and vary in thickness laterally. (c) Beds of shelly silty limestone or marly siltstone. Most shells are small gastropods of freshwater origin. Frequently the beds are highly carbonaceous and may contain coal fragments; occasionally they are rooted.

Coal-seams several centimetres in thickness occur throughout the section. They usually alternate with thin layers of highly carbonaceous silty clay.

Bentonite layers are common. In the measured section, twenty-three layers have been encountered, the thickest measuring 25 cm. Occasionally they have an irregular base.

Facies sequence. The vertical succession of the various facies types is not random, but cyclic. As a rule, the base of each cycle is characterized by thin, bioclast-supported shelly limestone beds, less frequently by shelly silty clay. These may alternate with beds of silty clay and clayey silt in which shells are scattered or absent. At this level poorly fossiliferous siltstones may also be found. Then follows a zone of carbonaceous silty clays, sometimes laminated and often associated with thin coal-seams. Intercalated between these and often terminating the cycles are beds of mud-supported silty or marly limestones that frequently contain plant or lignite fragments and sometimes roots. The cycles range from 50 (a very incomplete cycle) to 500 cm in thickness, most of them being 150 to 300 cm thick.

Fauna. The fauna of the Bear River Formation is generally of low diversity but high abundance and this is also true of the Bear River section. The faunas from the type locality and other localities were first described by Meek (1860, 1870a, b) and more fully by White (1895), but not all Meek's species have been found (for list of species see Table 1). In addition, some are interpreted here as representing only variants of one and the same species. For example, *Corbula engelmanni* Meek (White 1895, p. 40, pl. 4, figs. 10–11) is clearly the juvenile form of *Ursirivus pyriformis* (Meek). Similarly the two species of *Pyrgulifera* (*P. humerosa* and *P. stantoni*) described by White (1895, p. 55, pl. 8, figs. 1–11; pl. 9, figs. 1–8) are here considered only variants of the same species (as also recognized by White) with *P. humerosa* Meek having priority. A similar case can be made for *Mesoneritina naticiformis* (White) and *M. stantoni* (White), the latter being regarded as a junior synonym of the former.

Later descriptions of the macrofauna, in particular the gastropods—although from other localities—are by Yen (1951, 1954). The microfauna and microflora were described by Jones (1893), White (1895), and more recently by Peck (1951) and Peck and Craig (1962). The latter authors list thirteen species of ostracods and charophytes from the Bear River Formation. Palynological investigations were carried out by Tingey (1978).

In the Bear River section gastropods dominate in number of species (twenty) and in abundance. Both fresh- and brackish-water species are present, as is the case among the less diverse bivalves (seven species). In most cases, fresh- and brackish-water species are found in the same bed, but beds with only freshwater or only brackish-water faunal elements are also present. In many beds several species of ostracods and charophytes occur.

It was soon recognized that the Bear River Formation represents a marginal marine environment and White (1895) distinguished clearly between a freshwater and a brackish-water fauna. The assignment of ancient species to a certain salinity regime is particularly difficult in the case of the Bear River fauna where mixing plays a significant role. Criteria such as the preferred occurrence with undoubtedly freshwater forms (e.g. unionids) or brackish-marine forms (e.g. *Crassostrea*, *Ursirivus*, *Brachidontes*) were used to establish the broad salinity range

TABLE 1. List of species found in the Bear River Formation at the Bear River Locality. Familial classification of gastropods based mainly on Yen (1951, 1954)

FRESHWATER		
Bivalves:	Unionidae	<i>Loxopleurns belliplicatus</i> (Meek) <i>Protelliptio (Plesielliptio) vetustus</i> (Meek)
Gastropods:	Valvatidae	<i>Valvata praecursoris</i> (White)
	Viviparidae	<i>Lioplacodes stachei</i> (White)
		<i>Viviparus couesi</i> White
		<i>Campelema macrospira</i> Meek
	Neritidae	<i>Mesoneritina naticiformis</i> (White)
	Amnicolidae	<i>Parateinostoma occultum</i> (White)
		<i>Parateinostoma latense</i> (White)
		<i>Parateinostoma</i> cf. <i>P. altispirale</i> Yen 'Tornatellina?' <i>isocline</i> White
	Pleuroceratidae	<i>Pachychiloides cleburni</i> (White)
		<i>Pachychiloides turriculus</i> (White)
<i>Pachychiloides chrysalis</i> (Meek)		
<i>Pachychiloides chrysalloides</i> (White)		
<i>Pachychiloides macilentus</i> (White)		
	<i>Goniobasis</i> sp.	
	Cyclophoridae	<i>Pseudarinia</i> sp.
	Lymnaeidae	<i>Lymnaea nitidula</i> (Meek)
BRACKISH WATER		
Bivalves:	Corbiculidae	<i>Veloritina durkeei</i> (Meek)
	Corbulidae	<i>Ursirivus pyriformis</i> (Meek) corbulid sp. A
Gastropods:	Mytilidae	<i>Brachidontes multiliuigera</i> (Meek)
	Ostreidae	<i>Crassostrea soleniscus</i> (Meek)
	Pleuroceratidae	<i>Pyrgulifera humerosa</i> (Meek)
	Ellobiidae	<i>Rhytaphorus meeki</i> White
		<i>Zapytchius haldemani</i> (White)

of doubtful species. Thus *Pyrgulifera humerosa* is regarded as a brackish species (in contrast to Yen 1952; LaRocque and Edwards 1954) as is *Rhytaphorus meeki* (see Table 1).

The vertical distribution of the fauna, like the sediment, reveals a cyclic pattern; within a cycle the relative abundance of freshwater forms in individual beds invariably increases towards the top. At the base, shell beds are dominated by brackish-water bivalves whilst at the top brackish-faunal elements are usually missing or do not constitute more than 5% of the fauna, the rest being small freshwater gastropods and unionid bivalves.

SIGNIFICANCE OF ENVIRONMENTAL CONDENSATION FOR THE PALAEOECOLOGICAL INTERPRETATION OF MARGINAL MARINE FAUNAS

Palaeosynecological interpretation of faunas requires that they have undergone only minimal disturbance. This is particularly true of marginal marine faunas where environments and faunas may change drastically across short lateral distances and transport lead to mixing of communities from different biotopes. On the other hand, relatively uniform marginal marine environments such as large protected lagoons and bays may exhibit only insignificant lateral faunal mixing (e.g. Peterson 1976). Of far greater importance in such environments is a process called environmental condensation (Fürsich 1975), whereby faunas representing different environments in time are telescoped into one stratigraphic horizon. Prerequisite for such a process is a low rate of sedimentation and rapid change in environmental parameters such as seasonal or larger scale fluctuations in

salinity in connection with monsoonal type climates or variations in freshwater discharge of rivers. Under such circumstances fresh- and brackish-water to marine faunas, both autochthonous and partly even in life position, can become mingled in one single bed.

The recognition of environmental condensation is relatively easy where ecologically incompatible faunas such as marine and freshwater elements are mixed. If this mixing involves faunas representing different brackish-water regimes, it is more difficult to recognize. Interpretation of such condensed faunas as relics of a single former community will lead to erroneous conclusions with regard to faunal composition, diversity, and evenness and consequently to incorrect ecological inferences (see also Peterson 1977).

Recognition of environmental condensation is therefore crucial for any ecological analysis of Recent and ancient faunas. The following features may facilitate the recognition of environmental condensation:

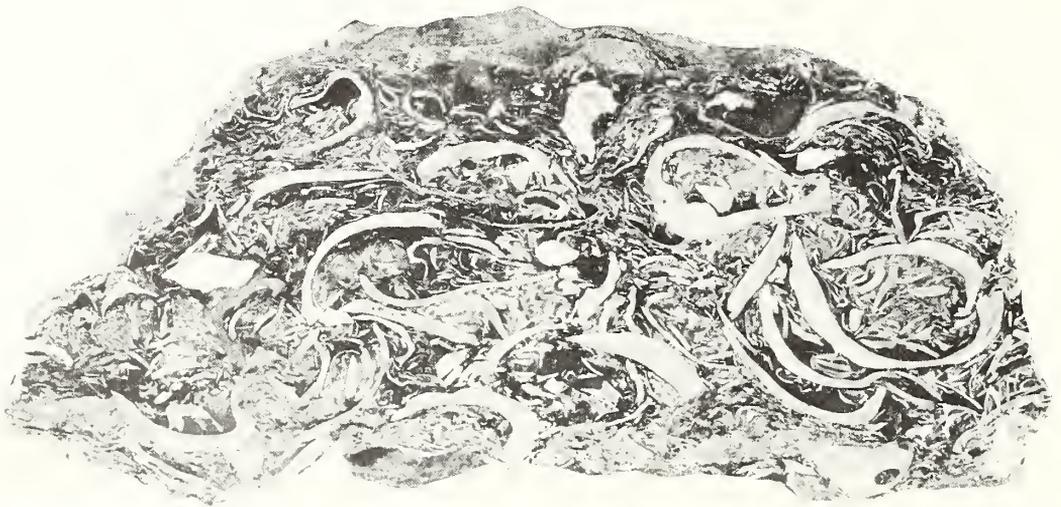
- (1) differences in sediment fill of shells;
- (2) preservational differences (e.g. degree of abrasion, breakage, encrustation) where they are not due to differences in life habits (such as infaunal versus epifaunal);
- (3) a less pronounced repetition of assemblages;
- (4) ecological incompatibility; and
- (5) morphological differences among individuals of the same species, such as co-occurrence of dwarfed and normal-sized, or thin- and thick-shelled individuals.

Environmental condensation played a significant role in shaping the faunal assemblages of the Bear River Formation.

BIOSTRATINOMIC AND SYNECOLOGICAL ANALYSIS OF THE BENTHIC FAUNA

Methods of study

Most of the fossiliferous part of the exposure was measured in detail and eighty-six bulk samples representing over 10,000 specimens of the benthic fauna were collected. The samples were broken up in the laboratory and the fossils counted as described in Fürsich (1977). In addition, the percentage of fragmentation among shells was noted and the right/left valve ratio calculated. Where possible, the size of the dominant faunal elements (*Ursirivus*, *Pyrgulifera*, *Veloritina*) was measured. Two aspects of faunal diversity were calculated: species



TEXT-FIG. 3. Typical example of *in situ* reworked shell bed. Bear River Reference Locality. Polished section, $\times 1$.

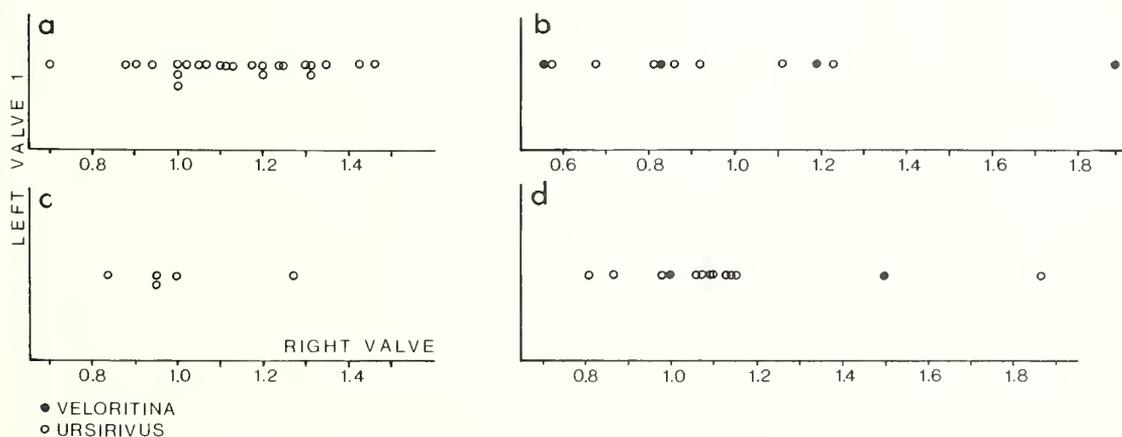
richness, expressed by the number of species present, and evenness which was calculated as $D = 1/\sum p_i^2$ whereby p_i is the relative frequency of the i th species (MacArthur 1972, p. 197). As diagenetic distortion of the fauna can be excluded with confidence (aragonitic faunal elements are invariably preserved, although aragonite has been replaced by calcite or silica) and selective transport was not a major factor, the fossil assemblages can be regarded as relics of former communities. Samples from individual beds frequently contain both fresh- and brackish-water elements, which were analysed separately.

Biostratinomy

The most conspicuous features of the Bear River Formation are the shell beds. Varying in thickness between 3 and 40 cm, they are usually packed with shells of bivalves and gastropods (text-fig. 3). Most shells are disarticulated; only 4 to 12% of brackish-water bivalves in the various associations (see below) are still articulated. This figure is higher for freshwater unionids: over 90% may still be articulated in individual samples. Only very rarely are individuals encountered in life position: the unionids *Loxopleurus* and *Protelliptio* occur predominantly in growth positions within two beds, the corbulid *Ursirivus* in another. In most shell beds a large proportion of the fauna is fragmented, in particular small specimens. In shell beds dominated by brackish-water bivalves estimated fragmentation percentage is generally in the range of 75 to 95; only rarely the percentage is 10 to 50. In contrast, shell beds dominated by freshwater elements have a lower fragmentation percentage, usually between 50 and 75, occasionally even zero.

The dense packing in most shell beds is expressed by a variety of biofabrics. Particularly common are nesting (text-fig. 3) or small-scale oblique imbrication. In contrast to the usual random orientation of shells within the shell bed, shells exhibit a preferred convex-up orientation near the top. The size range of shells and shell fragments is very large in most shell beds and individual species show often bi- or even polymodal size/frequency distribution patterns. The right/left valve ratios of dominant faunal elements (*Ursirivus*, *Veloritina*) are surprisingly close to 1 in most samples (text-fig. 4).

The matrix of many shell beds is not homogeneous. For example, in a silt or clayey-silt matrix, silty carbonaceous clay may be found under shells, in pockets, or as thin discontinuous or rarely continuous layers.



TEXT-FIG. 4. Right/left valve ratios of *Ursirivus pyriformis* and *Veloritina durkeei* in samples representing four subsets of the brackish-water *U. pyriformis* association. Minimum count per sample, 25. a, *U. pyriformis*/*Pyrgulifera humerosa* subset; b, *U. pyriformis*/*V. durkeei* subset; c, *P. humerosa* subset; d, *U. pyriformis*/*Crassostrea soleniscus* subset.

Discussion

At a first glance the shell beds appear to have undergone extensive transport resulting in significant distortion of original benthic communities. The high percentage of fragmentation, the largely disarticulated valves, and mixing of fresh- and brackish-water faunas as well as biofabrics clearly indicate reworking of the shells. However, the biostratigraphic data do not support extensive lateral transport: lack of size sorting, bimodal size/frequency distributions, and the right/left valve ratios all favour within habitat reworking. Faunal mixing was most likely caused by rapidly changing environmental conditions rather than by lateral mixing, and accentuated by local reworking. The case for environmental condensation is strengthened by the occurrence, in some of the shell beds, of 3- to 5-mm thick layers of silty clay that contain only freshwater species whilst the remainder of the bed consists of largely or only brackish-water species. During preparation of the shell beds, these thin layers could not be separated effectively from the rest, leading to samples that exhibit a mixed fauna.

Another example of environmental condensation is a bed of shelly dark-grey silty clay in which large *Pyrgulifera* and articulated *Ursirivus*, some in life position, are found between a host of small disarticulated *Ursirivus* and freshwater gastropods. In this case, at least three different environmental situations are recorded: a freshwater environment represented by the *Lioplacodes stachei* association (see below); a marginal brackish environment represented by juvenile members of the *Ursirivus pyriformis* association that were killed off before reaching maturity; and a more favourable brackish environment in which members of the *U. pyriformis* association reached normal adult size.

Differences in the matrix and faunal composition within single shell beds show that they represent a period of time during which sedimentation regime and environmental conditions changed at least once, if not several times. The extensive reworking was most likely caused by waves in connection with storms. Accordingly, the shell beds are interpreted to represent an environment below fair weather, but above storm-wave base, and thus not exposed to constant reworking as evidenced by the lack of widespread abrasion and the, albeit rare, individuals preserved in life position.

As the biostratigraphic analysis shows, the fauna has not undergone significant lateral transport and can be taken to represent relics of former benthic communities. Two problems, however, remain. First, how far did the extensive breakage act selectively, thereby distorting the original relative abundance of taxa with hard parts? Apart from *Brachidontes multiliniger* and *Crassostrea soleniscus* all brackish-water species have relatively thick shells and even small specimens appear fairly sturdy. The likelihood of fragmentation not only depends on shell size and thickness, however, but also on shell structure and crystal size, and it is very difficult to evaluate the combination of these features with regard to breakage. Observations on shell beds indicate, as one would expect, that small individuals have indeed undergone more breakage than large ones (see Hallam 1967) and thus distorted size frequency curves to some degree. The fact that in twenty out of twenty-four samples of the *U. pyriformis* association right valves are more numerous than left valves, although usually only barely so, probably does not reflect selective transport as the species is nearly equivalved; it is more likely that left valves were slightly more prone to fragmentation than right valves.

No differences with regard to fragmentation were noted between *Veloritina*, *Ursirivus*, and *Pyrgulifera*. In the case of the extremely thin *Brachidontes* and the thin to moderately thick *Crassostrea*, differential breakage was taken into account when the relative abundance of species was established. Nearly all freshwater gastropods were small and thin shelled, in contrast to the large and thick-shelled unionids. However, in both groups the percentage of fragmented shells was relatively low and apparently none of the two groups experienced preferential breakage, except that in most gastropods parts of the aperture and last whorl were damaged.

The second problem is the vertical mixing of different communities which may drastically alter faunal composition and diversity (e.g. Peterson 1977; Fürsich 1978). The fresh- and brackish-water faunas are separated relatively easily, but what about environmental condensation within the fresh- or brackish-water regime? Of the eight brackish-water species only three (*Ursirivus*, *Veloritina*, and *Pyrgulifera*) are abundant, two more occur in moderate to low numbers (*Brachidontes*, *Crassostrea*), whilst the remaining three are rare. The three abundant species and *Crassostrea* recur in sets with different relative abundances and these sets have been grouped into associations. The low and fairly

constant diversity, the lack of preservational differences, and ecological links between species (e.g. the large size of *Veloritina* in the *U. pyriformis*/*C. soleniscus* subset as opposed to its predominantly small size in the *P. humerosa* subset) do not favour extensive environmental condensation within the brackish regime. Furthermore, the salinity range represented by the brackish fauna is thought to be relatively small.

In the freshwater fauna five recurring sets of species were recognized, four of which are closely related and differ largely in the relative abundance of dominant species. There is no evidence to suggest or discount condensation of different faunas.

THE BRACKISH-WATER FAUNA

As has been demonstrated above, the benthic fauna of the Bear River section represents relics of former communities. In the following, five repetitive sets belonging to two associations (Table 2) are

TABLE 2. Composition of the brackish-water associations and subsets. EC—epifaunal cemented; SI—semi-infaunal; SHI—shallow infaunal; EM—epifaunal mobile; S—suspension-feeder; H—herbivore; HD—herbivorous detritus-feeder.

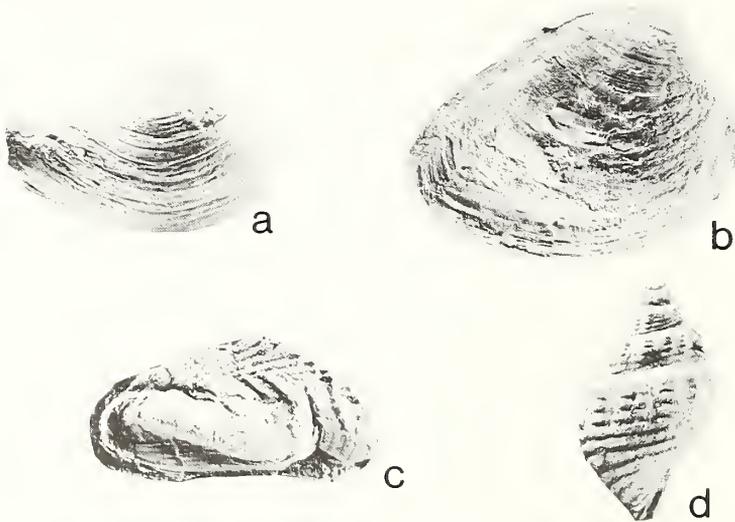
	Rel. abundance	Presence percentage	Rank position	Life habit	Feeding mode
A. <i>Crassostrea soleniscus</i> association (1 sample; 73 specimens)					
<i>C. soleniscus</i>	100	100	1.0	EC	S
<i>Ursirivus pyriformis</i> association:					
B. <i>U. pyriformis</i> / <i>C. soleniscus</i> subset (11 samples; 1054 specimens)					
<i>U. pyriformis</i>	66.0	100	1.1	SHI	S
<i>Veloritina durkeei</i>	15.4	100	2.4	SHI	S
<i>Pyrgulifera humerosa</i>	13.5	100	2.7	EM	HD
<i>C. soleniscus</i>	3.4	100	3.8	EC	S
<i>Bracluidontes multilinigera</i>	0.8	18.2		SI	S
C. <i>U. pyriformis</i> / <i>V. durkeei</i> subset (8 samples; 907 specimens)					
<i>U. pyriformis</i>	67.8	100	1.1	SHI	S
<i>V. durkeei</i>	21.3	100	1.9	SHI	S
<i>P. humerosa</i>	10.2	87.5	3.0	EM	HD
<i>B. multilinigera</i>	0.4	25		SI	S
<i>Rhytophorus meeki</i>	0.1	12.5		EM	H
corbulid sp. A	0.1	12.5		SHI	S
D. <i>U. pyriformis</i> / <i>P. humerosa</i> subset (24 samples; 2,154 specimens)					
<i>U. pyriformis</i>	69.6	100	1.0	SHI	S
<i>P. humerosa</i>	22.1	100	2.0	EM	HD
<i>V. durkeei</i>	7.4	70.8	3.1	SHI	S
<i>B. multilinigera</i>	1.3	20.8		SI	S
corbulid sp. A	0.2	4.1		SHI	S
<i>Zaptychius haldemani</i>	0.04	4.1		EM	H
<i>R. meeki</i>	0.04	4.1		EM	H
E. <i>P. humerosa</i> subset (13 samples; 761 specimens)					
<i>P. humerosa</i>	75.9	100	1.0	EM	HD
<i>U. pyriformis</i>	20.1	92.3	2.2	SHI	S
<i>V. durkeei</i>	4.2	76.9	3.2	SHI	S
<i>B. multilinigera</i>	2.9	38.4		SI	S
<i>R. meeki</i>	0.6	15.4		EM	H
corbulid sp. A	0.3	7.7		SHI	S

briefly described and interpreted ecologically with particular regard to their salinity ranges. The sets were defined by using presence/absence as well as relative abundance data. The dominant faunal elements are shown in text-fig. 5.

The Ursirivus pyriformis association

The U. pyriformis/C. soleniscus subset. Represented by eleven samples and 1,054 specimens, this subset is dominated numerically by the corbulid *U. pyriformis*, followed by the corbiculid bivalve *V. durkeei* and the gastropod *P. humerosa*. *C. soleniscus* represents only 3.4% of the fauna, but is present in each sample. The mean number of species is 4.3. Only 4.4% of the bivalves are articulated and fragmentation varies between 75 and 95%. The subset occurs in shell beds; the matrix ranges from clayey silt to silty micrite. In one sample, coal fragments were common. The mean right/left valve ratio was 1.18 for both *Ursirivus* and *Veloritina* (text-fig. 4). The size distribution of *Ursirivus* was measured in four samples and was invariably bimodal with one peak at 4–6 mm height and the other, broader, at 18–24 mm. Both peaks were pronounced in three cases, while in the fourth the larger size range dominated by far. For *Veloritina* and *Pyrgulifera*, the size distribution could be established in one case each; the two species also exhibit a bimodal distribution pattern with peaks at 3–6 and 15–21 mm in diameter (*Pyrgulifera*), and 5–10 and 25–40 mm height (*Veloritina*). In both cases the larger size group dominated. *Veloritina* reaches a relatively large size in most samples. *Brachidontes*, occurring only in two samples, reached its largest size within the Bear River section within one sample, but is small in the second. In the eleven samples of the subset, freshwater faunal elements ranged from 0 to 25% of the total fauna with a mean of 6.6%.

The U. pyriformis/V. durkeei subset. A second subset occurring in eight samples with 907 specimens was also dominated by *U. pyriformis*, followed by *V. durkeei*. *P. humerosa* occurs in seven of the eight samples and constitutes 10.2% in terms of relative abundance. The remaining three species (*B. multilinigera*, *Rhytophorus meeki*, and the corbulid sp. A) are rare and occur only in few of the samples. The mean number of species in the association is 3.4. Of the bivalves, 11% are articulated; the fragmentation percentage ranges from 50 to 95 and is 90 for most samples. The sediment is either clayey silt, silty clay, or silty limestone (in one case with plant fragments) and the shell density is high in all cases. The mean right/left valve ratio is higher than in the preceding subset, both for *Ursirivus* (1.26) and *Veloritina* (1.51), in the latter case possibly indicative of either selective transport or breakage.



TEXT-FIG. 5. Dominant brackish-faunal elements of the Bear River Formation. *a*, *Ursirivus pyriformis* (Meek); *b*, *Veloritina durkeei* (Meek); *c*, *Brachidontes multilinigera* (Meek); *d*, *Pyrgulifera humerosa* (Meek); all $\times 1$. Bear River Reference Locality.

The size/frequency distribution of *Ursirivus* is bimodal in four cases with the smaller size group usually more pronounced; in one case, only one peak, at 3–6 mm is present. A similar pattern (one bimodal, one unimodal) is exhibited by *Veloritina*. *Brachidontes* is small to tiny in all samples. *Veloritina* exhibits a wide size range except in one sample where all individuals are tiny. In this particular sample, all other faunal elements are equally of small size. The percentage of freshwater elements in the total fauna of each sample ranges from 0 to 60 with a mean of 13.1.

The U. pyriformis/P. humerosa subset. The *U. pyriformis/P. humerosa* subset is very widespread in the Bear River section, represented by twenty-four samples and over 2,000 individuals. *U. pyriformis* is by far the dominant species followed by *P. humerosa* and *V. durkeei*. The remaining four species are rare (corbulid sp. A and the gastropods *Zapychius haldemani* and *R. meeki*) or encountered occasionally (*B. multilinigera*). The mean number of species is 3.1.

Of the bivalves, 11.5% are articulated; percentage of fragmentation varies from 30 to 95 and in most samples is close to the latter. In one sample, *U. pyriformis* was found in life position. The mean right/left valve ratio of specimens of *Ursirivus* is 1.18 with individual values ranging from 1.0 to 1.41 (text-fig. 4). The sediment range in which the *U. pyriformis* subset occurs is like that of the two preceding subsets except that about 16% of the samples occur in silt. About 20% of the sediments are carbonaceous containing either plant debris or wood fragments.

The size/frequency distribution of *Ursirivus* could be established in eighteen samples. Except in one case, where only small individuals are present, the curves are bimodal. Both size clusters are either roughly equal or show a dominance of smaller forms. The size/frequency distribution of *Pyrgulifera* was unimodal in one case, most specimens belonging to the 12 to 21 mm size range, and polymodal in a second case with peaks at 3–6 mm (pronounced), 12–15 mm, and 24–27 mm in diameter. *Ursirivus* and *Pyrgulifera* are generally large, whilst *Veloritina* is small in some samples and occurs in a wide size range in others. In some samples, all specimens of *Ursirivus* are small as are all other faunal elements. *Brachidontes* is tiny in one sample, but relatively large in others. The relative abundance of freshwater elements in samples ranges from 0 to 89.5% with a mean of 19.9%.

The P. humerosa subset. Seven hundred and sixty-one specimens in thirteen samples constitute the subset which is strongly dominated by the pleuroceratid gastropod *P. humerosa*. *U. pyriformis* is also common, occurring in all but one sample. The remaining four species (*V. durkeei*, *B. multilinigera*, *R. meeki*, and corbulid sp. A) are all uncommon or rare. In individual samples, two to five species occur; the mean number of species is 3.3. Of the bivalves, only 9.5% are articulated. The right/left valve ratio of *Ursirivus*, measured in five samples, is extremely close to one (mean 1.1) with individual values ranging from 1.0 to 1.33. The percentage of fragmented shells varies from 10 to 95 but is usually between 50 and 90.

Most samples occur in argillaceous silt or calcareous siltstone; some are found in silt, silty clay, or siliceous fine sandy siltstone. Two samples were rich in plant debris; bioturbation (*Chondrites*-like burrows) was encountered in one case.

In three samples, the size/frequency curves of *Ursirivus* were bimodal, with small specimens strongly dominating. In contrast, *Pyrgulifera* was represented predominantly by large specimens, three out of the four samples having a bimodal distribution pattern, the fourth a unimodal one. In general, specimens of *Ursirivus* often did not reach maximum size. Specimens of *Brachidontes* and *Veloritina* are small or tiny in all except one sample. Freshwater elements constitute from 1.5 to 87% of the total fauna of individual samples with a mean of 51.6.

The Crassostrea soleniscus association

Only represented by seventy-three specimens in one sample, the *C. soleniscus* association nevertheless appears to represent a true recurring association, as it has been mentioned from several horizons at different localities in the Bear River Formation, usually in thin, mono-, or near monotypic shell layers. At the Bear River locality, *C. soleniscus* alone occurs near the top of the measured section in a silty clayey limestone. The oysters occur in thin patches not more than 10 cm high and are preserved *in situ*. Over two-thirds of the shells are articulated and encrust each other. Life orientation of the specimens was horizontal to oblique. The shells of *Crassostrea* are thin to moderately thick and relatively small (most specimens being less than 7 cm in height). In contrast to most Recent or fossil oyster patch reefs, the shells are not encrusted or bored. There is no freshwater fauna associated with the oysters.

Discussion

Apart from the monotypic *C. soleniscus* association, the remaining four sets of species are similar in composition and are best grouped within a single association, the *Ursirivus pyriformis* association.

Within this major association, however, the relative abundance of individual species varies considerably. Samples in which *Ursirivus* strongly dominates are found as well as samples in which *Pyrgulifera* accounts for more than 80% of the fauna. *Crassostrea* occurs only in some samples. *Veloritina* accounts for a quarter of the individuals in some samples, but is rare in others.

Among marine ecologists there are two schools: one which regards marine benthic communities as discrete entities with sharp boundaries, and one which recognizes only species gradients and regards communities as artificial subdivisions of such gradients (e.g. Mills 1969). Community boundaries are usually shaped by the nature of environmental gradients. Sharp gradients such as the sudden change from a soft to a hard substrate will result in discrete community boundaries, weak gradients in turn will result in gradual replacement of species and therefore at most in blurred boundaries.

Within the brackish-water faunas from the Bear River relative abundance and, to some extent, species composition changed along a gradient of an overriding ecological parameter. In an attempt to learn more about this parameter, the *U. pyriformis* association was subdivided into four subsets which are artificial in that they grade into each other, but are interpreted as occupying different positions along a continuous environmental gradient. Thus, we do not suggest that these subsets represent relics of discrete communities. They are simply the means by which we can illustrate changes in community composition and structure along an environmental gradient. Indeed, that these subsets appear to have occupied different positions along an environmental gradient is supported by the fact that size/frequency distribution, size range, diversity, and percentage of freshwater elements in samples differ systematically between the various subsets.

Autecology. All species could apparently tolerate low salinities as indicated by their close association with non-marine sediments and faunas.

Ursirivus pyriformis (text-fig. 5a) is a nearly equivalve corbulid with a tapering posterior. This, and the presence of a shallow pallial sinus (Vokes 1945) suggests that the bivalve lived as a shallow burrower in the sediment with the anteroposterior axis in a more or less vertical position. Like other corbulids it was a suspension-feeder. Corbulids have several adaptations (such as being able to close their valves very tightly) to withstand environmental fluctuations, especially with regard to salinity, oxygen level, and temperature (e.g. Lewy and Samtleben 1979) and are consequently eurytopic. This is true not only of Recent, but also of fossil species which are particularly common in marginal marine environments (e.g. Fürsich 1981) where they typically occur in large numbers in low diversity assemblages. Being slow burrowers they are preferentially found in low-energy environments with fine-grained substrates, and this was clearly also the preferred habitat of *U. pyriformis*.

Corbulid sp. A is a small, 3–4 mm long species that exhibits the sharp posterior ridge seen in many corbulid species. As no hinge line was seen, a generic designation was impossible. Most likely this fairly rare species lived, like other corbulids, as a shallow infaunal suspension-feeder.

The corbiculid bivalve *V. durkeei* (text-fig. 5b) belongs to a family whose Recent members either live in fresh or brackish waters. The pallial line of this trigonal species is posteriorly truncated and the species most likely possessed a pair of short siphons and lived as a suspension-feeder close to the depositional interface. Species of *Veloritina* and *Corbicula* are characteristic of marginal marine environments elsewhere in the Cretaceous of the Western Interior Basin (e.g. in the Fox Hills Formation of northern Colorado) and may there form monotypic shell beds. In the Bear River Formation, *V. durkeei* is generally less abundant than *Ursirivus* or *Pyrgulifera*.

The oyster *Crassostrea soleniscus* lived in small clusters as an epifaunal-cemented suspension-feeder. Elsewhere (e.g. in the Cenomanian Woodbine Formation of Texas; Stephenson 1952) it reaches a considerably larger size and may form extensive patch reefs. The relatively small and thin valves of the Bear River occurrence as well as the small size of the patches most likely indicate that there the species lived close to the limit of its environmental range.

B. multilinigera (text-fig. 5c) is extremely thin-shelled and consequently frequently fragmented. Judging from its cross-sectional shape, it appears to have lived semi-infaunally as an endobysate suspension-feeder. The small to tiny size of most specimens compared with occurrences elsewhere in the Cretaceous suggest a largely unfavourable environment for this species.

Of the three gastropods regarded as having lived in brackish rather than freshwater, *P. humerosa*

(text-fig. 5d) is by far the most abundant, whilst *R. meeki* and *Z. haldemani* are rare. *P. humerosa* most likely fed on plant detritus. Little is known about the ecology of Mesozoic gastropods and more detailed interpretation would be speculative.

Nature of environmental gradients. It is clear that the fauna lived on or in a moderately soft substrate. No specific substrate preferences have been noted, but all associations occur in a range of fine-grained substrates, and individual species appear to have been fairly eurytopic. The scarcity of sedimentary structures, the presence of laminated shales, and the fine-grained nature of the sediments indicate a low-energy environment except when, during storms, the wave base was lowered and shells accumulated in beds. This does not necessarily imply a great water depth. On the contrary, the presence of root horizons and coal layers suggests deposition in water depth of less than 5 m for most of the time.

Other environmental parameters exerting a major influence on the distribution of benthic faunas are the oxygen level, variations in food supply, temperature, and salinity. There are no indications of anoxic conditions at or near the sediment/water interface with the possible exception of the laminated, often carbonaceous silty clays and clayey silts that are usually devoid of fauna and may well represent periods of poor oxygenation. Variations in temperature are difficult to assess, but may have been pronounced in the shallow extensive water body represented by parts of the Bear River Formation. Such variations would favour eurytopic, opportunistic species, but exclude most stenotopic forms. Variations in food supply, characteristic of estuaries, are apparently less pronounced in lagoons, which are frequently rich in nutrients (e.g. Mee 1978). Marginal marine environments are strongly influenced by extreme salinity values or salinity fluctuations. The close association of freshwater and marine species in the Bear River Formation shows that salinity was the major factor controlling distribution and growth of the benthic fauna possibly amplified by fluctuations in temperature, resulting in a high stress environment. Coal beds, freshwater gastropods, unionid bivalves, and the absence of features indicative of hypersaline conditions suggest that salinity values were lower than normal marine and that one end of the salinity spectrum was represented by the freshwater environment. As stenohaline faunal elements are totally lacking (this is true also of the microfauna where foraminifera are absent and only fresh- and brackish-water ostracods occur) the highest salinity values probably were considerably below normal marine values. This is not surprising as even the offshore Skull Creek Seaway supported only a restricted fauna possibly influenced by low salinities (e.g. Eicher 1962). Considering the very low species diversity of all samples, it is safe to assume that the faunas did not live in waters of a salinity much higher than the mid-mesohaline regime (about 12‰).

Distribution of the fauna along the salinity gradient. Within meso- and oligohaline regimes of Recent estuaries, the fauna can be classified as euryhaline opportunists or estuarine endemics with freshwater species encroaching within the 1 to 2‰ range (Boesch 1977). Considering that *U. pyriformis*, *V. durkeei*, and *P. humerosa* are confined to the marginal marine Bear River environments and are not known from anywhere else in North America, it is most likely that they were endemic within this salinity range and specifically adapted to life in lowered and fluctuating salinity regimes. This is corroborated by the fact that all these species reach a large size and are fairly thick shelled. In contrast, *B. multilinigera* and *C. soleniscus* are known to occur in more saline waters elsewhere and, when occurring in the Bear River Formation, are relatively small and thin-shelled. They may be more correctly classified as euryhaline opportunists close to their environmental limit.

Using information on absolute size of individual taxa in connection with data on species richness and evenness, it is possible to arrange the five sets of species along a salinity gradient (text-fig. 6). Accordingly, the *U. pyriformis*/*C. soleniscus* subset occupies the upper end of the salinity scale, followed by the *U. pyriformis*/*V. durkeei* and *U. pyriformis*/*P. humerosa* subsets. These three subsets and the monospecific *C. soleniscus* association are thought to have occupied the lower part of the mesohaline regime, whilst the *P. humerosa* subset occupied the oligohaline regime. Within this proposed sequence the evenness declines as does species richness (except in the case of the *P. humerosa* subset). *Ursirivus* and *Veloritina* decrease in maximum size towards lower salinity whereas the size of *Pyrgulifera* remains unchanged. The proposed arrangement of associations is

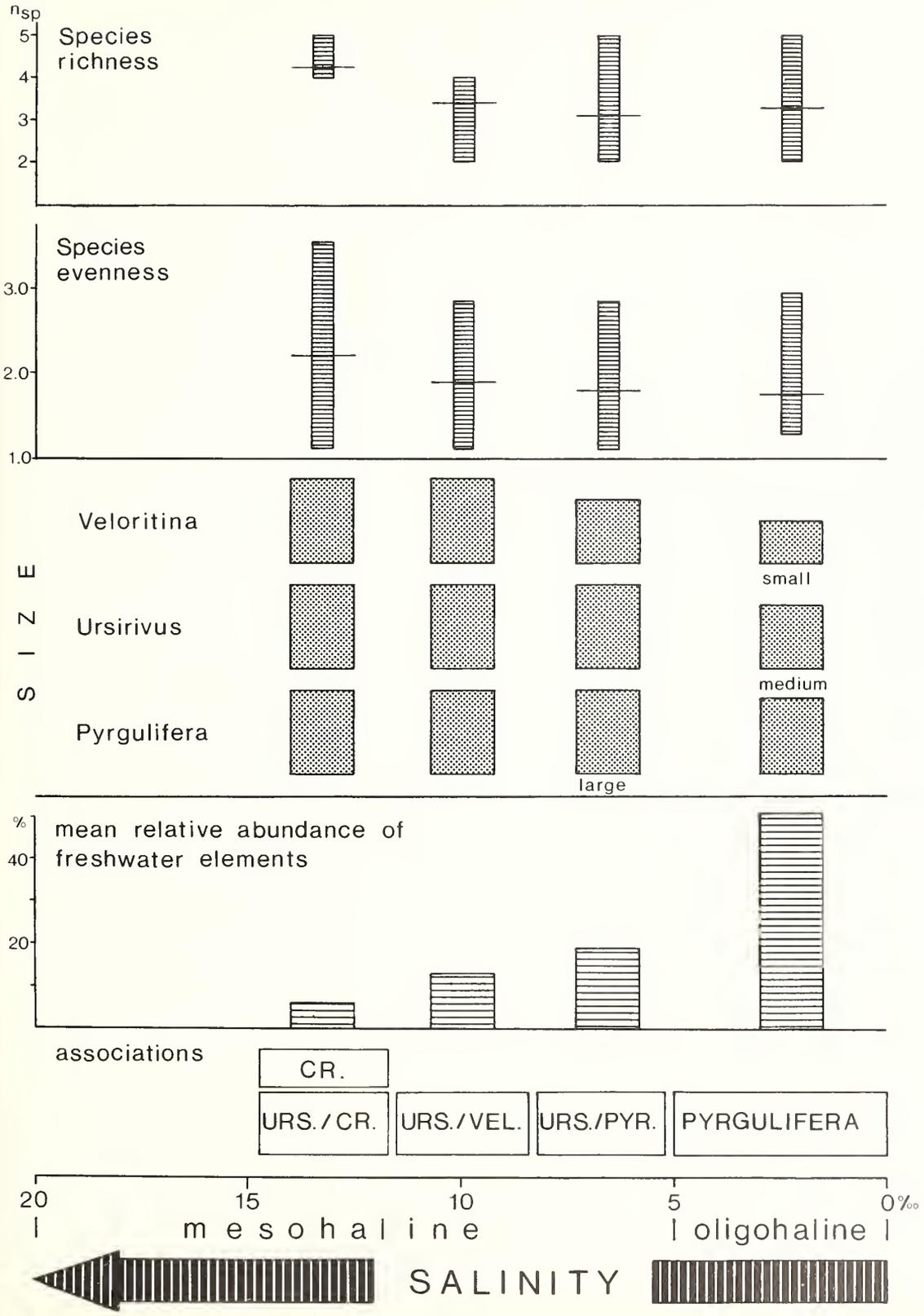
corroborated by the increase of the mean percentage of freshwater elements along the gradient, thus substantiating the decrease of marine influence. The exact position, along this gradient, of the *C. soleniscus* association is difficult to establish. According to its species richness and evenness values, it would have to occupy the zone closest to the freshwater edge. However, this seems unlikely, as *Crassostrea* was not found outside the *U. pyriformis*/*C. soleniscus* subset. The monospecific oyster patches more likely occupied a position near the upper part of the salinity range. The lack of other species may be caused by other factors than salinity. For example, the biogenic hard substrate would have prevented burrowers such as *Veloritina* and *Ursirivus*.

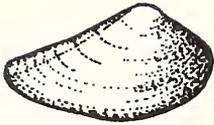
Lowered salinities versus salinity fluctuations: the significance of size/frequency curves. Recent environments rarely exhibit long-term stable salinity reductions. Fluctuations may be seasonal (variations in river discharge, monsoon-like rainy seasons), diurnal (caused by tides), or random (e.g. caused by tropical rain storms, removal of barriers). Interpreting size/frequency distribution patterns of dominant taxa, the wave length and amplitude of such fluctuations can be estimated. Text-fig. 7 shows variations in the size/frequency pattern of *Ursirivus*. *Veloritina* and *Pyrgulifera* show similar curves. The pattern is bimodal or unimodal and small or large individuals may dominate. The first mode is in the size classes 0–9 mm (*Veloritina*) or 3–9 mm (*Ursirivus* and *Pyrgulifera*), whilst the second mode lies between 24 and 40 mm (*Veloritina*), 15–27 mm (*Ursirivus*), and 12–21 mm (*Pyrgulifera*). The second size group is nearly always broader than the first one. The first mode most likely represents juveniles, whilst the second mode reflects adult populations. The size/frequency distributions do not include post-larval mortality, as those shells were too small to be recovered during the mechanical breaking up of the samples. Some individuals may be stunted, exhibiting extreme crowding of growth lines, but the majority are not. Compared with data from Recent bivalves (e.g. Hallam 1967) the smaller size group most likely represents one season's growth. Samples with only the smaller size group present thus consist of individuals that were killed after roughly one year. The reason for the death was probably a drastic reduction in salinity and this would imply strong seasonal salinity fluctuations.

Size/frequency distribution patterns with a strong dominance of juveniles in the population can also be caused by biological factors, in particular predation. An example to indicate that predation may play a significant role in marginal marine environments is the high abundance of blue crabs feeding on oyster banks in Chesapeake Bay (Levinton 1982, p. 345). Within the Bear River faunas signs of predation are extremely rare (some cases of repaired shells have been found). Predators such as starfish are unrepresented by isolated skeletal elements. The second important group preying on mollusks are crustaceans, in particular crabs. They usually leave marks on the shell when prying them open which should be preserved in the fossil record. Apart from the very rare cases of repaired shells—obviously representing unsuccessful attacks by predators such as crabs—no shell damage indicative of predation was encountered. Another indication that at least some individuals were not killed by predation is that they are still articulated. Finally, the occasional occurrence of severe growth restrictions in larger individuals at the size represented by the juvenile peak (text-fig. 8) strongly suggests that environmental rather than biological factors caused the death of many individuals after one season's growth.

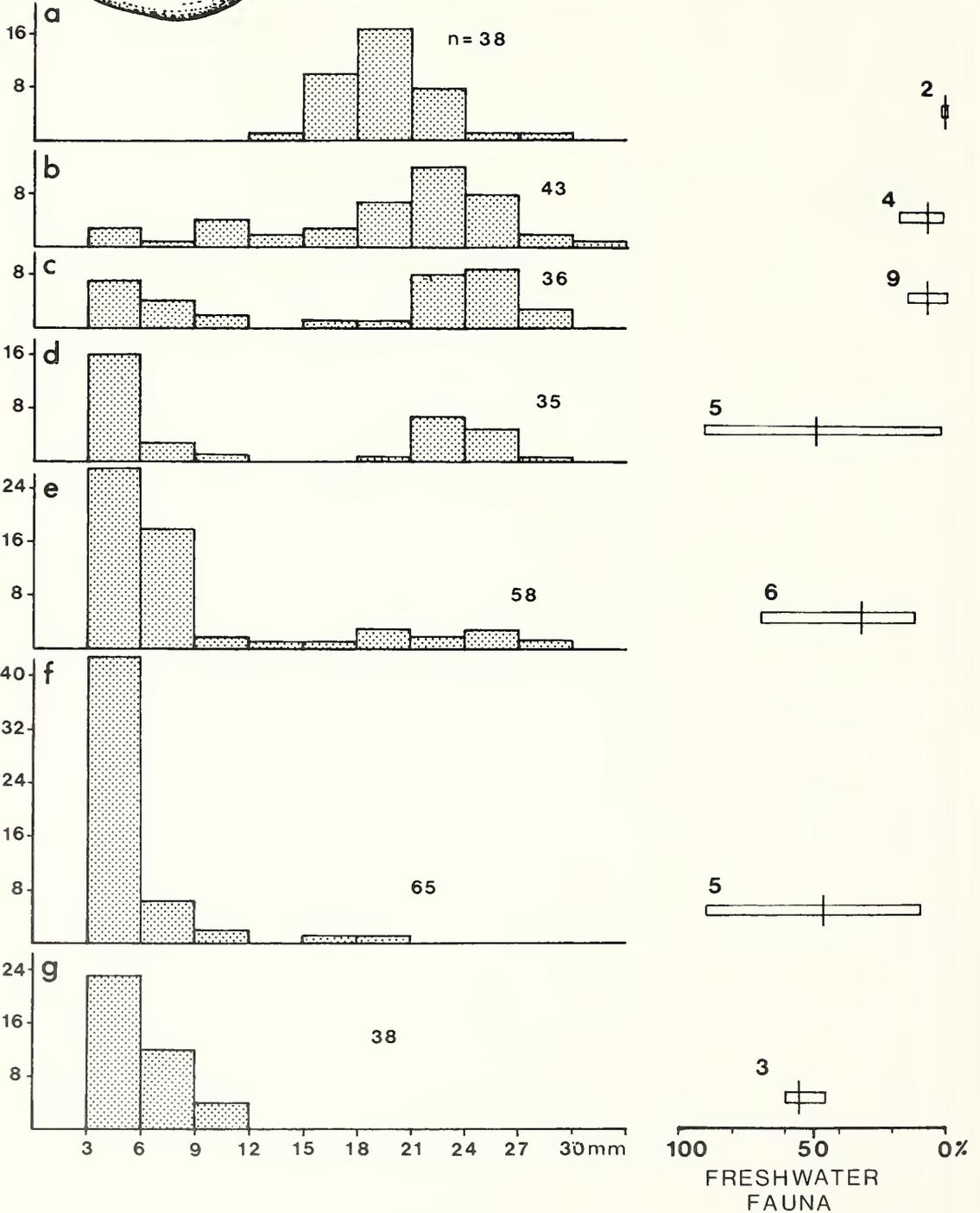
Another explanation of the size/frequency pattern would be migration of individuals from a nursery area to their adult habitat. This is apparently common among shallow water and intertidal

TEXT-FIG. 6. Inferred distribution of brackish-water associations along a salinity gradient. Note that species richness, evenness, and size of dominant species decline, whilst the relative abundance of freshwater elements in individual beds increases. For species richness and evenness both ranges and means are given. CR.: *Crassostrea soleniscus* association; *Ursirivus pyriformis* association—URS./CR.: *U. pyriformis*/*C. soleniscus* subset; URS./VEL.: *U. pyriformis*/*Veloritina durkei* subset; URS./PYR.: *U. pyriformis*/*Pyrgulifera humerosa* subset; PYRGULIFERA: *P. humerosa* subset.

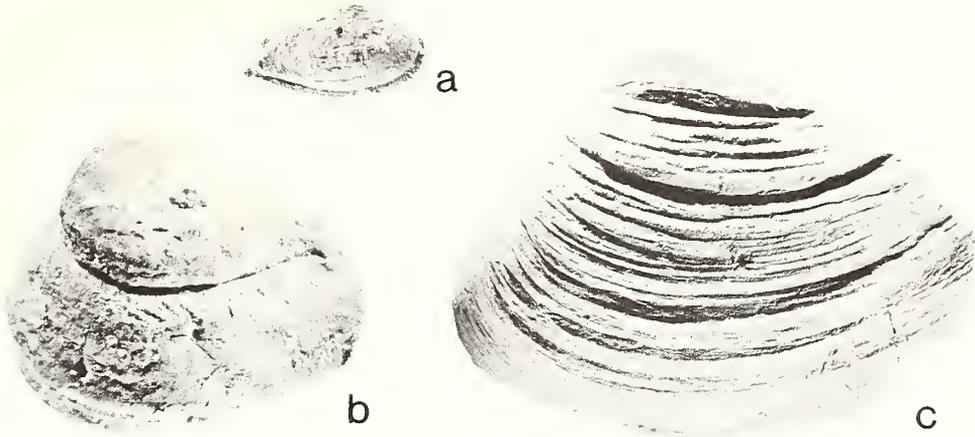




URSIRIVUS



TEXT-FIG. 7. Examples of size/frequency histograms of *Ursirivus pyriformis* related to the percentage of freshwater faunal elements in individual samples. Each histogram is representative of several samples (numbers at right side of text-fig). Note that the relative increase of large individuals is matched by a decrease in the relative abundance of freshwater faunal elements.



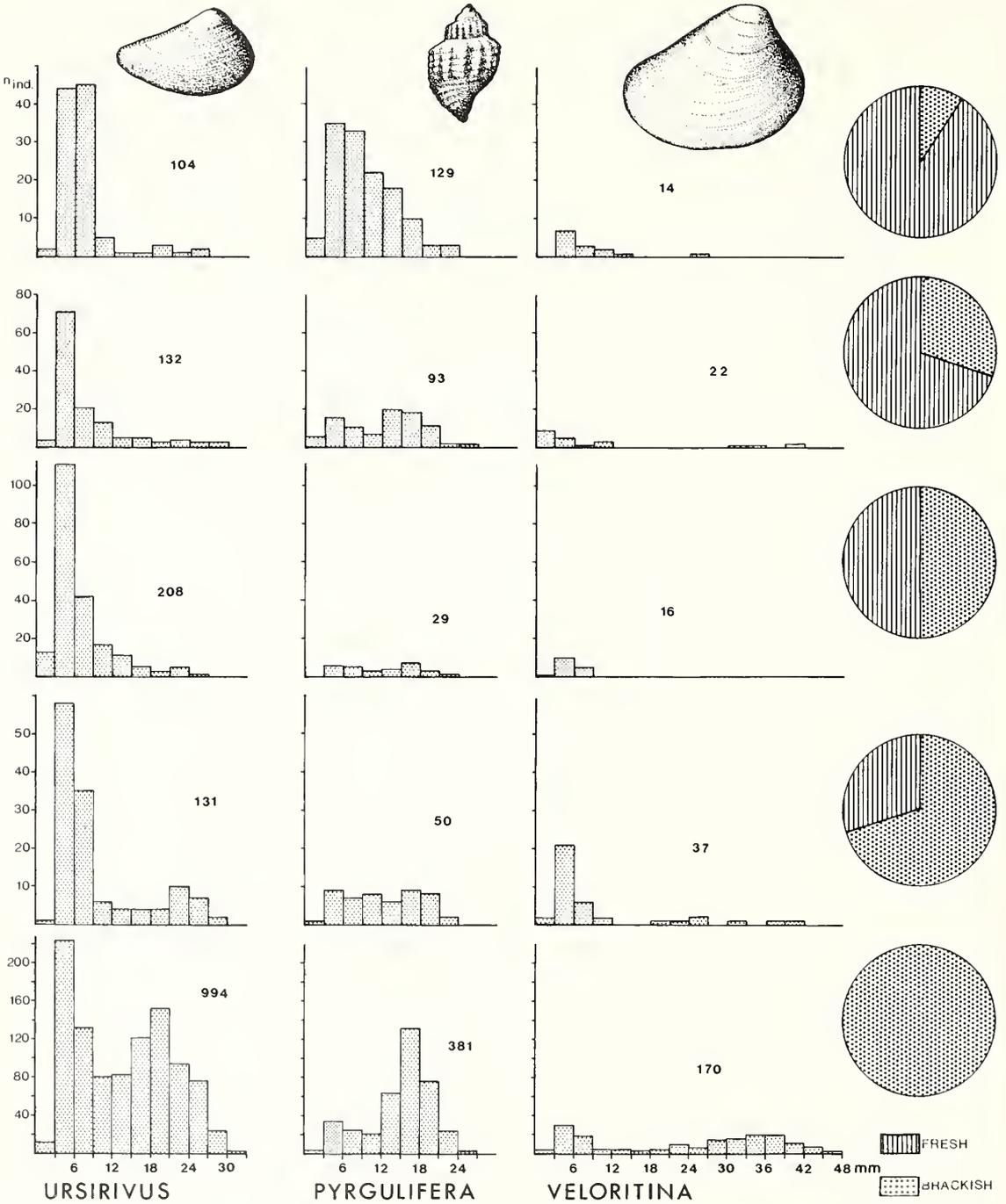
TEXT-FIG. 8. Growth restriction in *Ursirivus pyriformis*. *a*, juvenile specimen, $\times 3.5$; *b*, *c*, adult specimens, $\times 3.2$. Bear River Reference Locality.

species and by no means confined to mobile organisms (for recent summary see Cadée 1982). However, the clear relationship between size/frequency distribution and influence of freshwater (expressed by the percentage of freshwater faunal elements; see text-figs. 7 and 9) makes salinity the overriding factor explaining mortality patterns of the brackish-water mollusks.

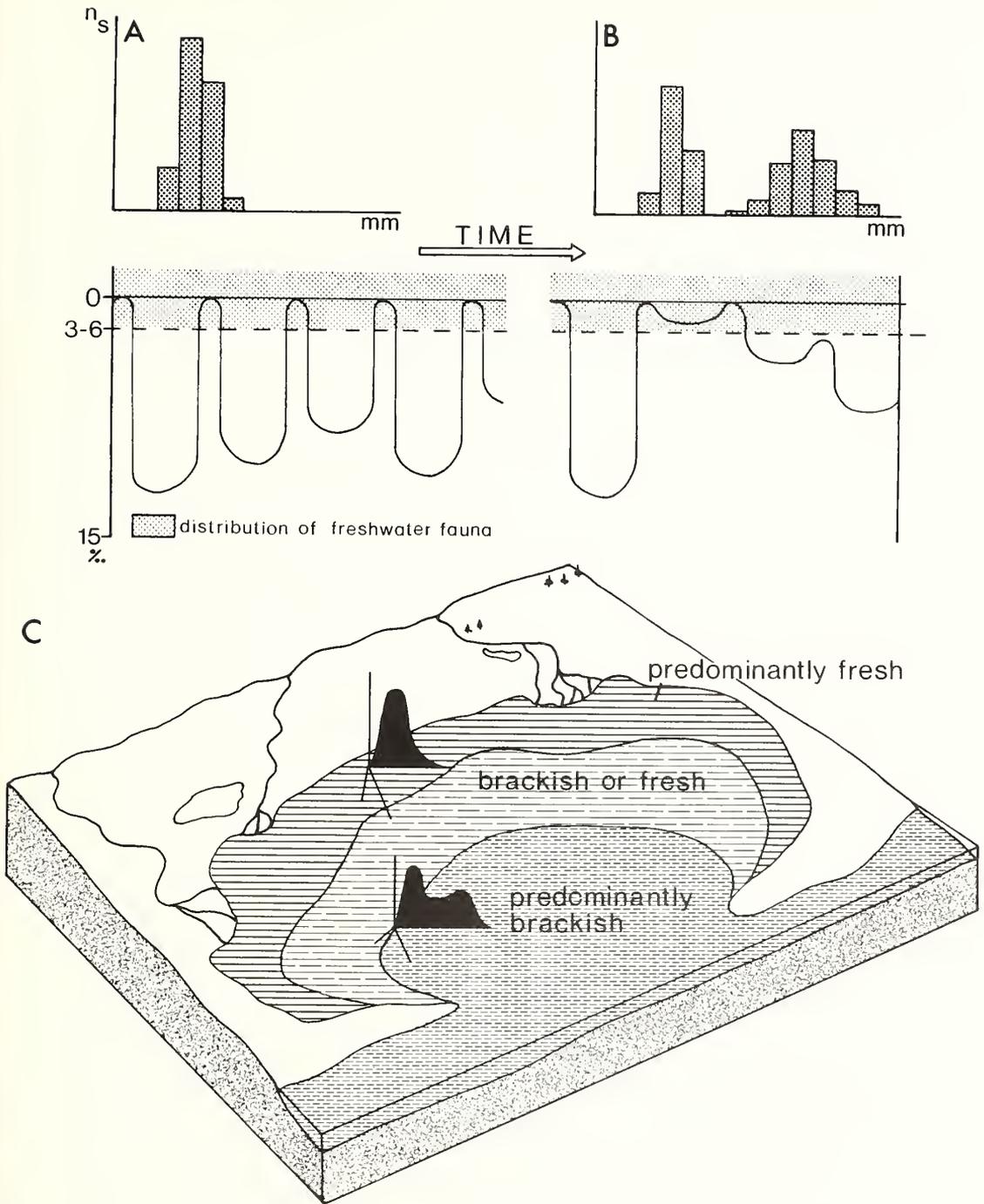
Some samples exhibit a unimodal distribution at the adult size range or a bimodal distribution with the adult population strongly dominating. In this case, the salinity fluctuation was apparently not severe enough to lead to the death of all animals. However, these samples have probably undergone some differential breakage resulting in an under-representation of small individuals. Numerous intermediate cases illustrate variations in the amplitude of the salinity fluctuations. No samples represent single generations but hundreds or even thousands of generations, and what we see is therefore the cumulative effect of salinity fluctuations of varying amplitudes.

In order to kill off a well-adapted brackish-water fauna, freshwater influx must have been very high. This can be demonstrated by the presence of an essentially autochthonous freshwater fauna. As one would expect, there is a relation between the percentage of freshwater elements and the size distribution pattern (text-fig. 7). Whilst the curves in text-fig. 7 show signs of bias—the lack or scarcity of juveniles in text-fig. 7*a-c* is difficult to explain in samples that represent numerous generations (e.g. Hallam 1972)—the cumulative histograms for *Ursirivus*, *Veloritina*, and *Pyrgulifera* from beds with different proportions of fresh- and brackish-water elements (text-fig. 9) are more realistic. Along a gradient representing a decrease in the relative abundance of freshwater faunal elements, the relative proportion, in the histograms, of larger size groups representing adults increases. Assuming the same degree of distortion, in all samples, by under-representation of small individuals, this would indicate that conditions for survival into adulthood were clearly more favourable in beds that exhibit no or only little freshwater influence. The main factor governing size frequency distribution of the brackish-water species would therefore be fluctuations in salinity.

Assuming salinity fluctuations to be largely seasonal, the following model is proposed (text-fig. 10): If the amplitude of salinity fluctuations were fairly high, ranging from freshwater to the mesohaline regime, the brackish fauna would not be able to survive and be represented only by juveniles. Were the fluctuations less pronounced, the brackish-water fauna might be able to survive seasonally reduced salinity values and be represented by juveniles and adults. Less pronounced fluctuations near the brackish/freshwater interface may also favour the establishment of a freshwater fauna over a longer period of time (text-fig. 10*B*). Text-fig. 10*C* presents a model of the water body most easily



TEXT-FIG. 9. Cumulative size/frequency histograms of the dominant brackish-water species arranged according to percentage of freshwater faunal elements in the same bed.

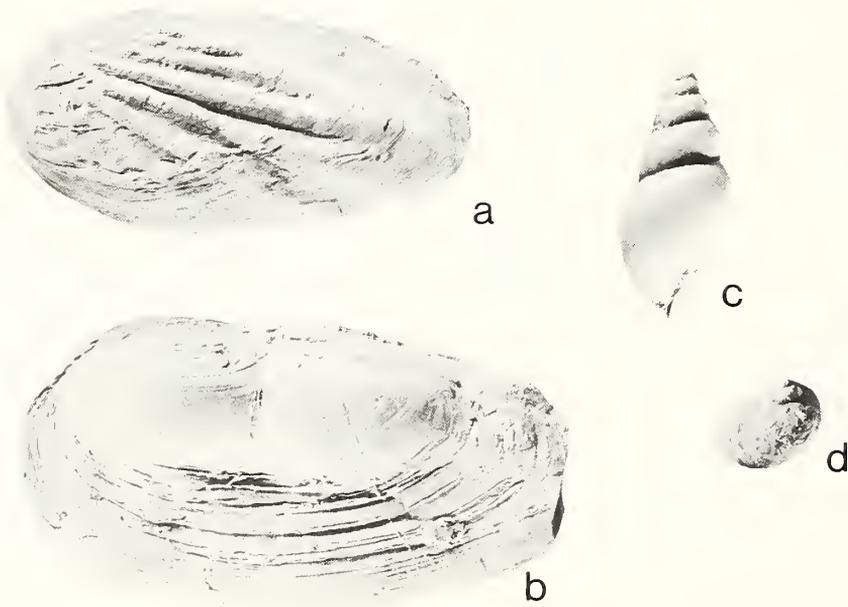


TEXT-FIG. 10. Model of the relationship between seasonal salinity fluctuations and size/frequency distribution of brackish-water species in an extensive embayment. A, model of salinity fluctuations and resulting histogram indicative of complete juvenile mortality; B, model of less regular salinity fluctuations resulting in histogram indicative of 'normal' juvenile mortality; C, palaeogeographic model of salinity zonation within an extensive embayment lacking barriers.

producing such distribution patterns: an extensive embayment is connected with the open sea at one end, while rivers enter it at the other. It is plausible to assume a predominantly freshwater mass near the river mouths and in neighbouring shallow areas—provided the climate is humid to subhumid. In contrast, a predominantly brackish-water mass would characterize the region close to the open sea and in the deeper parts of the embayment (Barnes 1980). In between these two areas there would be a zone in which salinity fluctuates greatly from brackish to fresh, depending on the amount of the seasonal freshwater input (be it by rivers or rain). Considering that, during Middle Albian time, the Skull Creek Seaway did not connect southwards to the Proto-Gulf of Mexico, but the area in southwestern Wyoming represented a cul-de-sac (text-fig. 1) with generally lowered salinity values even offshore, it is not necessary to invoke the existence of extensive barrier island systems to close off the highly brackish to fresh embayment from the open sea. It is envisaged that a salinity gradient without barriers could have been effective provided the freshwater influx was high and mixing of water masses was insignificant.

THE FRESHWATER FAUNA

The freshwater fauna is represented by small, thin-shelled gastropods and large, thick-shelled unionid bivalves. Five associations and one assemblage have been recognized on grounds of presence/absence and relative abundance of important taxa (Table 3). A modified χ^2 test performed on the relative abundances indicates that the associations are significantly different from each other at the 99% level. Dominant faunal elements are shown in text-fig. 11.



TEXT-FIG. 11. Dominant faunal elements of the freshwater. *a*, *Loxopleurus belliplicatus* (Meeke), $\times 1$; *b*, *Protelliptio vetustus* (Meeke), $\times 1$; *c*, *Lioplacodes stachei* (White), $\times 3$; *d*, *Mesoneritina naticiformis* (White), $\times 3$. Bear River Reference Locality.

TABLE 3. Composition of the five freshwater associations. EM—epifaunal mobile; SI—semi-infaunal; H—herbivore; S—suspension-feeder.

	Relative abundance	Presence percentage	Rank position	Life habit	Feeding mode
A. <i>Lioplacodes stachei</i> association (6 samples; 815 specimens)					
<i>L. stachei</i>	84.8	100	1.0	EM	H
<i>Mesoneritina naticiformis</i>	4.4	100	2.8	EM	H
<i>Protelliptio vetustus</i>	4.8	50		SI	S
<i>Campeloma macrospira</i>	3.4	33.3		EM	H
<i>Loxopleurus belliplicatus</i>	1.1	16.7		SI	S
<i>Parateinostoma occultum</i>	0.5	33.3		EM	H
' <i>Tornatellina</i> ' <i>isoclina</i>	0.5	33.3		EM	H
<i>Lymnaea nitidula</i>	0.4	33.3		EM	H
<i>Parateinostoma latense</i>	0.1	16.7		EM	H
B. <i>Lioplacodes stachei</i> / <i>P. occultum</i> association (3 samples, 477 specimens)					
<i>L. stachei</i>	68.8	100	1.0	EM	H
<i>Pachycholoides macilentus</i>	21.9	100	2.3	EM	H
<i>Parateinostoma occultum</i>	5.2	100	2.7	EM	H
<i>P. latense</i>	2.9	100	4.0	EM	H
<i>Valvata praecursoris</i>	0.2	33		EM	H
<i>M. naticiformis</i>	0.2	33		EM	H
<i>Pachycholoides cleburni</i>	0.2	33		EM	H
<i>Protelliptio vetustus</i>	0.2	33		EM	H
C. <i>L. stachei</i> / <i>Pachycholoides macilentus</i> association (14 samples, 2,607 specimens)					
<i>L. stachei</i>	71.1	100	1.2	EM	H
<i>Pachycholoides macilentus</i>	9.9	100	2.8	EM	H
<i>M. naticiformis</i>	10.3	85.7	3.4	EM	H
<i>Protelliptio vetustus</i>	2.5	64.3		SI	S
<i>V. praecursoris</i>	2.1	57.1		EM	H
<i>Goniobasis</i> sp.	0.8	14.3		EM	H
<i>C. macrospira</i>	0.7	42.8		EM	H
<i>Loxopleurus belliplicatus</i>	0.6	64.3		SI	S
<i>Viviparus couesi</i>	0.5	21.4		EM	H
<i>Lymnaea nitidula</i>	0.4	28.5		EM	H
<i>Parateinostoma occultum</i>	0.3	14.3		EM	H
<i>P. latense</i>	0.3	21.4		EM	H
<i>Pachycholoides cleburni</i>	0.1	7.1		EM	H
D. <i>M. naticiformis</i> / <i>L. stachei</i> association (8 samples, 1,016 specimens)					
<i>M. naticiformis</i>	70.1	100	1.0	EM	H
<i>Lioplacodes stachei</i>	19.1	100	2.1	EM	H
<i>P. macilentus</i>	4.9	100	3.1	EM	H
<i>C. macrospira</i>	1.4	25		EM	H
<i>Protelliptio vetustus</i>	1.2	37.5		SI	S
<i>Pachycholoides cleburni</i>	1.1	25		EM	H
<i>Loxopleurus belliplicatus</i>	0.3	25		SI	S
<i>V. couesi</i>	0.3	25		EM	H
<i>P. chrysalis</i>	0.3	25		EM	H
<i>Lymnaea nitidula</i>	0.2	12.5		EM	H
<i>Parateinostoma occultum</i>	0.2	12.5		EM	H
E. <i>Pachycholoides chrysalis</i> association (4 samples; 692 specimens)					
<i>P. chrysalis</i>	53.5	100	1.5	EM	H
<i>M. naticiformis</i>	19.9	100	2.2	EM	H
<i>P. cleburni</i>	19.4	100	2.5	EM	H
<i>P. macilentus</i>	7.2	100	3.7	EM	H
<i>P. chrysalloideus</i>	1.0	25		EM	H
<i>Lioplacodes stachei</i>	0.4	50		EM	H

The Lioplacodes stachei association

In six samples with 815 specimens, the viviparid gastropod *L. stachei* represents over 80% of the fauna. Six other gastropods occur in low to moderate numbers (*Mesoneritina naticiformis*, *Campeloma macrospira*, *Parateinostoma latense*, *P. occultum*, *Lymnaea nitidula*, 'Tornatellina' *isoclina*), only one of them (*M. naticiformis*) in all collections. Apart from the viviparid *C. macrospira* all gastropods are small to tiny (most of them not exceeding 1 cm in height). In contrast, the two species of unionids, *Protelliptio vetustus* and *Loxopleurus belliplicatus*, are large, measuring between 4 and 6 cm in height. They are more abundant than in other freshwater associations accounting for 4.8% (*P. vetustus*) and 1.1% (*L. belliplicatus*) in terms of relative abundance. The number of species varies from three to six; the mean number of species is 4.2.

Of the unionids, 50% are articulated. Percentage of fragmented shells ranges from 10 to 95, and in most samples is between 20 and 50. The association occurs in a range of sediments; in silty clays, silt, and, above all, in silty marls and limestones. Two samples are highly carbonaceous containing either coal fragments or plant debris. The percentage of brackish-water faunas in the total fauna ranges from 0 to 82, with a mean value of 15.3.

The Lioplacodes stachei/Parateinostoma occultum association

Three collections with 477 specimens were grouped in this association. *L. stachei* is the dominant species, followed by the pleuroceratid gastropod *Pachychiloides macilentus*. Two amnicolid gastropods, *Parateinostoma occultum* and *P. latense*, are also present in each sample, albeit in lower numbers. Three more gastropods (*Valvata praecursoris*, *M. naticiformis*, and *Pachychiloides cleburni*) are rare, as is the unionid *Protelliptio vetustus*. The number of species varies from five to six (mean 5.3). Fragmentation of shells ranges from 10 to 90%. Two collections are from argillaceous silt, the third from carbonaceous marly siltstone. The percentage of brackish-water elements in the total fauna ranges from 1.5 to 10.1 (mean 9.6%).

The L. stachei/Pachychiloides macilentus association

This is the commonest association in the freshwater regime, represented by 2607 specimens in fourteen collections. *L. stachei* is the dominant element followed by *M. naticiformis* and *P. macilentus*. Only *L. stachei* and *P. macilentus* occur in all samples. Eight gastropods occur rarely or sporadically only (Table 3), among them the relatively large *Viviparus couesi* and *C. macrospira*. Both unionid species are present with *Protelliptio vetustus* (2.5%) being far more common than *Loxopleurus belliplicatus* (0.6%). The number of species varies from four to nine with a mean of 6.1. 60.7% of the unionids are still articulated. Between 10 and 90% of the shells are fragmented (in most samples, however, not more than 20 to 50%). The fauna occurs in marly silts or calcareous siltstones. Over half the beds are carbonaceous with either abundant plant debris or coal fragments. In one case rootlets occur. The percentage of brackish elements of the total fauna of individual samples ranges from 0 to 85, with a mean of 15.6.

The M. naticiformis/Lioplacodes stachei association

In eight collections with 1016 specimens the neritid gastropod *M. naticiformis* dominates in terms of relative abundance followed by *Lioplacodes stachei* and *Pachychiloides macilentus*. The three species occur in all collections while six other gastropods (*P. chrysalis*, *P. cleburni*, *Parateinostoma occultum*, *Lymnaea nitidula*, *C. macrospira*, and *V. couesi*) and the two unionids are rare and occur only in one to three samples. The number of species varies from four to eight (mean 5.1). Only 25% of the unionids are articulated. The percentage of fragmentation ranges from 20 to 90 and most commonly is around 75%. In most samples the sediment is argillaceous silt, less commonly marly or calcareous siltstone. Nearly half the samples are carbonaceous containing plant debris or coal fragments. The percentage of brackish-water elements in individual samples is relatively high, ranging from 1.3 to 74%, with a mean of 38.9%.

The Pachychiloides chrysalis association

The *P. chrysalis* association differs drastically in species composition from the other associations. Found in four samples and represented by 692 specimens; it is dominated by the pleuroceratid gastropods *P. chrysalis*, *P. cleburni*, *P. macilentus*, and the neritid *M. naticiformis*. These four species occur in all samples, while the rare *Lioplacodes stachei* and *P. chrysalloideus* are found in only one or two collections. The number of species ranges from four to six (mean 4.8). Unionids are absent from this association. Fragmentation varies from 30 to 90%. The sediments are carbonaceous, non-calcareous, and range from argillaceous silt to silt and fine sandy siliceous siltstone. Two of the samples are bioturbated. The burrows consist of branching tubes, 1 mm in diameter, which are filled with dark, clayey silt. They resemble *Chondrites*, but their branching pattern is more irregular. The percentage of brackish forms within individual samples ranges from 6.9 to 24.7 (mean 16.9).

The Valvata praecursoris and corbulid sp. A assemblages

Found only in one sample, it is not known whether these assemblages represent recurrent associations. Occurring in low density in dark-grey shaley silty clay together with thin streaks of comminuted shell debris, the freshwater assemblage appears to be autochthonous. It consists of six species of small gastropods, with the tiny *V. praecursoris* most abundant (58.5%), followed by the amnicolid *Parateinostoma* cf. *altipsirale* (15.4%), the pleuroceratids *Pachytiloides chrysalis* (10.8%), and *P. chrysalloideus* (9.2%). *M. naticiformis* and *Parateinostoma occultum* account for the remaining 6.1%. Fish scales are found occasionally in the sediment that also contains a brackish-water assemblage (33% of the total fauna) that is dominated by the small corbulid bivalve sp. A (31.2%), followed by *Veloritina durkeei* (28.1%), *Brachidontes multilinigera* (25%), and *Ursirivus pyriformis* (15.6%). The two corbulid species are small, *Veloritina* and *Brachidontes* tiny.

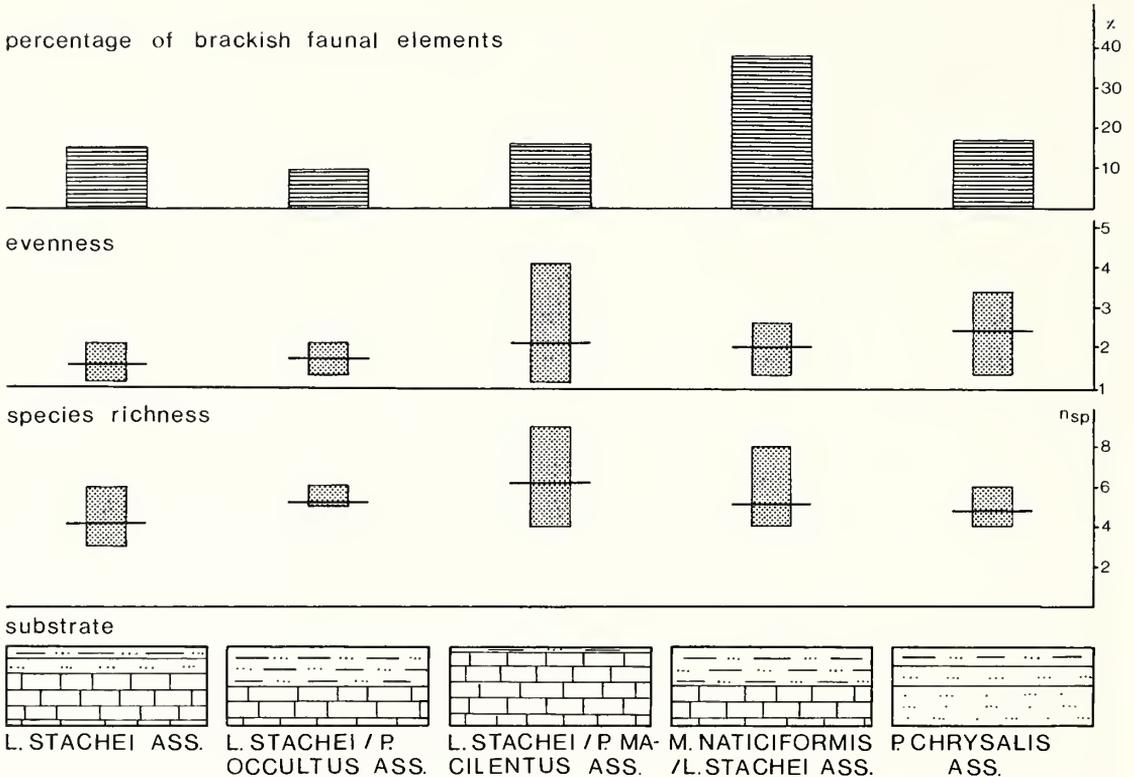
Discussion

Autochthonous nature of the freshwater associations. Few biostratigraphic data are available to indicate transport or the lack of it in the freshwater fauna. In most samples, unionid bivalves are predominantly articulated and in two cases they have been found in life position. Although transport of recently dead articulated unionids downstream into a nearshore area might appear plausible, it is unlikely considering the large and thick shells of both species (see also White 1895). The thin-shelled gastropods similarly underwent only little lateral transport, if any. The fragile shells would break very easily and the percentage of shell fragments would be much higher than it is. In most gastropods the aperture is damaged, but that can be explained by *in situ* reworking. Furthermore, the autecology of several species (see below) indicates that the fauna lived in the embayment and was not transported downstream from rivers. Finally, the pronounced relationship of some freshwater associations to silty limestones cannot be explained by transport. The freshwater fauna is therefore regarded as autochthonous or, at the most, parautochthonous.

Autecology. The unionids *Loxopleurus belliplicatus* and *Protelliptio* (*Plesielliptio*) *vetustus* exhibit features such as curved ventral margins and a well-expanded posterior which are more typical of species living in large lakes than in swiftly flowing rivers (e.g. van der Schalie 1938; Eager 1948; Tevesz and Carter 1980). Little is known about the life habits of Recent unionids and even less about fossil forms. It is, however, likely that both species lived partially buried in the sediment. Similarly, ecological studies of fossil freshwater gastropods are scant and little information is available. Most likely, all freshwater gastropods of the Bear River section were herbivorous, feeding either on live algae or on plant detritus. Recent members of the families represented by Bear River species vary considerably in their salinity requirements. For example, most members of the family Neritidae inhabit marine to brackish habitats at present day, but the genus *Neritina* tends to invade freshwater. A very transitional position is also assumed for the Cretaceous *M. naticiformis* as it occurs in large numbers where the percentage of brackish-water faunal elements is relatively high. This species is considered to have been able to live not only in freshwater, but also in oligohaline waters. Recent amnicolid gastropods also invade brackish water. How far this was true of the Cretaceous *Parateinostoma* is unknown. Recent members of the family Valvatidae and Viviparidae, although able to live in waters with a salinity of 2–3 permille (e.g. Ankel 1936) are typical representatives of freshwater environments and it appears safe to assume a similar habitat for Cretaceous species. In viviparids, the mantle cavity shows many features which may be associated with a muddy habitat (Fretter and Graham 1962, p. 594). This also fits the habitat preference of the Cretaceous *Viviparus couesi*. *Lymnaea nitidula* belongs to the freshwater pulmonate family Lymnaeidae and is the only representative of this group at the Bear River section.

In analysing similar faunas from the Cretaceous of Lincoln County, Wyoming, Yen (1951) concluded that they lived in relatively shallow, low-energy environments with an abundant aquatic vegetation. A freshwater assemblage from the Bear River Formation at Fossil Cut, south-east of Evanston (Wyoming), was interpreted by him (Yen 1954) as having lived in the lower part of the littoral zone (7–10 m deep), in a more or less closed and quiet bay with rich vegetation.

Analysis of the associations. Four of the five associations are closely related, with *Lioplacodes stachei* being present in moderate to high numbers in all samples. However, as in the case of



TEXT-FIG. 12. Evenness, species richness, and substrate relationships of the five freshwater associations. For key of substrate see text-fig. 2.

Ursirivus-dominated brackish associations, the relative abundance of species is thought to reflect subtle differences in the environment. Text-fig. 12 shows some ecological features of the five associations such as species richness, evenness values, and substrate relationships. All associations exhibit low species richness and evenness values suggesting that the faunas did not live under optimal conditions. However, they cannot be arranged along an environmental gradient as in the case of the brackish-water faunas. Faunal composition and diversity were probably influenced by several factors, not necessarily related. Substrate conditions appear to have influenced faunal distribution to some degree. Thus, the *Pachychiloides chrysalis* association occurs in coarser sediments than the others and the substrate was never calcareous. This biotope may have been close to river mouths and a slightly higher energy level than in the other associations probably prevailed. In contrast, the *Lioplacodes stachei*/*P. macilentus* association occurs nearly exclusively in calcareous siltstones or silty marlstones.

Another factor governing faunal distribution was *salinity*. According to Remane and Schlieper (1971) some freshwater species are able to tolerate waters of the oligohaline or even lower mesohaline regime. Segerstråle (1957, p. 779) records a number of freshwater gastropods from the Baltic Sea which live in oligo- or even low mesohaline coastal waters. Many of them are greatly reduced in size. Even some unionid bivalves tolerate salinities up to 3‰ in parts of the Baltic Sea (Segerstråle 1957; see also Remane 1958 for summary of the salinity tolerances of freshwater organisms). It is therefore

likely that several freshwater gastropods from the Bear River Formation could tolerate at least short-term small-scale salinity fluctuations. This may have been particularly true of *M. naticiformis* (see above). Consequently, the *M. naticiformis*/*L. stachei* association is thought to have lived closest to the brackish-water edge and was able to survive short-term incursions of oligohaline waters. This implies that there might have been a spatial and temporal overlap of members of this association with members of the oligohaline *Pyrgulifera humerosa* subset. The position of the *M. naticiformis*/*L. stachei* association close to the freshwater/brackish-water interface is supported by the relatively high percentage of brackish-water faunal elements in the total fauna as compared to that of other associations.

The *L. stachei* association appears to have lived furthest away from the freshwater/brackish-water interface: in three out of six samples no brackish faunas occur, in two more the brackish fauna accounts for less than 10%, and only in one sample is the brackish fauna very abundant (81.5%).

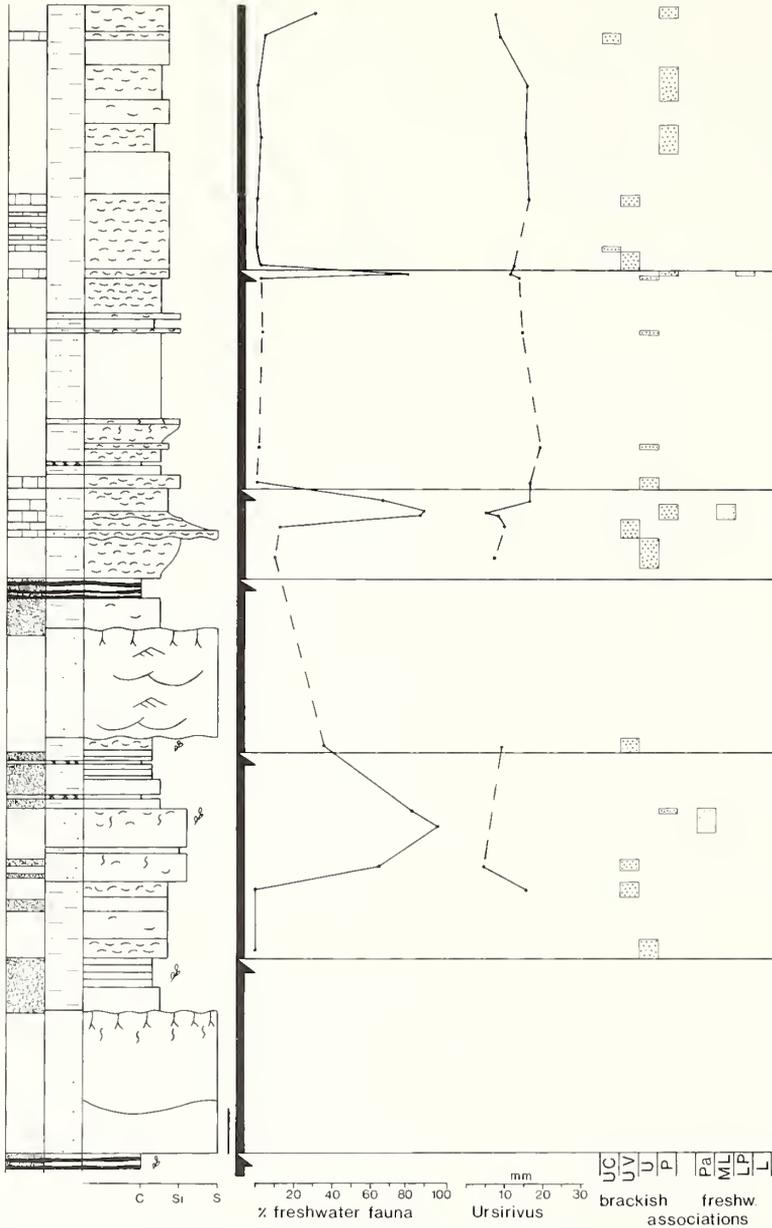
Other factors not readily recognized from the substrate must have exerted a strong influence on the freshwater fauna. Most likely they were water chemistry (e.g. concentration of Ca-ions), temperature and oxygen level. High temperature fluctuations combined with periods of poor oxygenation are very common in large, very shallow-water bodies, restricting the fauna to eurytopic species. That it was a high stress environment can also be demonstrated by the size of several faunal elements. At Shell Hollow, a locality of the Bear River Formation several miles north-west of Evanston (Wyoming), the gastropods *L. stachei*, *Pachychiloides chrysalis*, *P. chrysalloideus*, and *P. macilentus* were about 20 to 25% larger than at the Bear River locality (Shell Hollow data from unsorted collections in the Henderson Museum of the University of Colorado at Boulder). This implies that at least these species (data on other freshwater gastropods were not available) did not grow to their maximum size at the latter locality. Low oxygen conditions were most likely responsible for the small to minute size of all specimens in the *Valvata praecursoris* and corbulid sp. A. assemblages, which occur in a dark-grey laminated silty clay.

Summary of depositional environment. The freshwater faunas lived in a large shallow body of freshwater that was in direct contact with brackish water. Most associations lived in low-energy environments on soft substrate that was richly vegetated. The close association of coal-seams and freshwater faunas indicate that water depth was extremely shallow. Only one association appears to have preferred a somewhat higher energy level and coarser substrate, probably close to the rivers emptying into the embayment. The embayment was subject to fluctuations in temperature and oxygen levels that restricted the fauna to eurytopic species.

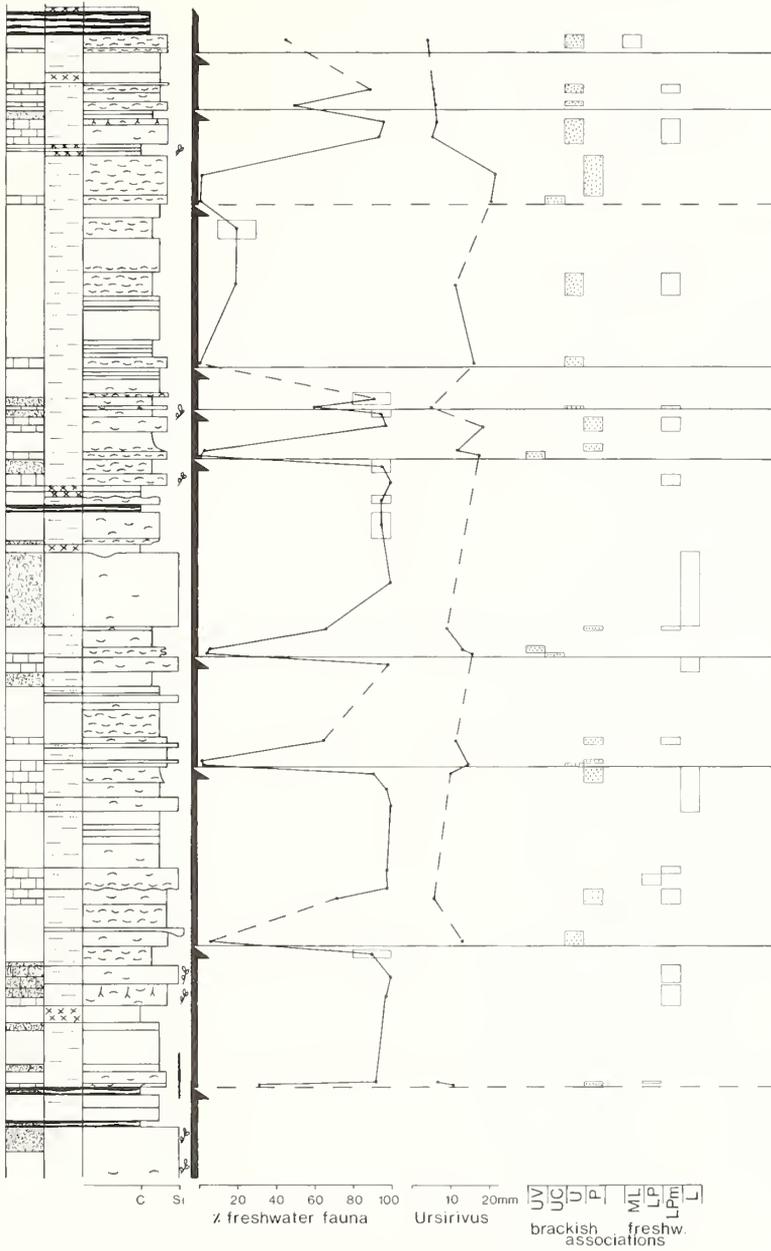
ANALYSIS OF CYCLES

In the Bear River section both sediment and benthic faunas occur in cycles. The base of each cycle is defined by shell beds dominated by brackish-water fauna, the top by coals, highly carbonaceous sediments and/or calcareous beds dominated by freshwater faunas. The boundaries between cycles are marked by the drastic change in the proportion of fresh- to brackish-water faunal elements. Text-figs. 13-15 show the lithological change, the variation in the proportion of fresh- to brackish-water species, the variation in mean size of the dominant brackish-water species (*Ursirivus*) and the distribution of fresh and brackish-water associations throughout the Bear River section. Although quantitative data are not available for each bed, the pattern is quite clear and can be interpreted as a series of regressive sequences each followed by relatively rapid transgressive pulses. In most cases, the transgressive phase did not leave any sedimentary or faunal record, but occasionally the change from freshwater-dominated faunas at the top of a cycle to brackish-water-dominated faunas at the base of the next cycle is represented by intermediate stages: part of the transgressive phase. The amplitude of the cycles may vary. Beds with exclusively brackish-water faunas may grade into beds with only freshwater elements at the top of each cycle. Alternatively, beds at the base may already exhibit a strong freshwater influence and beds at the top may still have a high percentage of brackish-water elements. Even where no faunas are preserved, the regressive nature of the cycles can be demonstrated easily: thus, at the base of text-fig. 13, carbonaceous sediments intercalated with thin seams of coal are overlain by a fine-grained channel sandstone which is bioturbated and rooted at the top and overlain by silty clays that grade into highly carbonaceous shales. This sequence can be interpreted as fluvial channel sands giving way to overbank deposits and finally swamps. Strong

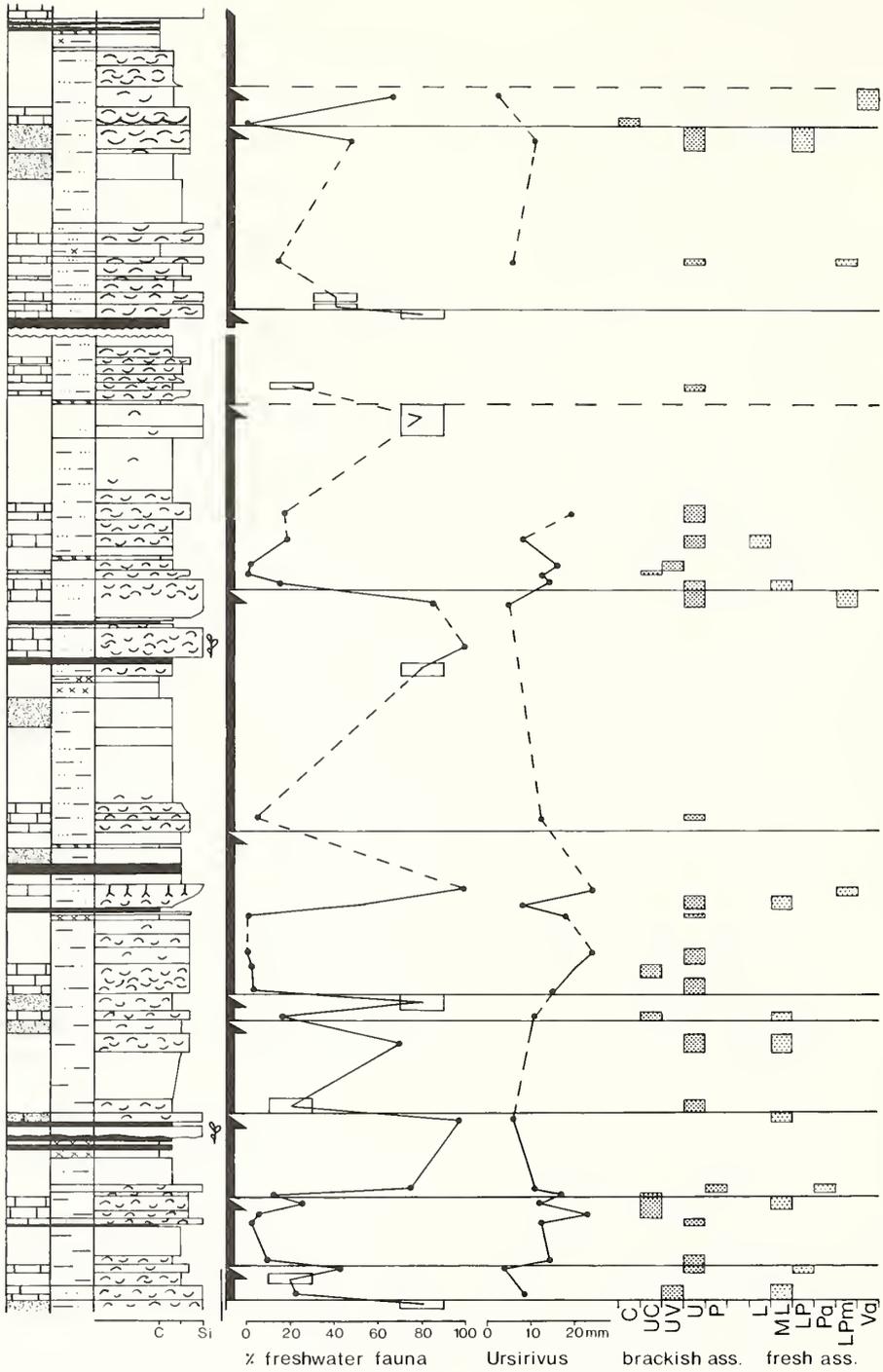
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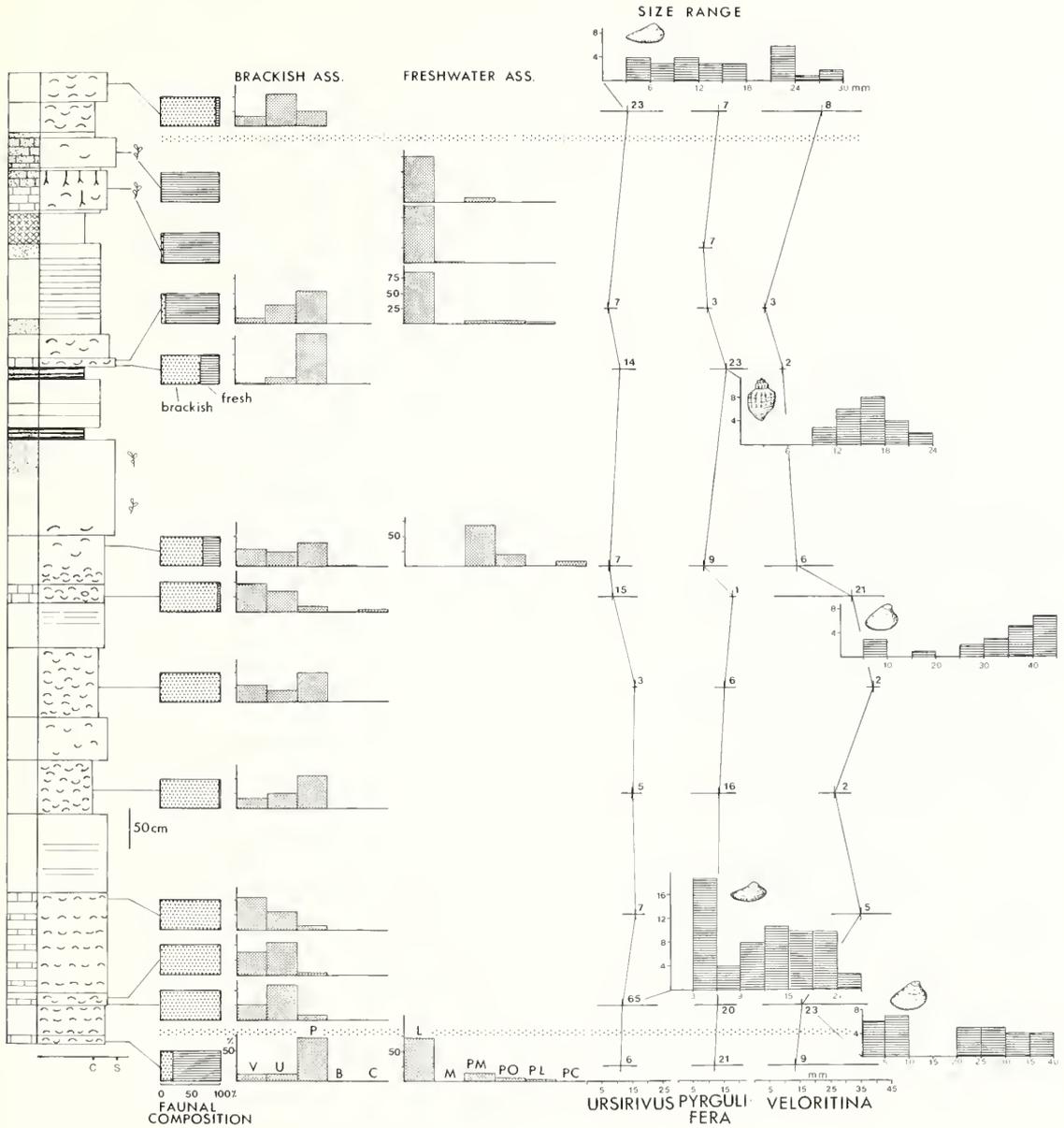
TEXT-FIG. 13. Sedimentological and palaeoecological data (percentage of freshwater faunal elements, mean size of *Ursirivus pyriformis*, and distribution of benthic associations) of the Reference Section of the Bear River Formation. For key to symbols see text-fig. 2. C—clay; Si—silt; S—fine-sand; C—*Crassostrea soleniscus* association; UC—*Ursirivus pyriformis*/*C. soleniscus* subset; UV—*U. pyriformis*/*Veloritina durkeei* subset; UP—*U. pyriformis*/*Pyrgulifera humerosa* subset; P—*P. humerosa* subset; Pa—*Pachytiloides chrysalis* association; ML—*Mesoneritina naticiformis*/*Lioplacodes stachei* association; LP—*L. stachei*/*Parateinostoma occultum* association; L—*L. stachei* association; LPm—*L. stachei*/*Pachytiloides macilentus* association; Va—*Valvata praecursoris* assemblage. Empty rectangles are semi-quantitative field estimations of the percentage of freshwater elements.



TEXT-FIG. 14. Continuation of section of text-fig. 13.



TEXT-FIG. 15. Upper part of marginal marine section at the Bear River Reference Locality. For key to symbols see text-fig. 2. Note disruption of section near top due to faulting.

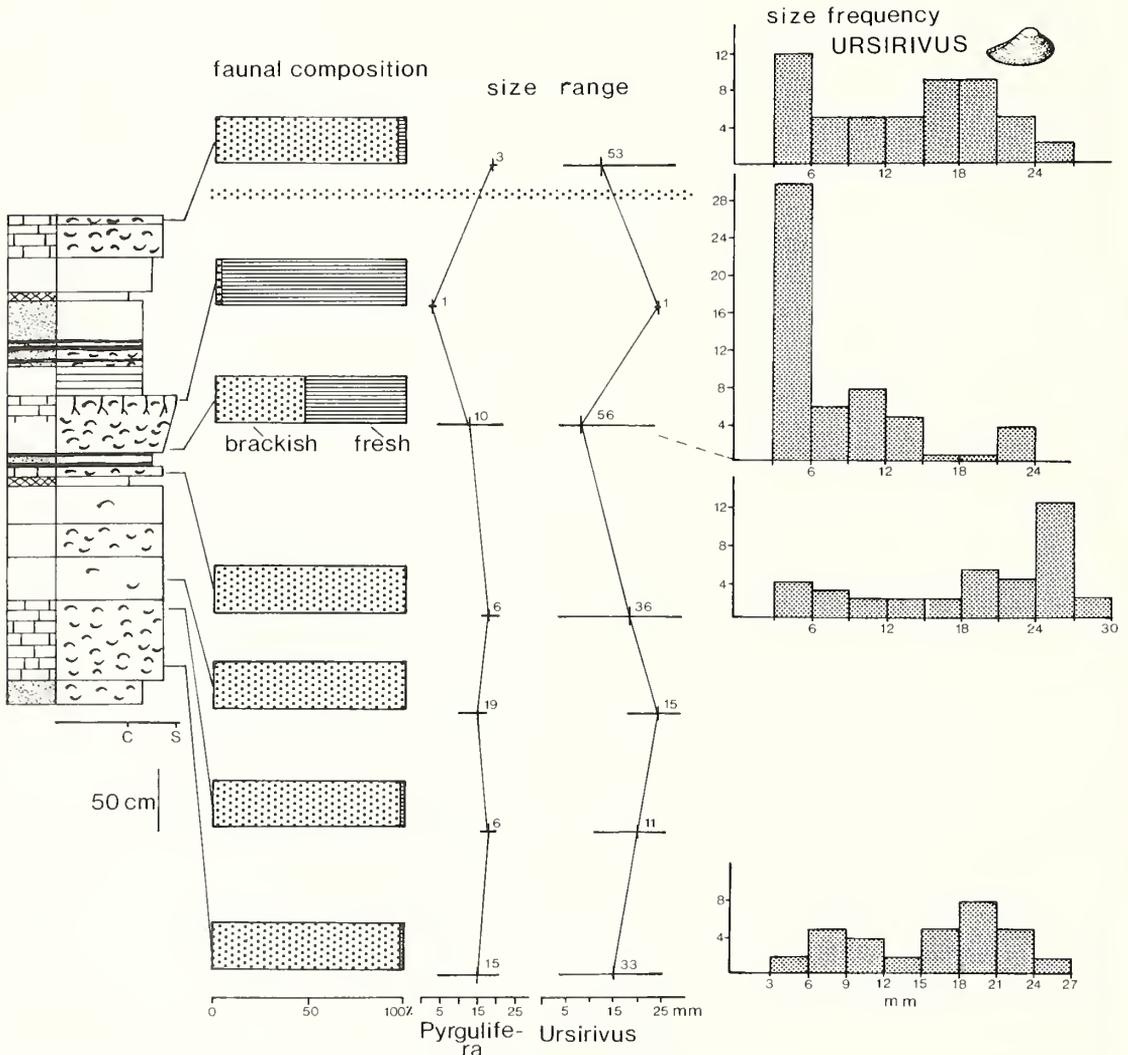


TEXT-FIG. 16. Detail of one regressive cycle. Both top of preceding and base of succeeding cycle have been included for comparison. Note increase in percentage of freshwater elements, changes in faunal composition, changes in the mean size of dominant brackish-water species, and size/frequency histograms towards the top of the cycle. For key to symbols see text-fig. 2. c—clay; s—silt; V—*Veloritina durkeei*; U—*Ursirivus pyriformis*; P—*Pyrgulifera humerosa*; B—*Brachidontes multiligera*; C—*Crassostrea soleniscus*; L—*Lioplacodes stachei*; M—*Mesoneritina naticiformis*; PM—*Pachytiloides macilentus*; PO—*Parateinostoma occultum*; PL—*P. latense*; PC—*P. cleburni*.

fluvial influence can only be recognized near the base of the measured section, while most other cycles record regression within a shallow embayment.

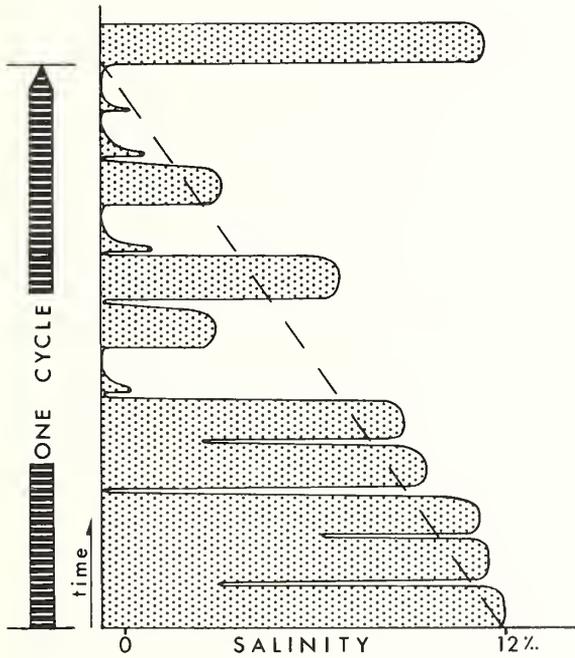
The distribution of the brackish-water associations follows the cyclic pattern, although with several exemptions. The oligohaline *Pyrgulifera lumerosa* subset is more commonly found near the top of cycles than at their base (text-figs. 13-15). Similarly, the mid-mesohaline *U. pyriformis*/*C. soleniscus* and *U. pyriformis*/*Veloritina durkei* subsets are more often found near the base. The freshwater associations show a fairly random distribution pattern except for the *L. stachei* association that usually occurs toward the top of the cycles.

In thirteen cases the mean size of *U. pyriformis* is larger near the base of the cycles than towards the top; in four cases it is not. Thus there is a general size decrease of *Ursirivus* within a cycle, notwithstanding a significant variability. This is true also of *Veloritina* and, although less pronouncedly, of *Pyrgulifera* (text-fig. 16). The picture may be distorted by preferential destruction of smaller valves.



TEXT-FIG. 17. Detail of one regressive cycle including base of the next cycle. Note increase in percentage of freshwater faunal elements, changes in the mean size of *Pyrgulifera* and *Ursirivus*, and dominance of juvenile individuals of *Ursirivus* near top of the cycle. For key to symbols see text-fig. 2.

The lack of an anticipated neat correlation between changes in size and benthic associations and the regressive cycles can be explained by the overprint of seasonal fluctuations on the cyclic pattern. The resulting pattern is therefore one of interference of two cycles of different magnitudes. In text-fig. 17 the size/frequency distribution of *Ursirivus* within one cycle is plotted as are mean size of *Pyrgulifera* and *Ursirivus*. As expected a strong peak of juveniles indicative of mass mortality during freshwater interludes shows up when the percentage of fresh-water faunas among the total fauna increases. However, there are also several examples of high juvenile mortality among the brackish-water species near the base of cycles where the percentage of freshwater faunas is low. In these cases the freshwater phase killed the brackish fauna, but did not last long enough for the establishment of a freshwater fauna. Similarly, presence of adult *Ursirivus* in time-averaged brackish-water populations of beds dominated by freshwater elements can be explained by occasional less severe salinity reductions which enabled the brackish fauna to survive for more than one season.



TEXT-FIG. 18. Model illustrating the overprint of seasonal cycles on the salinity reduction within one regressive cycle. Note that in reality thousands of seasonal cycles may be involved instead of the twelve shown here.

Text-fig. 18 presents a model of the salinity changes within cycles combining seasonal fluctuations with a general reduction in salinity. Both parameters can be reconstructed by using size/frequency data, proportion of fresh- and brackish-water faunas in one bed, and the nature of the brackish associations.

The cycles in text-figs. 13–15 vary in thickness, but also according to the dominant salinity regime. Groups of cycles in which brackish conditions dominate for most of each cycle followed by a short period of dominantly freshwater conditions alternate with groups where the brackish-water dominated phase is short and fresh-water conditions prevail for most of the time. The groups are composed of two to four cycles. Unfortunately for several cycles the data are insufficient to allow a more precise description of this feature. It seems, however, that yet another order of cyclicity is recorded by the fauna, but not by any features of the sediment.

INTERPRETATION OF CYCLES

Cyclicity recorded in the sedimentary or fossil record is either caused by climatic factors, by movements of the earth's crust in the broadest sense (be it by spreading of mid-oceanic ridges or small-scale tectonic movements), or by factors connected with mechanisms of sediment transport and deposition within basins (e.g. articles in Merriam 1964, Duff *et al.* 1967, Einsele and Seilacher 1982).

There can be little doubt that the seasonal cyclicality found in the Bear River section, expressed by the size/frequency curves of brackish-water organisms, is of climatic origin and records the alternation of dry and wet seasons similar to monsoon seasons in today's tropical and subtropical belts. This is in agreement with Tingey (1978) who, based on palynological data, postulated a subtropical to warm temperate climate for south-western Wyoming during the middle and late Albian.

The origin of the secondary cycles can be less easily assessed. What is recorded is the gradual infilling and freshening of a large embayment. The tectonic hypothesis would require rhythmic pulses of subsidence that would lead to a rapid transgression across the embayment and subsequent gradual infilling with sediment. Another variation of the tectonic model assumes increased uplift of the hinterland (ancestral Rockies) which would result in increased supply of sediment to deltas. Reworking of sediments by longshore currents would then lead to increased formation of barrier bar systems which could restrict marine influence in the embayment and finally seal it off completely. However, there are no signs of extensive barrier systems along the shorelines of the Skull Creek Seaway which apparently was bordered by very low-energy shore-lines. Moreover, the regressive cycles in the embayment are not coarsening-upward cycles, though an increase in the rate of sedimentation toward the top of the cycles is indicated in many cases by the decrease in the thickness and abundance of shell beds and by the lower density of shells within them.

Assuming a climatic origin of the cycles, with an increase of rainfall, there should be increased run off and consequently increased erosion and sediment supply to coastal waters. The same process of increased formation of barrier bars could then operate as in the tectonic model. As mentioned before, however, the existence of extensive barrier sands is unlikely. Increased rainfall could have resulted in a more extensive sheet of freshwater across the embayment and caused a long-term shift of the freshwater/brackish-water interface towards the open sea.

The third possibility is that the regressive pattern is autocyclic, caused by the switching of major distributaries within a deltaic system. This would cause sediment influx into the embayment to cease and, assuming subsidence to continue, would result in rapid transgression. From the available evidence it is impossible to decide which model is correct. An autocyclic explanation for the regressive sequences is, however, the simplest model and is therefore favoured.

The cause of the primary cyclicality, which is characterized by the relative duration of fresh- to brackish-water conditions within secondary cycles, is even more open to speculation. It may have been the result of climatic or tectonic factors, possibly expressed by slight eustatic fluctuations in sea-level. In this case, an allocyclic mechanism is more likely.

Text-fig. 19 presents a summary of the three orders of cycles. Whilst the tertiary cycles represent fluctuations on the scale of 10^0 years, the secondary cycles probably are in the range of 10^3 to 10^4 years, and the primary cycles possibly present periods of 10^4 to 10^5 years. Unfortunately, biostratigraphic and chronostratigraphic control on the Bear River section is not available. The time ranges for the three orders of cycles must therefore be regarded as very tentative. To what extent the primary cyclicality, should it prove to be of climatic origin, can be related to cycles of the earth's orbit (Milankovich 1930) remains unknown.

CONCLUSIONS

1. Part of the Bear River Formation represents an extensive embayment in which fine-grained sediments ranging from silty clays to silts and silty limestones accumulated in a predominantly low-energy environment. Within this sequence, numerous shell beds with a highly abundant but low diversity fresh- and brackish-water fauna of bivalves and gastropods occur.

2. Biostratigraphic data favour local reworking by storms rather than lateral transport by currents as the origin of the shell beds. Mixing of fresh- and brackish-water faunas in the same bed was caused by rapidly shifting environments and not by mixing of faunas from neighbouring habitats.

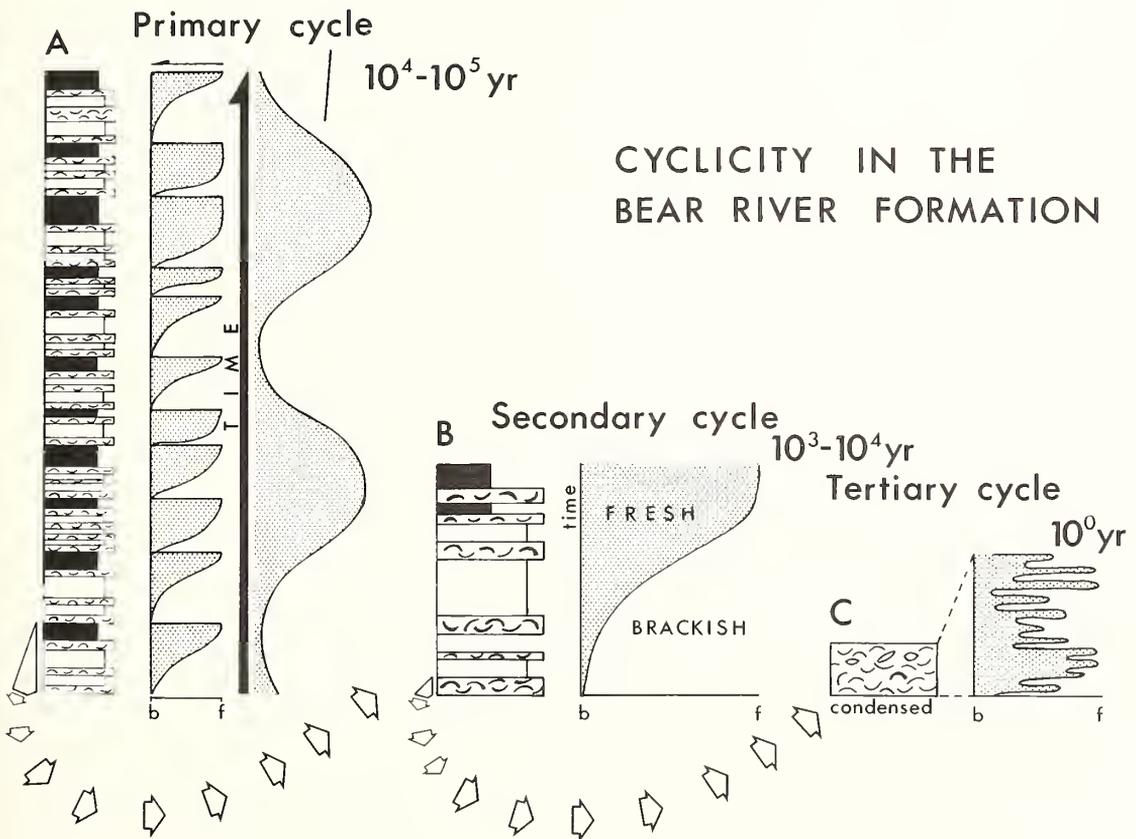
3. Sedimentological and palaeosynecological analyses demonstrate the presence of cycles that start with shell beds of predominantly brackish origin and end with thin seams of coal or beds of silty limestone dominated by freshwater faunal elements.

4. Two benthic associations, one of them with four subsets, are recognized in the brackish-water fauna. They can be arranged along a salinity gradient ranging from mid-mesohaline (about 12‰) to the freshwater edge. Along this gradient, species evenness and richness drops and most faunal elements decrease in size.

Five associations are recognized in the freshwater fauna. They are dominated by small gastropods, exhibit some substrate control, and, at least in one case, were probably able to invade oligohaline waters.

5. Size/frequency distribution patterns of the brackish bivalves *Ursirivus*, *Veloritina*, and the gastropod *Pyrgulifera* point to strong seasonal salinity fluctuations which, in many cases, caused a high juvenile mortality.

6. Altogether, three orders of cycles are recognized in the Bear River section of probably the following magnitudes: (a) 10^0 years (seasonal), recorded by size/frequency curves within shell beds; (b) 10^3-10^4 years, expressed by regressive sedimentary sequences and a consistent change from brackish to freshwater-dominated biota; and (c) 10^4-10^5 years, expressed by the dominance of fresh or brackish conditions within bundles of regressive sequences. Whilst the tertiary (seasonal) cyclicality is of climatic origin, the nature of the secondary cycles is probably autocyclic. The origin of the primary cyclicality remains unclear.



TEXT-FIG. 19. The three orders of cycles in the Bear River Formation at the Bear River Reference Locality. The terms primary, secondary, and tertiary cycles are used in order to avoid confusion with first, second, and third order cycles of Vail *et al.* (1977). *b*—brackish; *f*—freshwater.

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SCLEROCHRONOLOGY AND CARBONATE PRODUCTION IN SOME UPPER JURASSIC REEF CORALS

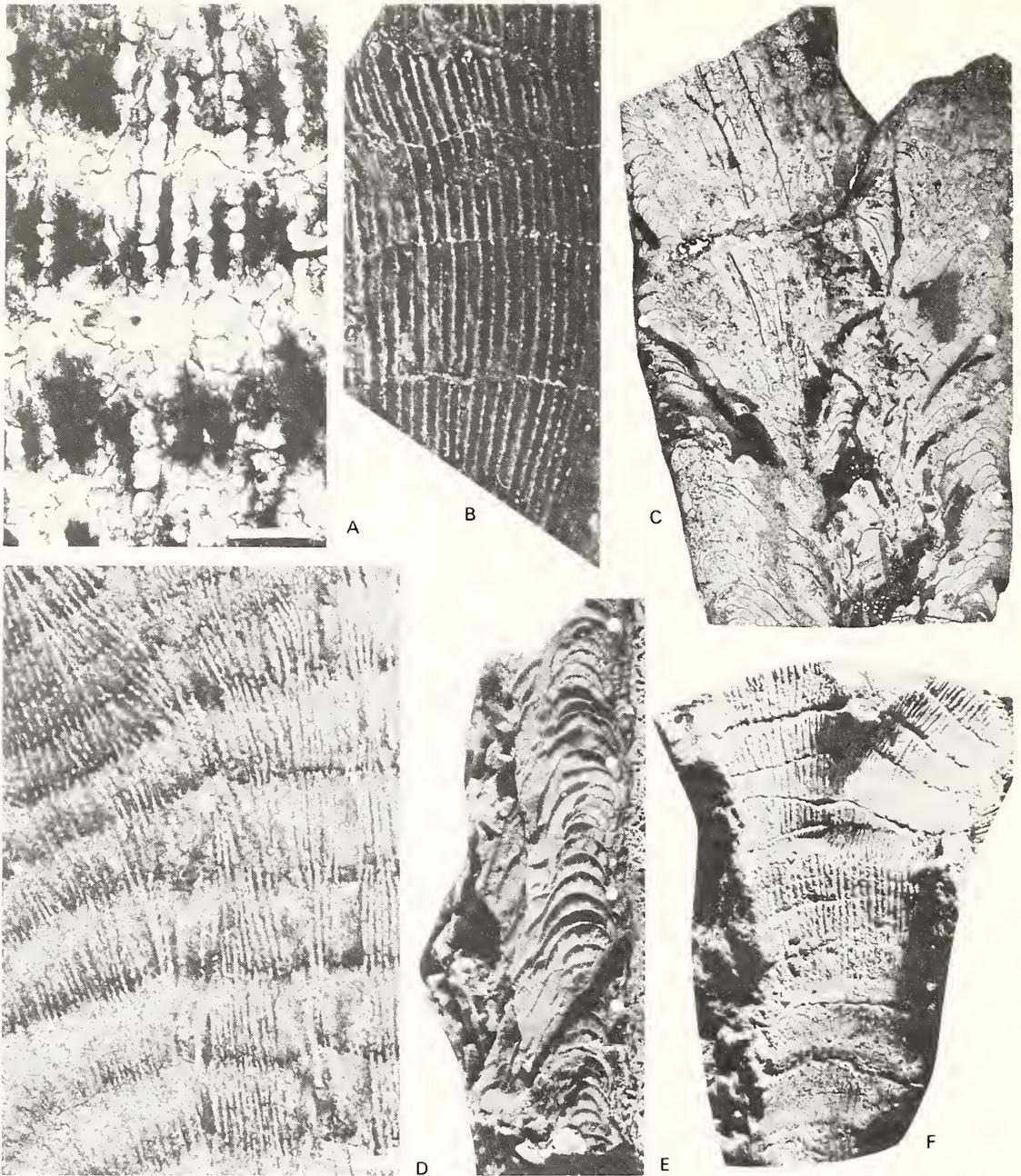
by OMER E. ALI

ABSTRACT. Annual banding evident from epithecal increments and associated internal structural changes in phaceloid and massive Oxfordian corals show a range in growth rate from 5 to 10 mm yr⁻¹ in branching colonies (*Thecosmilia*) and 1.5 to 3 mm yr⁻¹ for massive colonies (*Thamasteria*, *Fungiastraea*, *Isastraea*). High- and low-density growth bands are identified in massive colonies. The denser part of each couplet is consistently the broader, in contrast with that of most shallow-water modern corals. This is interpreted as due to high local turbidity. The formation time for two sections is estimated with gross carbonate production of 2000 to 3300 g CaCO₃ m² yr⁻¹.

GROWTH bands in organisms are of great interest to biologists and palaeontologists because, where their periodicity can be determined, a means is provided to estimate growth rate and age. Although growth bands have been studied in several groups of marine invertebrates most interest has been shown in scleractinian reef-building corals because of the extensive distribution of modern corals and ancient coralliferous sediments. Hudson *et al.* (1976) have coined the term sclerochronology to describe coral growth band studies, in comparison with the well-known term dendrochronology (e.g. Jefferson 1982). Research has been mainly concerned with the nature of the growth banding, its ecological significance and applications in the biological (Buddemeier and Kinzie 1976) and geophysical sciences (Rosenberg and Runcorn 1975; Scrutton 1978).

No growth studies have hitherto been made of Mesozoic corals but several British upper Jurassic corals display banding on well-preserved epithecae or in longitudinal section. The purpose of the present study is to examine the nature and periodicity of growth bands in the common branching and massive corals from the Oxfordian of England, and to assess their environmental implications, the time represented by particular coralliferous units, and the rate of carbonate production. Less-common genera such as *Rhabdophyllia* and *Montlivaltia*, which are seldom well preserved, and several genera recorded only from Steeple Ashton (Negus and Beauvais 1979) are not considered in any detail. Other invertebrates associated with coralliferous units, such as oysters, species of *Chlamys*, *Lithophaga*, and the alga *Solenopora* also show growth bands suggestive of annual periodicity but details are not included here.

Although there are many papers concerned with special aspects of the Oxfordian rocks of England, Arkell (1933, 1947) provides accounts of the distribution and stratigraphy of the outcrops and Cope *et al.* (1980) provides correlations. Material on which this paper is based was collected in the course of an investigation of coralliferous units in the Corallian (Oxfordian) of England (Ali, unpublished Ph.D. thesis, University of Reading, 1978) from the following: Shellingford Cross-Roads Quarry (SU 327941) (Arkell 1947, p. 87), Kingsdown Farm (temporary section) (SU 175885), Cumnor Hill by-pass (temporary section) (SP 465040) (see Arkell 1947, p. 89), Headington Cross-Roads Quarry (SP 550064) (Arkell 1947, p. 94), Steeple Ashton (ST 9057) (Negus and Beauvais, 1979); Yorkshire (Wright 1972), Ayton Quarry (TA 002856), Crossgate Quarry, Seamer (TA 028843), Pockley Quarry (SE 635846), Nunnington railway cutting (SE 649787), Stonegrave Quarry (SE 648787).



TEXT-FIG. 1. *Fungiastrea arachnoides*. A, photomicrograph of unstained thin-section with neomorphic preservation, showing banding and a few more complete upward-tapering septa, $\times 25$. D, positive print from stained longitudinal thin-section showing dark zones with thick septa and light zones with poor preservation of skeletal elements, $\times 6$. Shellingford Cross-Roads Quarry (Reading University 14876a, b). B, C, E, F. *Thecosmilia annularis*. B, latex peel from external mould of partly decorticated specimen, $\times 2$. C, longitudinal section with tabular dissepiments marked (for comparison with text-fig. 3B), $\times 1.5$. Shellingford Cross-Roads Quarry (RU 14879). E, periodic development of tabular (marked) and vesicular dissepiments, $\times 2$. Cumnor By-pass. F, external mould of partly decorticated specimen showing major concentric markings associated with abrupt thickening of septa, $\times 1.2$. Shellingford Cross-Roads Quarry (RU 14877). Bar scales: A, 0.5 mm; D, 1.0 mm.

GROWTH BANDS

MASSIVE CORALS

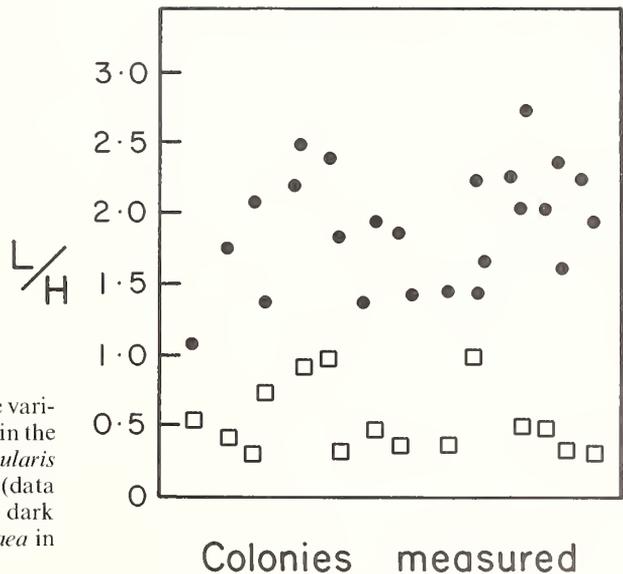
Thamnasteria concinna (Goldfuss), *Fungiastraea arachnoides* (Parkinson), and *Isastraea explanata* (Goldfuss).

The three species of massive corals show distinct banding on longitudinal sections and on differentially weathered material, mostly as an alternation of a broader dark zone with thicker septa and a narrower zone with less distinct and thinner skeletal elements (text-fig. 1A, D).

The two zones are similar to bands recognized in modern scleractinian reef corals by several authors (e.g. Knutson *et al.* 1972) and referred to as high- and low-density bands. Using x-radiographic techniques Knutson *et al.* (1972), Buddemeier (1974), Buddemeier *et al.* (1974), MacIntyre and Smith (1974), Dodge *et al.* (1974), Dodge and Thomson (1974), and Weber *et al.* (1975) showed that a high- and low-density couplet is deposited yearly by many tropical corals.

In the Oxfordian material the couplets have been diagenetically enhanced so that they are visually distinct. Both zones have undergone neomorphic replacement by calcite or ferroan calcite, but the skeletal relics are best preserved in the lower darker zone and relatively uncommon in the lighter zone (text-fig. 1A). Ferroan calcite is mainly in the upper zone. In thin section the change from one zone to another is generally sharp and distinct due to the contrasting degree of recrystallization. The differential recrystallization may be related to primary skeletal thickness and composition and to differences in the original skeletal porosity. An attempt was made to determine whether any variation in non-carbonate (clay) inclusions now occurs between the couplet zones. Selected specimens showing clear banding were analysed for Si, Ca, and Fe using electron probe. The results (in Ali unpublished Ph.D. thesis, University of Reading, 1978) show that there is no clear correlation between the slight variations in these constituents and position of individual bands.

Couplet widths were measured on sectioned specimens and peels where preservation of the skeletal elements was deemed satisfactory. Poor relic preservation often overemphasizes the light zone when it may be questioned which zone is equivalent to the high- and low-density band of modern corals. The light zone was also prone to recrystallization with void stage. Dr. D. Kinsey (Australian Institute of Marine Science, Townsville) suggested to Dr. R. Goldring that the low-density band with its inferred greater amount of organic matter (Highsmith 1979) might fossilize relatively better than the high-density band, but this does not seem to have been the case. No significant variation in width of the high- and low-density bands has been noted between the bottom and top of colonies investigated, although there is an irregular variation through and laterally across a colony. The zones are occasionally of equal width but the ratio of the width of the light zone to that of the dark zone is never greater than 1.0 (text-fig. 2). This contrasts with modern shallow-water reef genera where it is the dense band that is



TEXT-FIG. 2. Graphical representation to illustrate variation in ratio (L/H) of low- to high-density bands in the modern corals *Platygyra* sp. and *Montastrea annularis* from Indo-Pacific and Caribbean localities ● (data from Weber *et al.* 1975) and the ratio of light to dark zones in *Thamnasteria*, *Fungiastraea*, and *Isastraea* in the Oxfordian of England □.

thinner (e.g. Knutson *et al.* 1972; MacIntyre and Smith 1974; Baker and Weber 1975; Weber *et al.* 1975). Weber *et al.* (1975) show that the ratio low density/high density is always greater than 1.0 and up to 2.8. But Highsmith (1979) and Hudson (1981) find ratios of less than 1.0 associated with growth in deeper water.

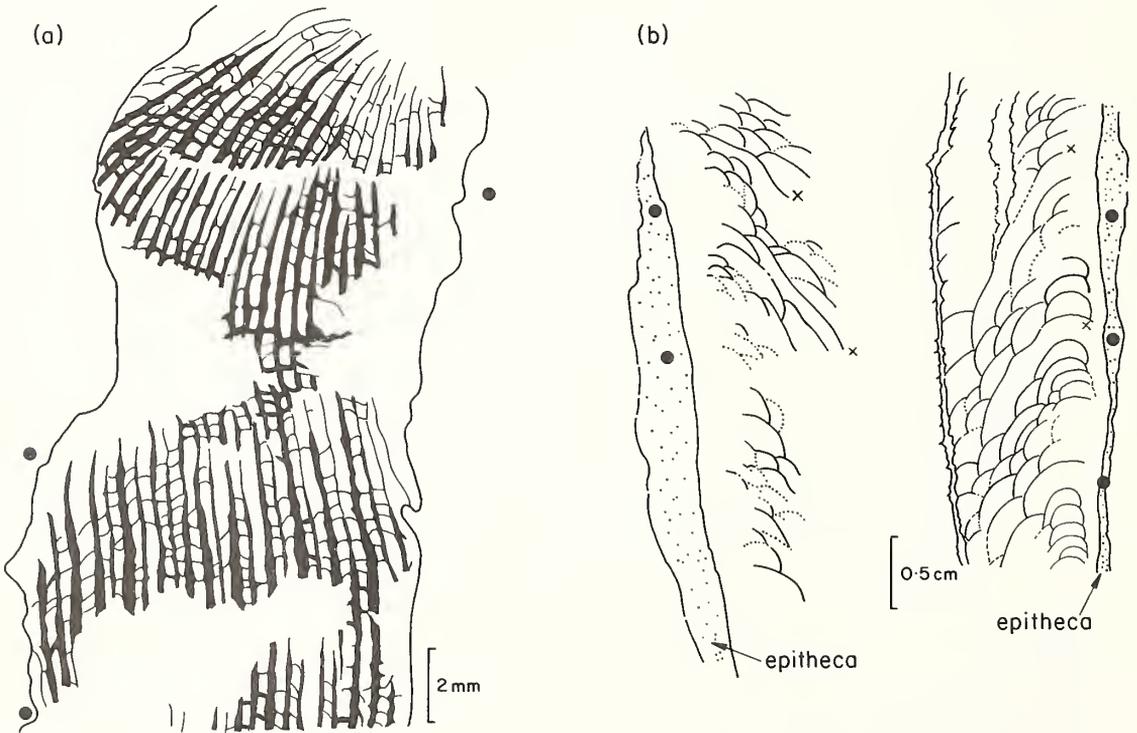
BRANCHING CORAL

Thecosmilia annularis (Fleming).

T. annularis is a common phaceloid coral in most sections. Incremental growth is evident on the epitheca and there are related structural changes to septa and dissepiments.

(a) *Epithecal banding.* Where the epitheca is well preserved, or on good external moulds a regular banding of major concentric markings separated by areas with finer incremental ridges may be seen. Whilst the major growth bands (4 to 6 in 50 mm) are well defined and easy to follow, the fine bands (more than 200 in 10 mm) are generally indistinct and very difficult to trace on the material available. It has not been possible to establish the number of fine bands between major growth bands.

(b) *Structural changes.* The major banding (above) is expressed internally by a sharp thickening of the septa (text-fig. 1B, F) which gradually thin upwards to the next thickening. This is best seen on partly decorticated specimens preserved as external moulds. The arrangement of tabular vesicular dissepiments shows a close relationship to the major growth banding (text-figs. 1C, E, 3). Following formation of a tabular dissepiment, the marginal vesicular dissepiments show a regular change mostly realized by transverse contraction towards the



TEXT-FIG. 3. *Thecosmilia annularis*. a, longitudinal section to show regular thickening and thinning of septa, b, longitudinal sections to show structural changes in dissepiments. ● Position of major epithecal banding, × tabular dissepiments (Reading University, 14878).

margin, abaxially. At the same time successively shorter dissepiments are introduced axially which maintain the general form of the calyx. Nevertheless, the introduction of a tabular dissepiment, which reached to about four-fifths the transverse length of a septum, led to a deepening and increased acuity of the thecal cone. The vesicular dissepiments are frequently thickened and crowded below the periodically introduced tabular dissepiment. This cyclicity or succession of dissepiment arrangement is rarely perfect, but the spacing of the tabular dissepiments corresponds with that of the major growth bands of the epitheca.

No such structural changes have yet been described in modern phaceloid corals but the general changes in thickness of septa and dissepiments are similar to those observed in modern massive corals and the Oxfordian genera. Ma (1934) described similar changes in the vesicular elements of modern and subfossil plocoid *Favia speciosa* though MacIntyre and Smith (1974) commented that dissepiment spacing does not differ between high- and low-density bands of *Pavona gigantea*. It seems reasonable to suppose that the periodic changes in *Thecosmilia* do represent annual changes and that the fine incremental ridges on the epitheca represent daily growth increments.

DISCUSSION

There can now be no doubt that each couplet of growth bands in modern corals represents an annual skeletal increment (Knutson *et al.* 1972; MacIntyre and Smith 1974; Moore and Krishnaswami 1974; Dodge and Thomson 1974; Weber *et al.* 1975). But what is not yet clear, as Scrutton (1978) and Scrutton and Powell (1980) discuss, are the environmental factors that contribute to the formation and seasonal timing of bands of different densities. (There is also as yet no detailed geochemical analysis of the differences between the different density bands and it would be premature to analyse, e.g. O₂ isotope, the banding of fossil corals.) Attempts to determine growth factors have, so far, led to somewhat contradictory conclusions. Some investigators (Dodge and Thomson 1974; Knutson and Buddemeier 1973; Buddemeier *et al.* 1974) suggest that high density is associated with seasonal low water temperature, whereas others (MacIntyre and Smith 1974; Weber and White 1974; Weber *et al.* 1975; Hudson *et al.* 1976; Isdale 1977) report that high skeletal density is correlated with periods of high water temperature. Buddemeier (1974) has correlated the dense bands with times of high seasonal rainfall and hence lower-light intensity. Stearn *et al.* (1977), using seasonal variations in the Barbados environment, suggest that the high-density bands are formed in the autumn in response to relatively abrupt decreases in the available light and the low-density bands are formed in the spring and summer.

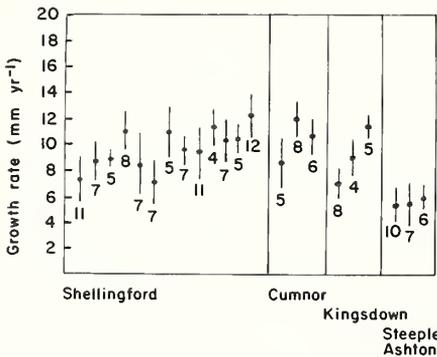
The paired zones in Oxfordian corals must represent periods of significantly different conditions of skeletal growth but it is difficult to draw from the fossil record what environmental factors led to the formation of different densities. England during the upper Jurassic was at about 40° N. (Smith *et al.* 1981) and a marked seasonality of climate is likely. If the negative correlation between skeletal density in corals and available light is accepted, then several characteristics of the corals may be explained.

The contrast in thickness ratios of low- to high-density growth between the Oxfordian corals and *Platygyra* and *Montastrea* (Weber *et al.* 1975) might be explained by presuming generally reduced light conditions in the local ancient seas because of either greater water depth or turbidity (see Highsmith 1979 for discussion). This would have allowed growth of a wider band of high-skeletal density and a much thinner band of low-skeletal density. In *Montastrea* (Baker and Weber 1975) the relative thickness of the band changes with depth. Whilst at depths of less than 18.0 m the less-dense band is consistently more than twice the width of the denser band, at greater depths this value changes to less than 0.5 coinciding with a sharp change in linear growth rate, skeletal density, and growth form. However, the actual thickness of the denser band shows relatively little change with depth. Hudson (1981) reported decrease in growth-rate of *Montastrea* in deeper fore-reef locations. The local reduced light intensity may better be attributed to high turbidity in the Corallian reefs (Ali, in preparation). Evidence in support of this is the absence of calcareous algae and foraminiferal encrusters, except for rare occurrences on massive corals. Although detritus trapped within the coral skeleton is widespread (e.g. Ali 1983), it is not possible to prove that in any instance it was introduced during growth as described by Bernard *et al.* (1974).

GROWTH RATES

In reviewing growth rates of modern scleractinian corals Buddemeier and Kinzie (1976) conclude that linear growth-rate ranges from 4 to 20 mm yr⁻¹ and that normal average growth rate is about 10–12 mm yr⁻¹. They mention examples of faster growth and the extreme growth rate exhibited by *Acropora*. Dodge and Vaisnys (1977) give a vertical growth rate of about 3.5 mm yr⁻¹ for Bermuda corals. Such growth rates for modern corals may be used as a background for the study of growth rate of related forms from the fossil record.

The growth rate of the branching corals *Thecosmilia* in southern England (text-fig. 4) and *Rhabdophyllia* have been obtained by examination of the epithecal banding. (*T. annularis* is not common in most of the coralliferous localities in Yorkshire and the few specimens collected show only an indistinct banding.) Few measurements were available from Steeple Ashton (though many specimens were examined), but an appreciably lower growth rate is indicated. *R. phillipsi* is not common in the Oxfordian of southern England, and where it occurs, rarely shows well-defined periodic bands. Specimens from a temporary section at Cumnor Hill (SP 465041) show a banding which suggests rates of about 5.0–6.5 mm yr⁻¹. The same range of values is suggested by specimens from Yorkshire localities.

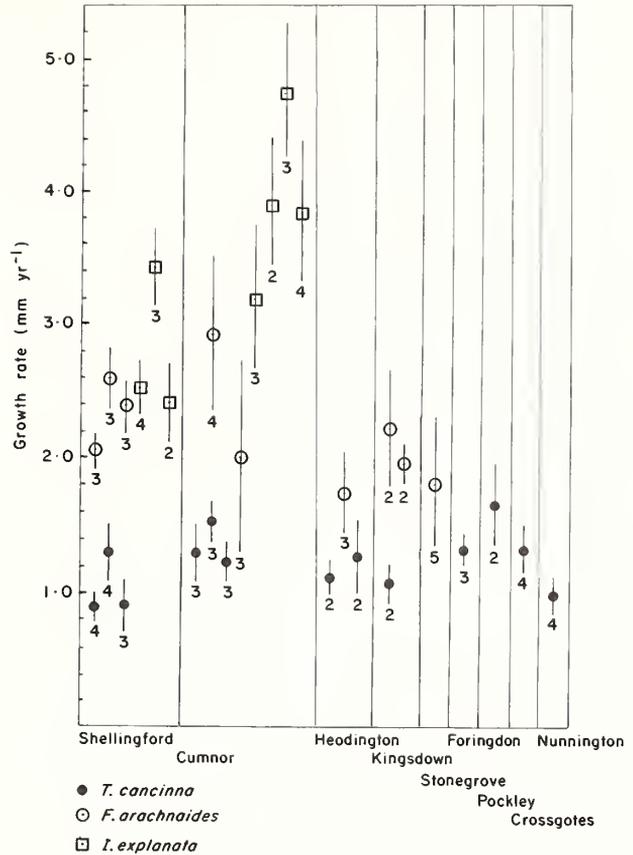


TEXT-FIG. 4. Mean and standard deviation of growth rates of thecosmilian colonies from four localities in the Oxfordian with number of measurements made on each colony.

Growth rates of the massive corals were determined from measurements of the high- and low-density couplets in thin section and cut surfaces. Similar values have been obtained by measurement of epithecal banding. In general there is considerable variation in the thickness of the bands though this is matched by a similar variation in the thickness of individual bands over a colony.

Thamnasteria concinna (text-fig. 5) has the lowest growth rate of the three species but the values show the least variation between colonies and between localities. The growth rate of *Fungiastraea arachnoides* is higher but the variability in the rate is greater. The relatively poor preservation of *Isastraea explanata* has allowed fewer measurements to be made. Values of growth rate vary from 2.5 mm yr⁻¹ to about 5.0 mm yr⁻¹. Individual variability in linear growth rate, of much higher magnitude, is reported in modern scleractinians by Lewis *et al.* (1968) for *Acropora* and other corals, and by Weber and White (1974) for *Platygyra*. Weber and White suggest that individual variations in growth rate among the different members of a population are probably attributable to a combination of environmental and genetic factors. Dodge *et al.* (1974) who studied the effect of sediment suspension on growth of *Montastrea annularis* from Jamaica, noted a decrease in the variability of growth with increasing resuspension. They speculated that the ability of the coral to respond to other favourable, or at least less-limiting, environmental variables is reduced by high resuspension. This factor may have applied to the Oxfordian corals under discussion.

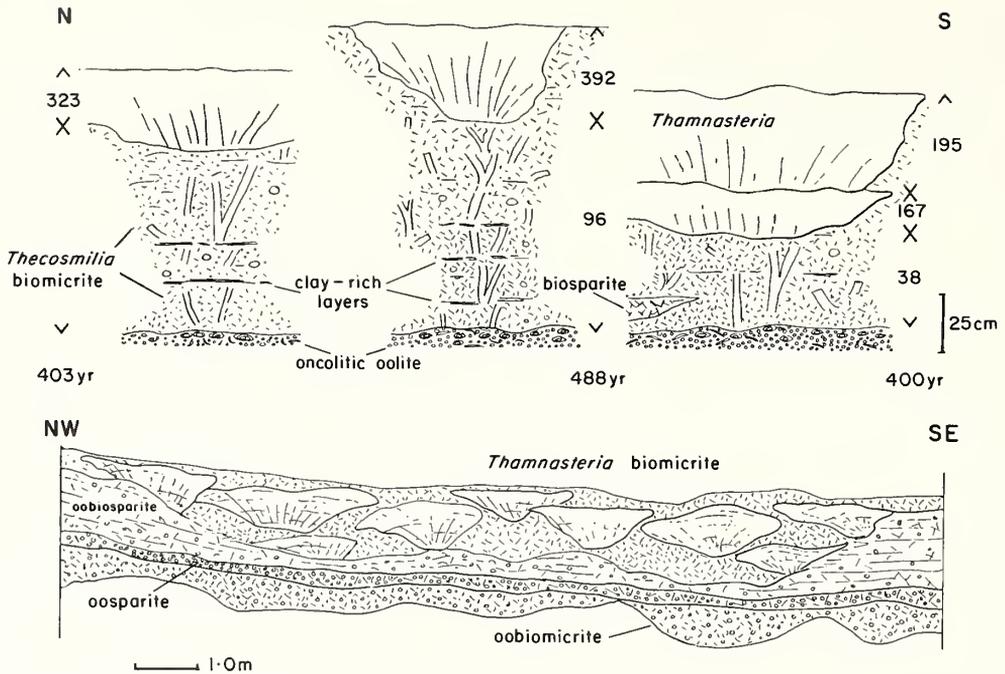
TEXT-FIG. 5. Mean growth rates and standard deviation of colonies of *Thamnasteria concinna*, *Fungiastrea arachnoides*, and *Isastraea explanata* from Oxfordian localities with number of measurements made on each colony.



When compared with modern scleractinians the average growth rates of the massive fossil species are low. However, corals such as *Agaracia* (3.5 mm yr^{-1} , Stearn *et al.* 1977), *Solenastrea* (1.5 mm yr^{-1} , Moore and Krishnaswami 1974), and *Siderastrea* (4.1 mm yr^{-1} Stearn *et al.* 1977) are amongst the slow-growing genera. There are no data available on modern phaceloid genera such as *Caulastrea* and *Astraemorpha*, which are morphologically more similar to *Thecosmilia* and *Rhabdophyllia* than ramose thamnasteroid genera. Vaughan (1915) noted that, in general, the more massive and denser the skeleton the slower the growth, whilst the more ramose and porous the skeleton the more rapid the growth. The growth rates of some Dinantian rugose corals (Johnson and Nudds 1975) are, surprisingly, relatively high ($40\text{--}60 \text{ mm yr}^{-1}$): though Scrutton and Powell (1981) quote $5\text{--}18 \text{ mm yr}^{-1}$ for Silurian favositids.

Extension of growth-rate analysis to estimates of geological time represented by actual sections is fraught with difficulties but two sections were selected in the Oxfordian to attempt to determine the time taken for their formation. Sections at Shellingford Cross-Road Quarry and Ayton Quarry (text-fig. 6) are sufficiently extensive to locate profiles where growth was uninterrupted or where successive generations of coral colonies could be traced. This method was adopted by Hoffmeister and Multer (1964) to estimate growth rate of the Pleistocene Key Largo coral reef of the Florida Keys.

An account of Shellingford Cross-Roads Quarry is being prepared. Arkell (1947, p. 87) gave a general description and Ali (1977) described the effects of penecontemporaneous erosion and mantles of shelly biosparite, and smectite seams which interrupted coral growth. There are three intervals of smectites and three intervals of biosparite but the interruptions ('hazards') to coral growth and



TEXT-FIG. 6. Successive sections used for estimating growth rate of the coralliferous unit at Shellingford Cross-Roads Quarry (above). Sections chosen at about 50-m intervals along quarry face. Lithology and coral distribution at Ayton Quarry (below).

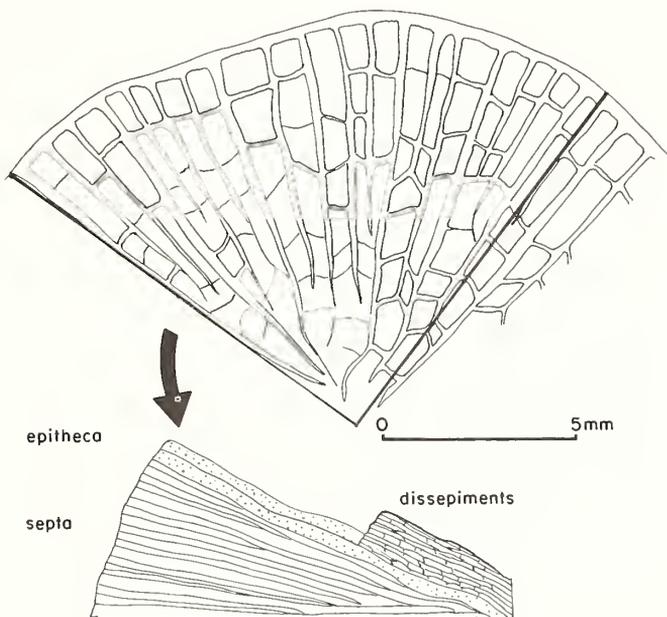
sedimentation were not continuous along the section. When specimens of massive coral are sectioned further local growth discontinuities are evident that are not visible in the field. But such interruptions probably represent only a few years at most. The estimated age for the coralliferous unit is 359 years giving an average growth rate of 3.7 mm yr^{-1} . (This estimate is based on seven sections: data in Ali, unpublished Ph.D. thesis, University of Reading, 1978.)

The section at Ayton Quarry was described and figured by Blake and Hudleston (1877) and referred to by Wright (1972). The coralliferous unit is composed of biolithite with lens-shaped colonies of 1.0 m height forming discrete but closely packed hemisphaeroids averaging 30 cm across, the roundheads of Blake and Hudleston (1877), with little matrix (biomicrite). There are rare colonies of *Rhabdophyllia*. The growth rate of *Fungiastraea arachnoides* forming the column in the centre is about 2.4 mm yr^{-1} and the thickness of this column is about 1.3 m. The minimum period of time required for the formation of the coralliferous unit at Ayton is about 550–600 years.

CARBONATE PRODUCTION

Calcium carbonate production today varies greatly from temperate to tropical environments (Chave *et al.* 1972; Smith 1970, 1971; Stearn *et al.* 1977; Bosence 1980). The data for these studies are based on some assumptions and estimations because of the complexity of the processes within reefs and carbonate banks. As well as the skeletons of the corals and other frame-builders, their epizoa and associated biota, and the sedimentary particles produced by physical and biological erosion and dispersed within and without the reef by currents and waves must also be evaluated.

Chave *et al.* (1972) defined potential production as the amount of calcium carbonate produced by a single organism, or colony of organisms per unit area of the surface covered by that organism. This definition is useful in providing a unit of measurement by which carbonate-producing abilities of different organisms can be compared. With fossil corals the problem is aggravated because not only is it seldom possible to trace time surfaces with any degree of accuracy through a unit, but primary production has been modified subsequently by diagenesis, solution, and precipitation of cements.



TEXT-FIG. 7. Part of a thecosmilian cross-section to illustrate method used for estimating proportion of skeleton per unit area of corallite.

The method to determine skeletal density of the coral species is shown in text-fig. 7. Successive septa were individually traced, using a low-power projection microscope, on to paper, the paper being moved to give a cumulative value of the septal cross-sectional areas. Epitheca and dissepiments were then added and the total cross-sectional area determined. It is assumed that *Thecosmilia* had a circular cross-section. The average diameter at Shellingford is about 2.7 cm and aragonite S.G. is 2.94 (Goreau 1963). The skeleton in *Thecosmilia* occupies about 31.5 % of the cross-sectional area. Skeletal proportions of massive corals were determined by the same method and the mass of CaCO_3 per unit volume of the organism (g/cm^3) obtained for each species. Potential production, expressed as CaCO_3 mass per unit volume \times growth rate (cm yr^{-1}) is given in Table 1.

It is clear from the above data that the differences in linear growth rates for the Corallian species are represented by much smaller differences in actual calcification rate because the mass per unit volume of the slower-growing colonies is much higher than in those with faster growth rates.

The estimated values of potential production of massive coral species from Shellingford and from Ayton (Table 1) are quite similar to productivity values of some modern scleractinians off Barbados determined by a different method (Stearn *et al.* 1977), though the calcification rate of *Thecosmilia* is considerably greater.

The gross production is the amount of CaCO_3 produced per unit area of the reef (Chave *et al.* 1972). It is obtained by summing the product of potential production of each organism in a given reef, times the proportion of the reef area covered by the organism. The approximate coverage by

TABLE 1. Potential production of coral species and gross production at Shellingford Cross-Roads Quarry and Ayton Quarry

	(a) skeleton per sq. cm	(b) growth rate cm yr ⁻¹	(a × 2.94) mass per unit vol. g/cm ³	(a × b × 2.94) potential prodn. g CaCO ₃ m ² yr ⁻¹	(d) mean coverage ^x per unit area	gross prodn. a × b × 2.9 × d
Shellingford, Oxfordshire						
<i>Thecosmilia</i> <i>annularis</i>	0.315	0.98	0.926	9074.8	0.301	2731.5
<i>Thamasteria</i> <i>concinna</i>	0.588	0.104	1.729	1797.8	0.091	163.6
<i>Fungiastraea</i> <i>arachnoides</i>	0.424	0.235	1.246	2929.4	0.128	367.7
<i>Isastraea</i> <i>explanata</i>	0.312	0.28	0.917	2567.6		
						3262.8 g CaCO ₃ m ² yr ⁻¹
Ayton, Yorkshire						
<i>Fungiastraea</i> <i>arachnoides</i>	0.424	0.24	1.246	2990.4	0.4	1196.2
<i>Thamasteria</i> <i>concinna</i>	0.588	1.04	1.729	2421	0.28	677.8
<i>Rhabdophyllia</i> <i>phillipsi</i>	0.58	0.5	0.90	4500	0.02 ^y	90.0
						1964.0 g Cal O ₃ m ² yr ⁻¹

x—based on seven sections (data in Ali, unpublished thesis for Ph.D., University of Reading 1978) *Isastraea* (2%) included with *T. arachnoides*.

y—estimated.

corals at Shellingford is shown in Table 1, together with an estimate of the gross calcium carbonate production of the coralliferous unit. (Where coral cover is extensive gross production on modern reefs is a reasonable approximation of net production: the carbonate permanently retained by the reef after allowance for carbonate dissolution and mechanical gains and losses. In the ancient examples discussed it is appropriate to take net production as equivalent to gross production.)

The coralliferous unit at Ayton is composed mainly of *Thamasteria* and *Fungiastraea*, but branching *Rhabdophyllia* also occurs forming about 2% of the rock. Estimates of calcium carbonate production for this unit are made by the same method and values are shown in Table 1. Differences in productivity between the two sections are due to small differences in growth rates but mainly to differences in productivity of the species present.

DISCUSSION AND CONCLUSIONS

In upper Jurassic times scleractinians were still at an early stage of their evolution though some, such as the microsolenids (now extinct) had achieved a high degree of integration. Further, Jurassic corals in northwest Europe mostly formed localized banks or patch reefs on an extensive shelf area rather than fringing reefs. Such banks were subdued structures with amplitudes that could mostly be measured in centimetres. During its formation the coralliferous unit at Shellingford Cross-Roads Quarry probably consisted of scattered low domes of massive corals amongst short heads of candle-like thecosmilians and *Rhaxella* sponges emerging from a muddy sediment, with an associated fauna of vagile regular echinoids, brittle stars and small gastropods, and attached oysters and other bivalves as the preservable elements.

Thus it is surprising that this study shows a style of growth banding and values of growth rate and carbonate productivity that compare well with what is known from areas of modern tropical corals, and productivity an order of magnitude higher than temperate coralline algae (Bosence 1980). Indeed, the values are peculiarly close to the 3–5 kg/CaCO₃/m² yr⁻¹ characteristic of tropical Pacific reef flats (Kinsey 1979, unpublished Ph.D. thesis, University of Hawaii, quoted by Grigg 1982). The possibility that reefs in the Jurassic extended well beyond the 40° latitude to which they are restricted today (Beauvais 1973) cannot be excluded. But the present study is only preliminary and until similar studies have been carried out, particularly on the diverse coral faunas of the northern margin of Tethys, it would be unwise to consider these results as typical for the Mesozoic. The need for more detailed work on modern corals that can be applied to fossil corals is also evident.

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CONSTRUCTION AND PRESERVATION OF TWO MODERN CORALLINE ALGAL REEFS, ST. CROIX, CARIBBEAN

by DANIEL W. J. BOSENCE

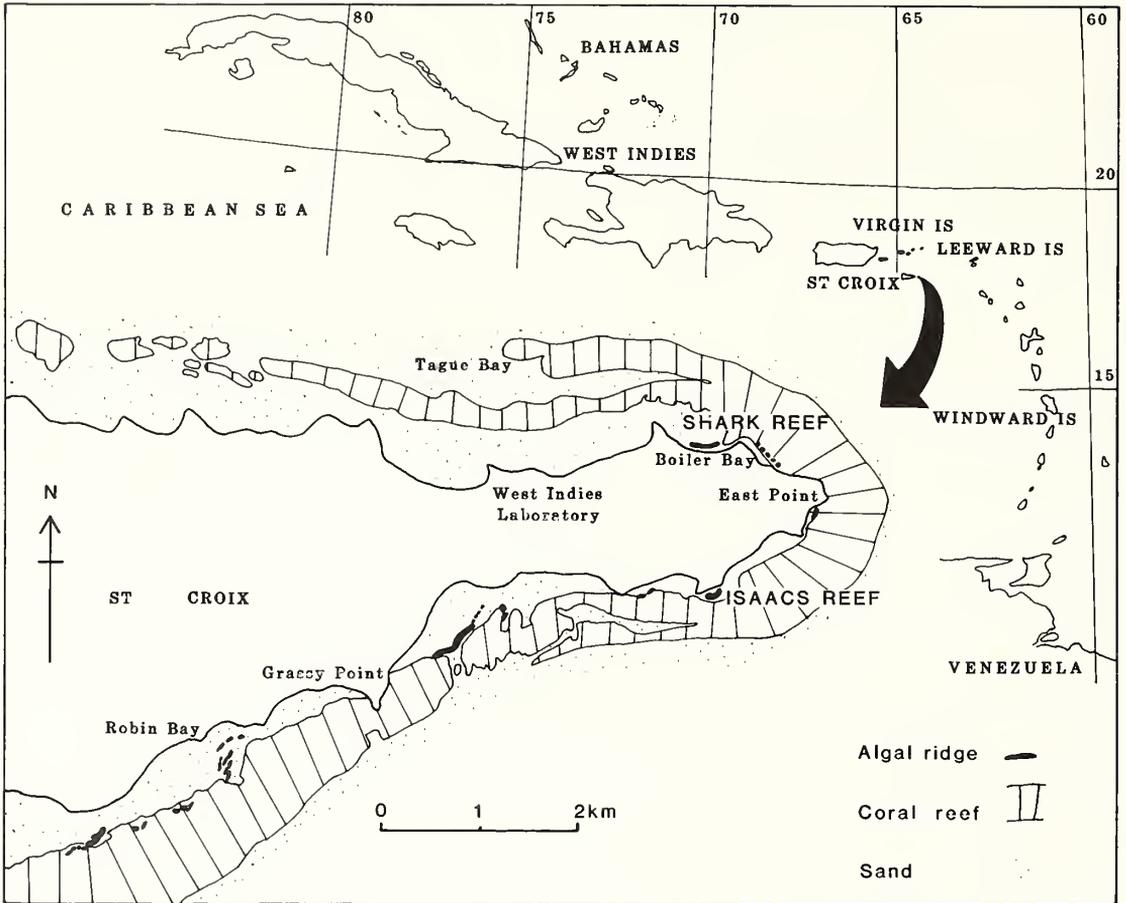
ABSTRACT. The internal structures of two coralline algal reefs from St. Croix are described. The primary framebuilders are *Lithophyllum congestum*, which dominates in exposed mid-intertidal situations, and *Porolithon pachydermum* from the high intertidal. Secondary frameworks are constructed by one of the following corallines: *Tenarea*, *Lithothamnium ruptile*, *Mesophyllum syntrophicum*, *Lithophyllum congestum*, and *Neogoniolithon* sp., together with *Homotrema* and vermetid gastropods. The environmental preferences of these corallines and their recognition in slabbed reef sections permits a reconstruction of past reef morphologies and environments. Predictable ecological successions are found within preserved coralline sequences which correspond with previous settlement plate experiments. The main agents of reef destruction are sponge and echinoid bioerosion. Inter-reef sediments are winnowed by wave currents and reflect the composition of surrounding coral reefs in addition to debris from the coralline algal reefs. A relatively low proportion of coralline algal debris in sediments around the reefs is thought to result from deposition of silt-sized sponge chips of corallines in quieter water elsewhere. Internal reef sediments reflect the composition of the reef constructors.

THIS work has arisen from research on Tertiary coralline limestones of the Tethyan region (Bosence and Pedley 1982; Bosence 1983a, b), during which it became evident that the interpretation of coralline limestones is limited by the paucity of studies on actuopalaontology of Recent tropical coralline buildups. The longevity of coralline algal species together with their narrow environmental tolerances makes them valuable palaeoenvironmental indicators in the Tertiary (Adey *et al.* 1982; Bosence and Pedley 1982). Similarly, late Palaeozoic ancestral coralline reefs require descriptions of Recent counterparts for detailed interpretations.

It is here shown that there are two main components involved in reef construction. The major reef framework is constructed by primary framebuilders which support later encrustations by secondary framebuilders. The characteristics of present-day species of coralline can be recognized in thin sections from the slabbed reef material, and this permits reconstruction of the form and the ecological succession in ancient coralline reefs. Study of the modern reef sediments shows that those around the reef do not accurately reflect reef composition, but that those from the internal reef cavities are similar in composition to the reefs.

The St. Croix algal reefs (algal ridges) described here (text-fig. 1) were selected for investigation because of the extensive previous work on the present-day corallines by Walter H. Adey (Smithsonian Institution) and his co-workers. Adey (1975) describes the setting, morphology, large-scale internal features (text-figs. 2, 3), and Holocene development of the reefs. Adey and Vassar (1975) describe the colonization, succession, and growth rates of the corallines from a series of settling plate experiments. The environmental control on morphology of the main ridge-building alga *Lithophyllum congestum* is studied by Steneck and Adey (1976). The systematics and morphology of the corallines are to be described by Adey (pers. comm.). Detailed discussion of the relevance of these earlier studies to this project is included in the appropriate parts of this paper.

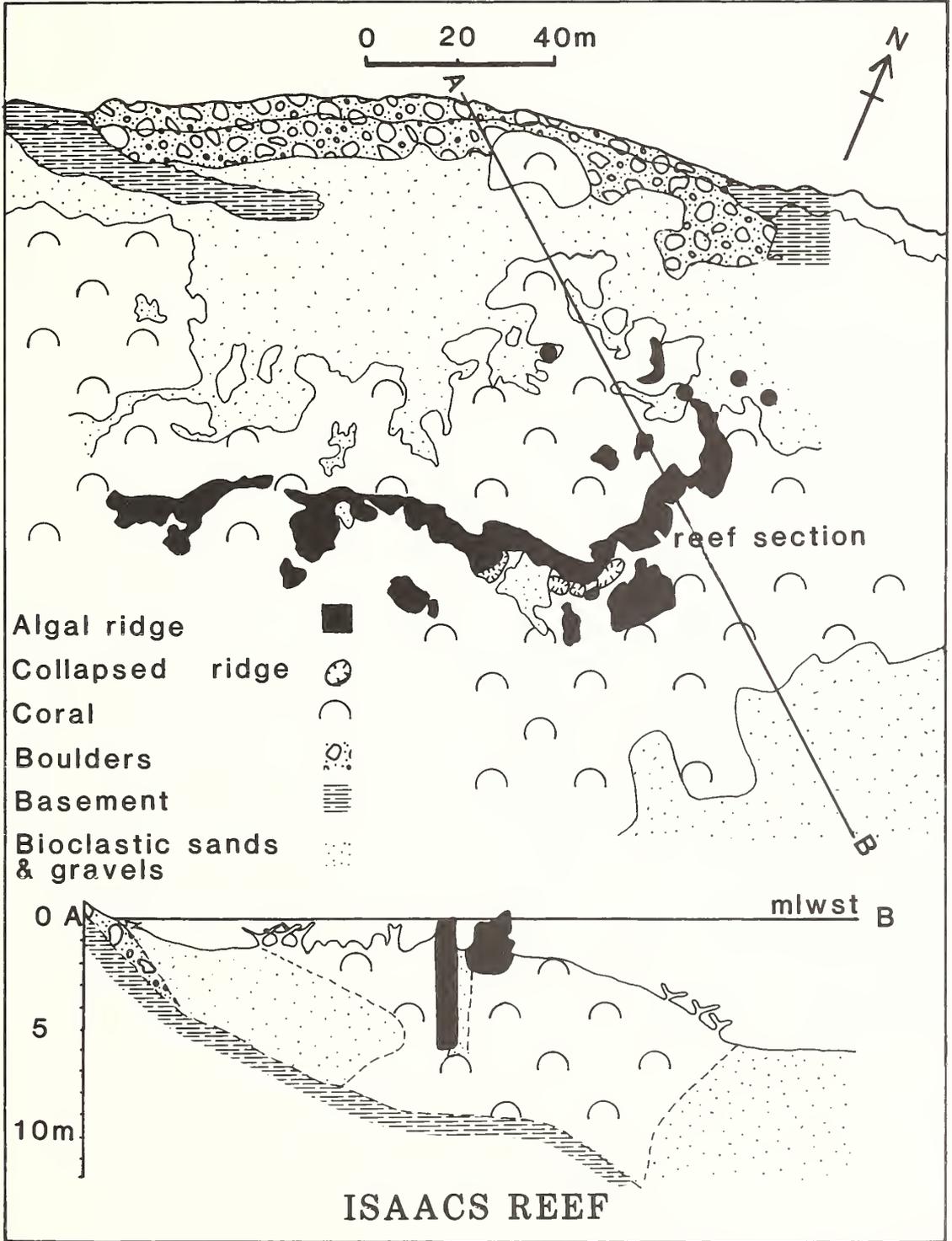
The ecology of the coralline algae (Adey 1975; Adey and Vassar 1975) provides the information for interpretation of the internal growth fabrics described below in this paper. In exposed situations in eastern St. Croix, a pavement of *Acropora palmata* exists in depths of 1–2 m. These coral pavements are coated by crusts of the coralline algae *Neogoniolithon* spp. and *Porolithon pachydermum*. If the



TEXT-FIG. 1. Location of Shark and Isaacs Reefs in St. Croix and the Caribbean (after Adey 1975).

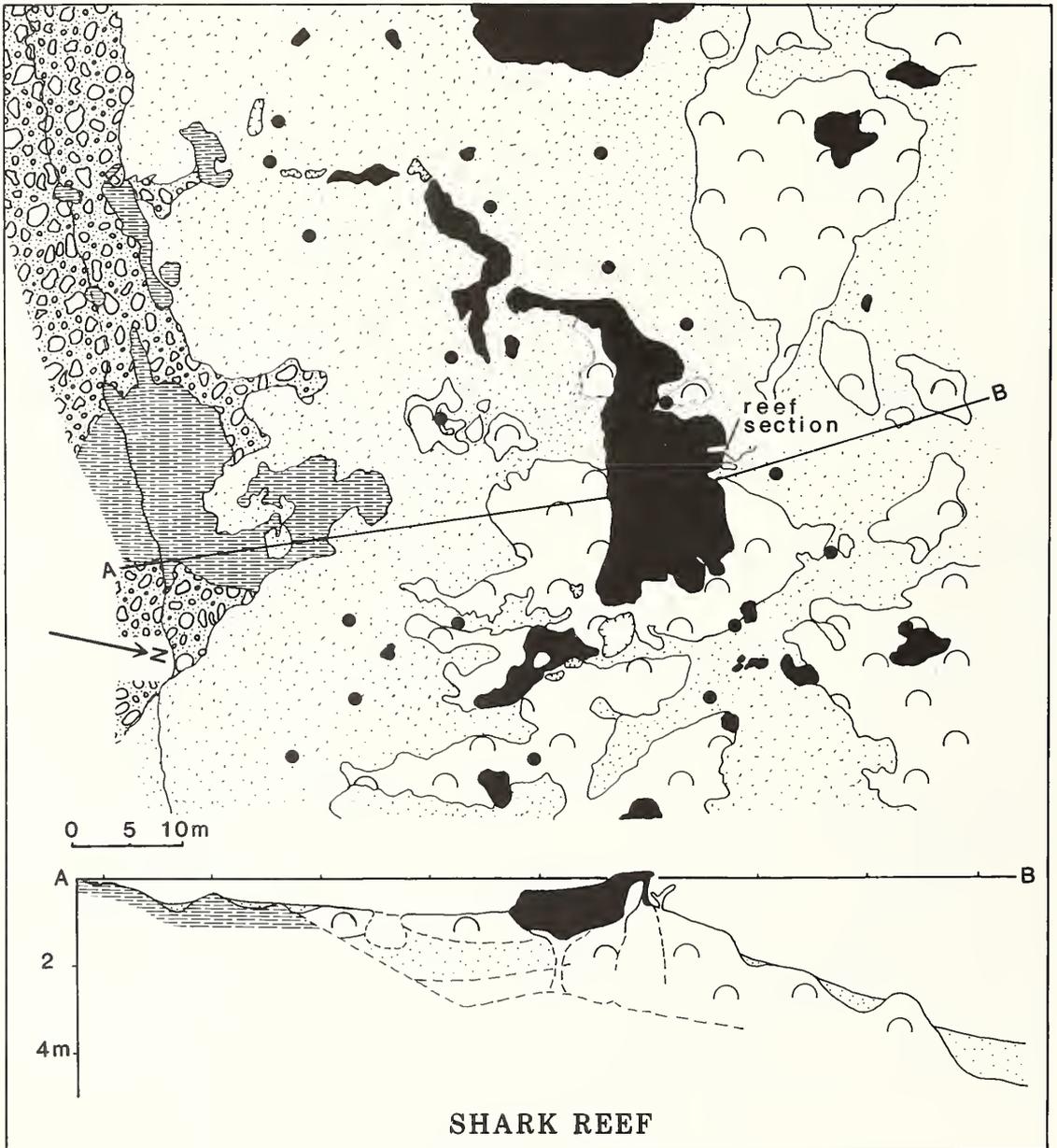
pavements extend to low-water level then *L. congestum* dominates up to 20–30 cm above m.l.w.s. tides. Above this height *P. pachydermum* is the major reef constructor. In the many reef cavities and overhangs the following corallines are important in reef building: *Lithothamnium ruptile*, *Mesophyllum syntrophicum*, *Neogoniolithon* sp., and *Tenarea*. In addition, the foraminifer *Homotrema* and vermetid gastropods are common.

Two coralline ridges or algal reefs were selected for this study on the basis of those drilled by Adey (1975). Isaacs Reef is located off the exposed south-eastern shore of St. Croix (text-figs. 1, 2, 4B) and is composed of a number of fused reefs or boilers. The reefs are very cavernous with a number of walls and pillars supporting a roof and crest. Present-day coralline growth is luxuriant (text-fig. 4D, E) and construction by *Lithophyllum congestum* and *P. pachydermum* has built the reef to a height of up to 50 cm above m.l.w.s. tides (Adey 1975). Adey and Vassar (1975) give a maximum accretion rate of 5 mm/year for reef crest environments of exposed ridges. Adey's (1975) drilling indicates coralline build-up over a previous *A. palmata* reef dated at the base as 4,040 yrs. B.P. The *Acropora* continues today in 3–4 m of water in front of the algal reefs. Coralline frameworks extending to a depth of 2.5 m were recovered. For the present study a large slot 1 m deep and extending back 1.5 m from the reef crest was excavated to provide a continuous cross-section (text-figs. 2, 5).



TEXT-FIG. 2. Plan and cross-section of Isaacs Reef showing location of algal reefs and excavated reef section (after Adey 1975). ● sediment samples.

Shark Reef, in contrast, occurs in the more sheltered Boiler Bay of north-eastern St. Croix (text-figs. 1, 3, 4A). It is further protected by a newly (c. 500 yrs. B.P.) emergent barrier reef extending across the bay (Adey 1975). Shark Reef was one of the most thoroughly studied of Adey's reefs (Adey 1975, figs. 39, 40). A large *A. palmata* stand (dated at 2,900 yrs. B.P.) is overgrown by about 1.5 m of coralline reef which extends today to a height of about 15 cm above m.l.w.s. tides. Because of the



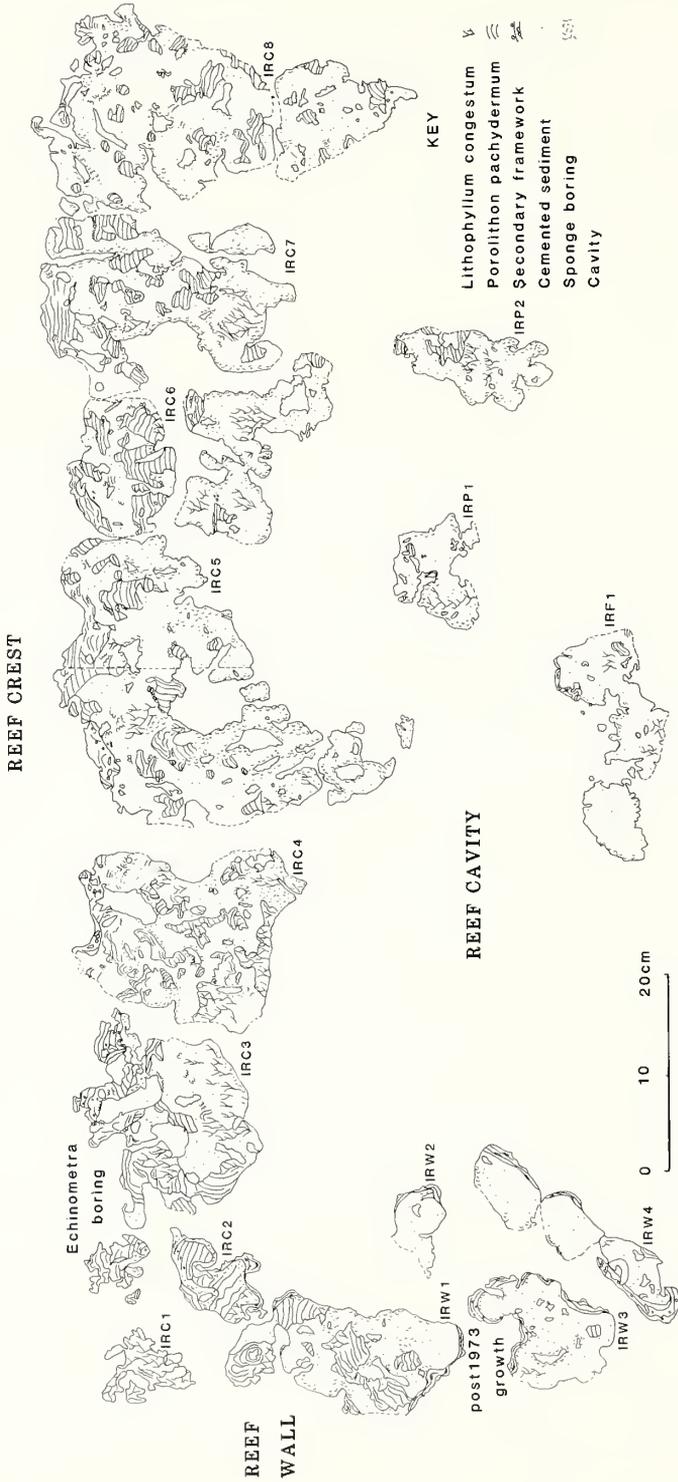
TEXT-FIG. 3. Plan and cross-section of Shark Reef showing location of algal reef and excavated reef section; symbols as for text-fig. 2 (after Adey 1975).

reduced hydraulic energy conditions there is little *Lithophyllum* and *Porolithon* growth on Shark Reef today (text-fig. 4C) although these algae are important in reef sections (text-fig. 6). Present-day surfaces are covered with non-calcified algae (Abbott *et al.* 1974) and penetrated by large borings of the echinoid *Echinometra*. Adey and Vassar (1975) have shown present-day accretion rates on these reef crests to be only 1–2 mm/year which apparently cannot keep pace with the heavy *Echinometra* boring (Adey 1975). As with Isaacs Reef a large slot normal to the reef crest was excavated (1.4 m deep and 1.2 m back from the crest), adjacent to and extending a previous slot of Adey (1975, fig. 40).

The depth/age relationships for these two reefs (Adey 1975) indicate an age of 2,200 yrs. B.P. for the base of my Isaacs Reef section and 3,300 yrs. for the base of my Shark Reef section. The slabbed reef sections (text-figs. 5, 6; Table 1) indicate five major components within the reefs. Primary reef frameworks are constructed by *L. congestum* and *Porolithon*. Secondary reef frameworks comprise



TEXT-FIG. 4. A, Shark Reef (arrowed); Boiler Bay, looking north-east. Note waves breaking on barrier reef across mouth of bay and small waves on beach. B, Isaacs Reef, looking south-west. Coralline algal ridges are clearly visible between waves. C, underwater photograph of Shark Reef crest, showing sparse crustose algal growth, white areas scraped by parrot-fish, and *Echinometra* in borings; $\times 0.12$. D, surface view of Isaacs Reef crest, showing branching heads of *Lithophyllum congestum* and columnar growths of *Porolithon pachydermum* (upper centre, white). Darker tufts are fleshy algae (right of hammer). *Echinometra* borings (2–5 cm diam.) occur throughout the area; $\times 0.12$. E, underwater photograph of front wall of Isaacs Reef (c. 1 m depth), illustrating competitive intergrowth of coralline crusts and vermetid (V) in secondary framework; note *Lithotrya* (L) borings; $\times 1$.



TEXT-FIG. 5. Section through Isaacs Reef crest, simplified from tracings of impregnated, cut, and polished reef blocks. Reef block labels refer to crest (IRC), wall (IRW), pillar (IRP), and floor (IRF) locations.

TABLE 1. Point counts from grid on slabbed reef surfaces (text-figs. 5, 6) indicating percentage abundance of frameworks, borers, sediment, and cavities ('Total' column includes counts from slabs and cavities; 'Preserved' column is recalculated for the preserved slabs only).

	Isaacs Reef (1378 counts)		Shark Reef (2272 counts)	
	Total	Preserved	Total	Preserved
Primary Frameworks	15	41	10	29
<i>Lithophyllum congestum</i>	5	14	2	7
<i>Porolithon</i>	10	27	5	14
<i>Millepora</i>	—	—	3	8
Secondary Frameworks	1	2	8	20
<i>Tenarea-Homotrema</i>	—	—	4	10
Sponge chambers	3	9	5	14
Cemented sediment	20	55	14	37
Cavities	61		62	

later crusts growing on and within the reef. Borings of sponges and other organisms account for 3% and 5% of Isaacs and Shark Reefs, respectively. Fourthly, cemented internal sediment forms a large part of the sections. Finally, reef cavities account for the majority of the cross-sectional areas (61% and 62% of Isaacs and Shark Reefs, respectively).

METHODS

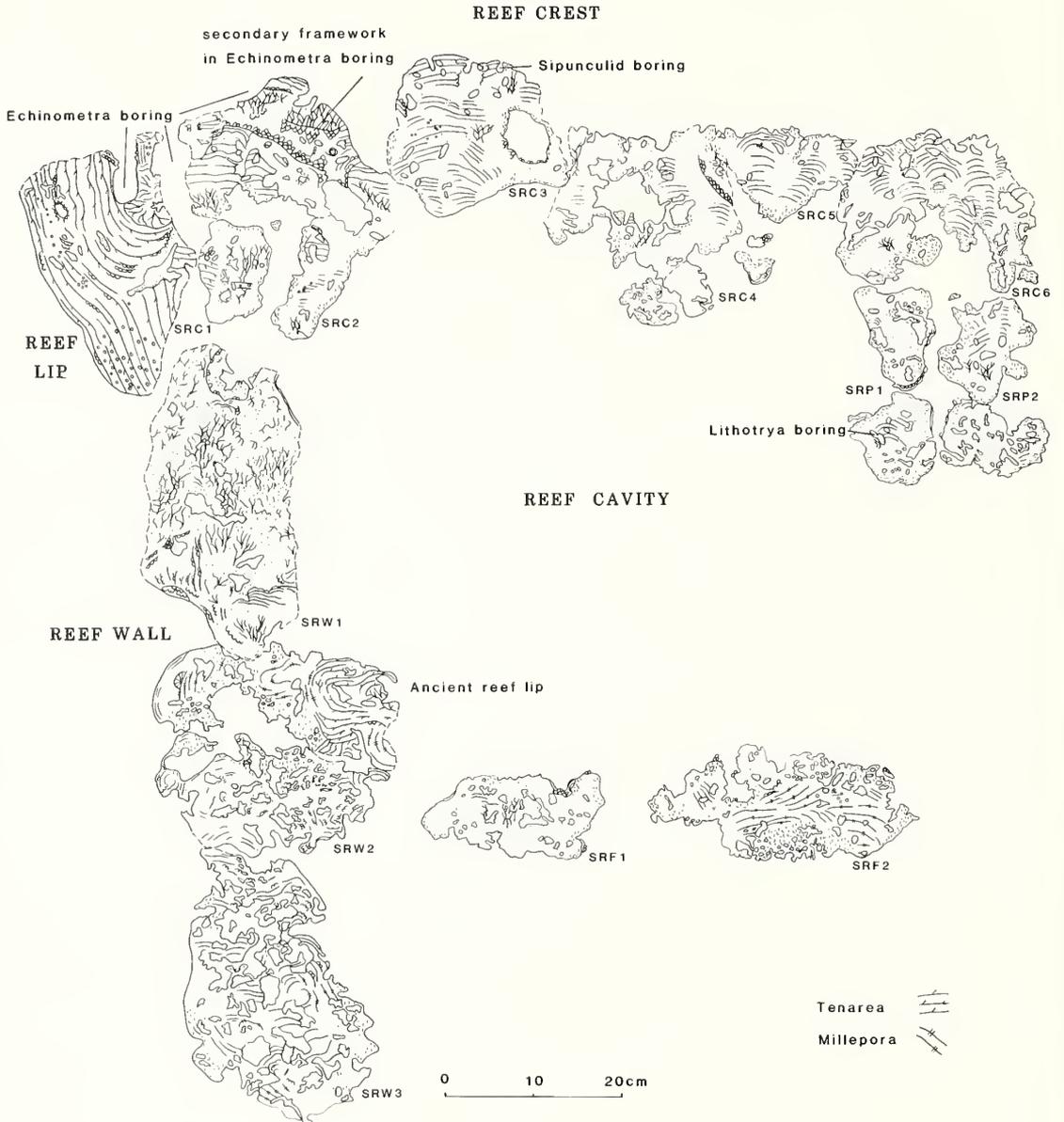
The material for this study was collected during January 1980. Large blocks of reef were removed by hammer, chisel, and bar to excavate cuttings normal to the reef crest. Work on Shark Reef was straightforward because of low energy conditions but Isaacs Reef was continuously pounded by 1.0 to 1.5 m waves and ropes were used to maintain a position on the reefs. The reassembled blocks were slabbed along one plane, impregnated with Araldite resin, ground, and polished. Text-figs. 5 and 6 were traced from these prepared surfaces. Thin sections were prepared from further impregnated chips of both reefs for identification of the corallines, successional data, and study of the internal fabrics and sediments. Specimens of reef material were fractured, or polished, and etched, coated with gold for investigation under a JEOL JM 35 S.E.M. operating at 25 kv. Inter-reef sediments were collected with a scoop and sieved at half phi intervals. For all samples, subsamples from each sieve were amalgamated and impregnated. Composition was determined by point counts made on stained acetate peels.

THE CORALLINE ALGAE

An important part of this investigation involved the identification of the recently preserved coralline algae. The identifications were based on Adey's representative collection of coralline thin sections together with the original descriptions from decalcified material. Measurements from micrographs provided data on crust thickness, hypothallus thickness, hypothallus and perithallus cell sizes and shapes, heterocyst and conceptacle size and shape for the eight species of coralline from the Cruzan reefs (Table 2). Six of these species were found to be common or abundant on the reefs: *Lithothamnium ruptile* Foslie, *Mesophyllum syntrophicum* (Foslie) Adey comb. nov., *Lithophyllum congestum* (Foslie) Foslie, *Porolithon pachydermum* Foslie, *Neogoniolithon megacarpum* n.s. Adey,

and *Tenarea* sp. The remainder were rare: *Porolithon antillarum* Foslie and *Neogoniolithon imbricatum* n.s. Adey.

One other common coralline in the reef sections is represented by thin monostromatic crusts with roughly cubic cells (c. $10 \times 12 \mu\text{m}$). These occur as early colonizers of hard substrates in the reefs (see discussion below on ecological succession). They possibly correspond to Adey's genus *Leptoporolithon* which is a common early colonizer on these reefs. *Leptoporolithon* occurs as thin



TEXT-FIG. 6. Section through Shark Reef crest, simplified from tracings of impregnated, cut, and polished reef blocks. Reef block labels refer to crest (SRC), wall (SRW), pillar (SRP), and floor (SRF) locations.

TABLE 2. Morphology of coralline algae. Measurement of each feature in microns expressed as mean (standard deviation), and range.

Taxon	Growth form	Hypothallus	Cell sizes	Perithallus	Cell sizes	Tetrasporic asexual conceptacles	Size width × height
<i>Lithothamnium ruptile</i>	Crusts of variable thickness	Non-coaxial 147 (4.5) 144-153 thick	29 (2.8) 25-34 × 11 (0.9) 10-13	Filaments dominant	29 (4.8) 25-36 × 12 (2.3) 8-15	Multipored	500-700 diameter
<i>Mesophyllum syntrophicum</i>	Follicaceous crusts	Coaxial 90 (12) 68-102 thick	24 (3.9) 19-32 × 7 (2) 5-10	Rows dominant	13 (3.6) 10-19.5 × 13 (6.2) 7-22	Multipored flat roofed	400-600 diameter
<i>Lithophyllum congestum</i>	Thick crusts and luxuriant branching in intertidal	Single layer sub-triangular or coaxial	13.5, 1-18.5 × 16, 5.5-24	Rows dominant branches zoned	5.5-11.5 × 7-8	Unipored	256 (60) × 106 (27)
<i>Porolithon antillarum</i>	Crusts and columns	—	—	Grid like, irregularly zoned Heterocysts in rows of 6-10	14 (2.4) 11-17 × 10 (2.1) 7-15 29.5 (4.8) 24-39 × 16 (3.3) 9-20	Unipored	253 (39) 235-272 × 111 (4.8) 105-117
<i>Porolithon pachydermum</i>	Crusts and columns	Coaxial	20 (2.2) 17-24 × 7 (1.4) 5-9	Filaments dominant regular grid	10 (3.7) 6-19 × 9 (1.7) 6-13	Unipored	101-185 68-88
<i>Neogoniolithon megacarpum</i>	Crusts c. 230 thick	Coaxial c. 50 thick	15 (1.7) 11.5-17 × 5 (0.8) 3-7	Heterocysts in rows of 3-4 Zoned irregular grid	28 (11) 19-48 × 18 (2.5) 17-22 5 (1.2) 3-6 × 4.5 (0.7) 3-6	Large raised unipored	326 × 161
<i>Neogoniolithon imbricatum</i>	Thick crusts imbricate by overgrowing	Coaxial 88-92	22 (4.2) 17-29 × 9 (1.2) 8-12	Filaments of 3-4 dominant Heterocysts in filaments of 2-3	7 (3) 3-10 × 10 (1.6) 8-12 13 (4) 7-19.5 × 7 (1.8) 5-11 14 (3.6) 10-19.5 × 13 (3.3) 10-15	Unipored	500-1000 outside diam.

monostromatic crusts or developing a single-layered perithallus with heterocysts similar to *Porolithon* (Adey and Vassar 1975). No perithallus or conceptacles are present in the preserved monostromatic crusts. Because of the uncertainty over identification of these thalli they are here labelled 'monostromatic crusts'.

Full morphological details of each coralline are to be treated by Adey (pers. comm.). The diagnostic features of each species as seen in thin sections are tabulated in Table 2 and illustrated where relevant in Plates 50–52.

REEF CONSTRUCTORS

Primary frameworks

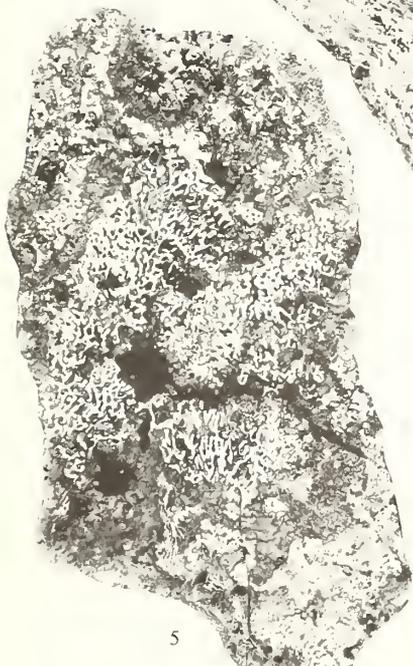
Lithophyllum congestum framework. Branching *L. congestum* may be abundant about 20 cm below to about 20 cm above m.l.w.s. tides in exposed ridges. The most exposed and therefore the highest ridges have the greatest cover of *L. congestum* (Adey 1975; Steneck and Adey 1976).

Of the two ridges investigated in the present study only Isaacs Reef supports live branching *L. congestum* (text-fig. 4D). This occurs as a 60 cm thick band on the outer crest of the reef. The lower part of this band has up to 2 cm thick crusts bearing incipient branches of *L. congestum* overgrowing old bored, infilled, and cemented reef (text-fig. 5, slab IRW1; Pl. 51, fig. 6). This represents new growth over a small slot cut by Adey in 1973 and gives an actual vertical crust accretion rate for crusts of 1 mm/yr. The branching *Lithophyllum* framework occurs as 5.3% of the area of the section (but 14% of the area of preserved reef—see table 1). The framework is preserved within the crest and the lower parts of the reef crest blocks (text-fig. 5, slabs IRC3–IRC7). Scattered areas are also preserved within the reef pillars and reef cavity floor (slabs IRP1–IRP2, IRF1). In contrast, Shark Reef, which has a similar porosity of just over 60%, has large areas of well-preserved branching framework in the front wall (text-fig. 6, SRW1; Pl. 50, fig. 3) but only small patches in other interior regions. The percentage area occupied by the framework is 2.5% or 14% of the preserved reef (area of slabbed surface).

L. congestum is preserved as an *in situ* irregular branching framework with or without a crustose base. Many areas are clearly remnants of previously more extensive frameworks because the margins are bioeroded (Pl. 50, fig. 1) and replaced by a secondary framework (Pl. 50, fig. 5) or cemented sediment. In addition to the areas of framework traced from the slabs, most thin sections contain small erosional relics of branching or crustose *L. congestum*.

EXPLANATION OF PLATE 50

- Fig. 1. Polished slab (upper part of IRC6, text-fig. 5) illustrating preserved columnar growth of *Porolithon pachydermum* succeeding *Lithophyllum congestum* (lower right). Note well-cemented internal sediment (grey) within centimetres of upper growth surface of reef, $\times 0.5$.
- Fig. 2. Bases of articulate corallines (*Amphiroa*) in laminar crust of *P. pachydermum*. Note horizontal rows of heterocysts (arrow) within perithallial tissue. Thin section micrograph from block SRC3 (text-fig. 6), $\times 26$.
- Fig. 3. Section of lower lip of Shark Reef crest (SRC1, text-fig. 6). Branching *L. congestum* framework (upper right) is firstly overgrown by thick secondary framework of *Mesophyllum*–*Tenarea*–*Homotrema*–vermetid association then *Tenarea*–*Homotrema*–vermetid association. *Echinometra* boring (upper right) has geopetal infill of uncemented sediment, $\times 0.3$.
- Fig. 4. Thin-section micrograph showing detail of *Tenarea*–*Homotrema* framework with *Homotrema* (bottom centre) overgrown by successive crusts of *Tenarea*. Block SRW2 (text-fig. 6), $\times 10$. Top to right of specimen.
- Fig. 5. Vertical slabbed section from front wall of Shark Reef (SRW1, text-fig. 6) illustrating well-preserved *L. congestum* branching framework, small area of *Porolithon* framework (lower right) and *Echinometra* borings partly infilled with secondary framework (top centre). Secondary framework overgrows primary framework in lower left. Grey areas are hard cemented internal sediment, $\times 0.25$.
- Fig. 6. Thin-section micrograph of *L. congestum* framework illustrating branch fusion. Where filaments from adjacent branches meet end on (centre) a gap remains. Isaacs Reef crest (Block IRC1), $\times 10$.



The initial colonization of *L. congestum* is in the form of crusts (Pl. 51, fig. 6). In lower reef wall positions, a laminar secondary framework of superimposed crusts may develop (e.g. slab IRCW1, text-fig. 5). The crusts may have grown in competition with *Homotrema* and/or *Tenarea* and this results in alternating layers of these organisms and *L. congestum* in vertical section (Pl. 51, fig. 6; text-fig. 8Dii). Similarly, crusts of *Lithophyllum* may be found within laminar and columnar growths of *Porolithon* (text-fig. 7). Branches arise from crust perithallial tissue to form branching frameworks (Pl. 50, fig. 5). Steneck and Adey (1976) give details of branch morphology which varies in different reef niches. Branch sections are frequently oval with minimum diameters of 1 mm and maximum diameters of 23 mm with a mean of 9.1 mm. Branches are constructed by a dominant central, zoned medullary hypothallus with elongate rectangular cells arranged in a grid of filaments and cell rows. The outer cortex of the branch is thin, with smaller square cells (Pl. 51, fig. 1). Branches may divide by apical or lateral division, but commonly fuse together (Pl. 50, figs. 5, 6) which increases the strength of the framework. Branch fusion occurs when filaments approach obliquely or laterally. However, when filaments from adjacent branches approach end on there is no fusion (Pl. 50, fig. 6) possibly due to a thick apical cuticle (cf. Cabioch 1972).

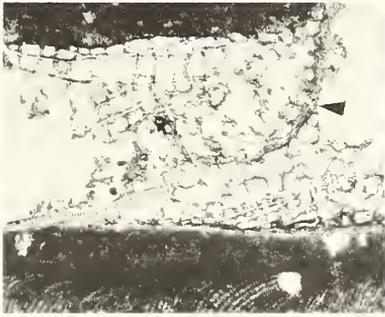
This framework is encrusted by *Homotrema*, vermetids, *Tenarea* sp. and monostromatic crustose corallines (Pl. 51, fig. 1) which all add to the branching framework. Less common encrusters are serpulids and bryozoans. Sediment, which is soon cemented, is added to the cavities between branches (Pl. 50, fig. 5) and is presumably brought in by waves.

Many outer surfaces are bored by dendritic algal borings (c. 10 μ m diameter) which may also mark growth discontinuities within branches (Pl. 52, fig. 1). Surrounding the borings are darkened areas of altered algal tissue which under the S.E.M. are seen to be cells infilled with micrite cement. This close association suggests that micritization of the thallus may be controlled by the algae or organic decay in and around borings (cf. Bathurst 1971, p. 388). Sponge boring is ubiquitous and may occur before or after colonization by the encrusters mentioned above.

Porolithon framework. Three species of *Porolithon* occur in the St. Croix reefs: *P. antillarum*, *P. fragilis*, and *P. pachydermum* (Adey and Vassar 1975). The latter species is the main reef builder and dominates in high reef crest environments (over 20 cm above m.l.w.s. tides). Here it outcompetes *L. congestum* as *Porolithon* is particularly well adapted to resist desiccation and high levels of illumination (Steneck and Adey 1976; Littler 1973). On Isaacs Reef *P. pachydermum* is common both live on the upper reef crest (text-fig. 4D) and as a dense framework throughout the reef interior where it forms 10% of area in cross-section (text-fig. 5). The abundance decreases with depth into the reef as bioerosion increases and cemented sediment becomes dominant. In Shark Reef *Porolithon* is not

EXPLANATION OF PLATE 51

- Fig. 1. Thin-section micrograph showing elongate zoned medullary cells and smaller, squarer cortical cells in outer part of branch of *Lithophyllum congestum*. Encrusting on coralline branches are *Homotrema rubrum* intergrown with monostromatic coralline crusts (arrowed). Isaacs Reef crest (IRC1), $\times 27$.
- Fig. 2. Thin-section micrograph showing detail of lacy intergrowth of *Lithothamnium ruptile* (note multipored conceptacle, mid left) and *Homotrema*. Block IRC3 (text-fig. 5), $\times 35$.
- Fig. 3. Thin-section micrograph of part of *Lithothamnium* (L)-*Tenarea*-*Homotrema* (H)-vermetid framework. Note early colonizers *Homotrema* and monostromatic crusts (M) on cemented internal sediment (lower right) giving way to *Lithothamnium* and *Homotrema* crusts (cf. text-fig. 8 Diii). Block IRW3 (text-fig. 5), $\times 24$.
- Fig. 4. *Mesophyllum* (M)-*Tenarea*-*Homotrema* vermetid (V) framework in Shark Reef Lip (SRC1; Pl. 50, fig. 3; text-fig. 6). Thin-section micrograph, $\times 10$. Top to right of specimen.
- Fig. 5. Thin-section micrograph of intergrowth of *Neogoniolithon* (N) and *Homotrema* (H) over earlier cemented sediment (upper right). Block SRW2 (text-fig. 6), $\times 10$.
- Fig. 6. Thin-section micrograph of laminar *Lithophyllum*-*Tenarea*-*Homotrema*-vermetid framework. Sponge-bored reef rock is overgrown in vertical sequence by *Homotrema* (H), *Tenarea* (T), *L. congestum* (L), vermetid gastropod (V) (infilled with aragonite cement), and *L. congestum*. Block IRW3 (text-fig. 5), $\times 25$.



5

6

found living but it occurs in reef sections with a similar distribution to that found in Isaacs Reef. In the reef crest blocks it occurs as 8.4% of the area but *Porolithon* only makes up 4% of the reef floor blocks. *Porolithon* frameworks dominate over *Lithophyllum* frameworks in the inner crest regions whilst *Lithophyllum* dominates the outer crest and wall locations (cf. text-figs. 5, 6).

P. pachydermum occurs as thick crusts with a thin poorly developed hypothallus. The thick perithallus with cells arranged in filaments and with frequent heterocysts and conceptacles, is apparently of limitless growth. The perithallial tissue forms laminar crusts which normally develop into columnar growths (1.0–1.5 cm high and 1 cm wide) of undifferentiated tissue (Pl. 50, fig. 2). The growth of columns can be seen to have been discontinuous with breaks and rehealed surfaces being common. Algal borings (10 μm) persist throughout the columns suggesting continuous infestation of *Porolithon* during life (text-fig. 7). A common epiphyte is the articulate coralline *Amphiroa* (Pl. 50, fig. 2; text-fig. 7). Articulate corallines are not usually preserved *in situ* but here the bases have been overgrown by the live host to become incorporated in the *Porolithon* tissue.



TEXT-FIG. 7. Thin-section micrograph and tracing to illustrate structure and succession in primary frameworks (branching to laminar *Lithophyllum congestum*, then columnar *Porolithon pachydermum* followed by *Lithophyllum* and *Porolithon* crusts), and secondary *Lithothamnium* and *Lithophyllum* crusts. Note frequent intergrowths of *Homotrema* and vermetid gastropods, infilled sponge borings, minor growth breaks and subvertical algal borings in *Porolithon*.

This relationship is not found in any other coralline in the St. Croix section and appears to be host specific. *Amphiroa* debris is common in the reef sediments. Vermetids and *Homotrema* are commonly intergrown within the *Porolithon* framework. Sponge boring is ubiquitous.

Secondary frameworks

Within the many reef cavities and below overhangs exist associations of encrusting corallines and other epizoans. The term secondary framework is used to describe these cryptic crustose associations because they overgrow or infill cavities in primary frameworks or cemented sediment and they make up a minor part of the two reef sections (0.7% and 7.7% of Isaacs and Shark Reef, respectively).

The major taxa involved in the construction of secondary frameworks as seen in thin section are: *Lithothamnium ruptile*, *Mesophyllum syntrophicum*, *Lithophyllum congestum* (crustose forms), *Neogoniolithon* sp., *Tenarea* sp., Vermetid gastropods, and Homotrematid foraminifers. Adey (1975) also lists *Archaeolithothamnium dimotum* as a cryptic coralline but this has not been seen in these sections.

TABLE 3. Frequency of pairing (total 77) of taxa in encrusting associations in thin section.

	<i>Lithophyllum congestum</i>	<i>Lithothamnium ruptile</i>	<i>Neogoniolithon</i>	<i>Mesophyllum syntrophicum</i>	vermetid	<i>Homotrema</i>
<i>Tenarea</i>	6	3	3	5	8	19
<i>Homotrema</i>	5	6	3	4	9	
vermetid	1	2	1	2		
<i>Mesophyllum syntrophicum</i>	0	0	0			
<i>Neogoniolithon</i>	0	0				
<i>Lithothamnium ruptile</i>	0					

Of the 7 encrusting taxa only some (15 pairs out of a possible 21 pairings) are found together in these frameworks. The crusts normally occur as alternating layers of 3 or 4 taxa in an association. Table 3 shows the frequency of occurrence of pairs (substrate and overgrowth) of encrusting organisms in secondary frameworks. The coralline *Tenarea* is abundant and ubiquitous (accounting for 63% of pairings) whilst *Homotrema* and vermetids are respectively less and less common but still ubiquitous. The corallines *Neogoniolithon* sp., *M. syntrophicum*, *L. congestum*, and *Lithothamnium ruptile* commonly overgrow or are overgrown by *Tenarea*, *Homotrema*, and vermetids but do not occur together in secondary crustose frameworks. This pattern of association permits a classification into five principal secondary frameworks in which *Tenarea*, *Homotrema*, and vermetids may occur alone or together with one of four other diagnostic coralline taxa, viz.

Tenarea-*Homotrema*-vermetid framework;

Lithothamnium-*Tenarea*-*Homotrema*-vermetid framework;

Mesophyllum-*Tenarea*-*Homotrema*-vermetid framework;

Neogoniolithon-*Tenarea*-*Homotrema*-vermetid framework;

Lithophyllum-*Tenarea*-*Homotrema*-vermetid framework.

All these frameworks are constructed by laminar to foliaceous crusts of corallines intergrown with *Homotrema* and vermetids. The competitive intergrowth of these corallines can be seen today in close up underwater photographs (text-fig. 4E) from overhangs and reef cavities. In vertical thin sections an interfingering growth of adjacent encrusters indicates competitive growth (Pl. 51, figs. 2-6). Cavities within these frameworks may be common where thin, foliaceous crustose growth occurs (*Lithothamnium*-*Tenarea*-*Homotrema*-vermetid framework) or rare where thick laminar crusts are

involved (*Neogoniolithon*-*Tenarea*-*Homotrema*-vermetid framework). Similarly, bioerosion is commoner in the latter, denser frameworks than in the former, more open frameworks. Cavities are either open, infilled with sediment, or filled with fans of aragonite cement (Pl. 51, fig. 6).

The secondary frameworks listed above are found in different environments on and within the reefs. The *Tenarea* dominated framework (Pl. 50, figs. 3, 4) is commonest on the underside of Shark Reef crest (SRC1, text-fig. 6; Pl. 50, fig. 3) and in what is interpreted as a fossil reef crest on block SRW2 (text-fig. 6). In both situations it overgrows a branching head of *Lithophyllum congestum*. Occasional thin crusts of this association (but with *Homotrema* dominating) are found over growth breaks in the primary frameworks.

The *Lithothamnium*-*Tenarea*-*Homotrema*-vermetid framework is found in both reef sections in similar successional positions. Most occurrences follow erosion or overgrow fresh *Lithophyllum congestum* or *P. pachydermum* frameworks. Other occurrences are where it alternates with the *Lithophyllum*-*Tenarea*-*Homotrema*-vermetid framework. Normally this association occurs in reef cavities (i.e. infilling *Echinometra* borings: SRC2, text-fig. 6). However, with sections deeper within the reef it is not possible to reconstruct the surrounding niche due to later boring and reef growth.

The *Neogoniolithon*-dominated association is found in the lower reef front wall of Shark Reef (SRW 2, text-fig. 6) and the *Mesophyllum*-dominated association occurs in cryptic habitats on both reefs (Pl. 50, fig. 3; Pl. 51, fig. 3). This association occurs with the large *Tenarea*-*Homotrema*-vermetid framework on the underside of the Shark Reef crest. It is also found on blocks on the floor of reef cavities (text-fig. 5, IRF1; text-fig. 6, SRF1).

The main occurrence of the *Lithophyllum*-*Tenarea*-*Homotrema*-vermetid framework is in the recently exposed areas on Isaacs Reef crest (text-fig. 5, IRW2-IRW4; Pl. 51, fig. 6). This occurrence represents the first stage in the development of the *L. congestum* branching framework and has been described above.

Discussion

The occurrence of coralline frameworks in the reefs is shown above to be closely tied to the specialized ecological requirements of the different coralline algae. Therefore, the presence of preserved frameworks in the reef sections (text-figs. 5, 6) can be used to reconstruct ancient reef morphology and environments. In both reef sections there is no evidence of any major erosion surfaces or breaks in growth. Therefore, reef growth is considered to be more or less continuous.

Isaacs Reef. The presence of preserved remnants of branching *Lithophyllum* and *Porolithon* frameworks in the interior of blocks at the bottom of the Isaacs Reef section (IRF1, text-fig. 5) indicate the former (c. 2,200 B.P.) presence of a high-intertidal reef forming in high energy conditions. Nothing is preserved of the shape or position of the reef crest. The base of the present-day ridge crest blocks (particularly IRC3, 4, 6, 7, text-fig. 5) records the change from an exposed mid-intertidal *Lithophyllum* reef to a high-intertidal *Porolithon* reef. The downward-curving *Porolithon* growth laminae in block IRC3 suggest a former outer edge to this reef crest. A high intertidal *Porolithon* reef crest has continued through to the present day with *Lithophyllum* on the front of the seaward edge.

Shark Reef. Extensive drilling by Adey (1975) showed that Shark Reef was founded on heads of *Acropora palmata* and *Millepora*. The present section penetrates to the top of the *Millepora* colonies. Overgrowing the *Millepora* are alternating frameworks of *Lithophyllum* and *Porolithon* (blocks SRF1, 2, text-fig. 6). The inner part of block SRW2 (text-fig. 6) shows a branching *Lithophyllum* framework overgrown by 2-6 cm thick convex-outwards secondary frameworks of both *Tenarea* and *Mesophyllum*-*Tenarea*-*Homotrema*-vermetid type. These frameworks are only found together today on the outer crest and lip of the sheltered Shark Reef (block SRC1, text-fig. 6). Therefore, this structure may be interpreted as an ancient reef lip developing as a response to quieter hydraulic conditions. This sheltered reef crest is succeeded within a few centimetres by *Lithophyllum* then *Porolithon* and then nearly 50 cm of well-preserved branching *L. congestum*. This represents a return to an exposed intertidal reef crest, (block SRW1, text-fig. 6). The remaining 30 cm of reef crest blocks record a high intertidal *Porolithon* crest with occasional intergrowths of branching *Lithophyllum*. The upper reef surface today is not concordant with this growth framework. Extensive *Echinometra*,

sipunculid, *Lithotrya*, and algal borings are eroding this surface and no live *Porolithon* has been recorded. These sheltered conditions are also recorded by the thick *Tenarea-Homotrema*-vermetid and *Mesophyllum-Tenarea-Homotrema*-vermetid secondary frameworks on the outer and under surface of the lip. Adey (1975) has suggested that the sheltered conditions are due to the build up of an *A. palmata* barrier reef across the mouth of Boiler Bay (text-fig. 4A) in the last 500 years.

ECOLOGICAL SUCCESSION

The change, through overgrowth, of one association of corallines to another is recorded in vertical sections in the reef slabs. Large-scale changes in frameworks have been discussed in the preceding sections. The reef frameworks in thin section illustrate ecological succession on a smaller scale. This is shown where fresh (broken) substrates are colonized or where new individuals overgrow and replace previous corallines. In this investigation, 350 overgrowths were recorded and the nature of the junction (bored, broken, simple) was observed. Overgrowths by the same species were not recorded. The successions were analysed by the probability of one taxon being overgrown by another. The sequences were studied within primary frameworks, overgrowths to primary frameworks, and secondary frameworks in the reef crests, walls, and interiors (text-fig. 8).

Succession within primary frameworks

In primary frameworks the commonest growth sequences, with or without a time break (which is indicated by boring into the substrate), is from laminar to branching *Lithophyllum* followed by an overgrowth of first laminar then columnar *Porolithon*. Columnar *Porolithon* is most commonly overgrown by *Lithophyllum* crusts (text-figs. 7, 8A). These observations confirm the large-scale association of these two frameworks and, because of the differing tolerances to exposure of these taxa, reflect fluctuating conditions of emergence. This could result from breakage of portions of reef in storms (there is evidence of this happening on the present-day reefs) or fluctuating sea level. Adey and Vassar (1975) measure accretion rates of 1–5 mm/yr which means that successions without a time break represent changes measured in years or tens of years. This short time span suggests that growth or breakage of reef crest sections is the most likely cause of local alteration of conditions of exposure.

Primary framework encrusters

The frequencies of overgrowths by encrusters on the primary reef frameworks are illustrated in text-fig. 8B and C. Breaks within *Porolithon* thalli are colonized mainly by *Tenarea* and *Homotrema* which are also the commonest encrusters on the preserved outer surfaces. None of the growth breaks within *Lithophyllum* was found to be colonized by other taxa. This may reflect the rapid growth rate of this coralline (up to 8 mm/yr, Steneck and Adey 1976). The commonest encrusters, mostly over dead bored branches of *Lithophyllum*, are *Homotrema*, *Tenarea*, and monostromatic crusts.

Secondary frameworks

An analysis of secondary frameworks identified five associations of encrusters. Within these associations there were alternations of overgrowth resulting in the accreting frameworks. This analysis records the sequence of overgrowths within these frameworks and between one association and another. Results of recording successions from the reef crests and interior cavities from both reefs were similar and have been combined for discussion (text-fig. 8D). Overgrowths in the Shark Reef wall were markedly different and are discussed separately (text-fig. 8E). Reef crest and wall and interior cavities are characterized by a large number of combinations (36 out of a possible 72 overgrowths) of a relatively small number of encrusters (8 corallines + *Homotrema*). Text-fig. 8D therefore only shows the commonest recorded sequences. Bored and broken surfaces and reef rock are most commonly overgrown by *Homotrema*, *Tenarea*, and monostromatic crusts (Pl. 51, figs. 3, 6).

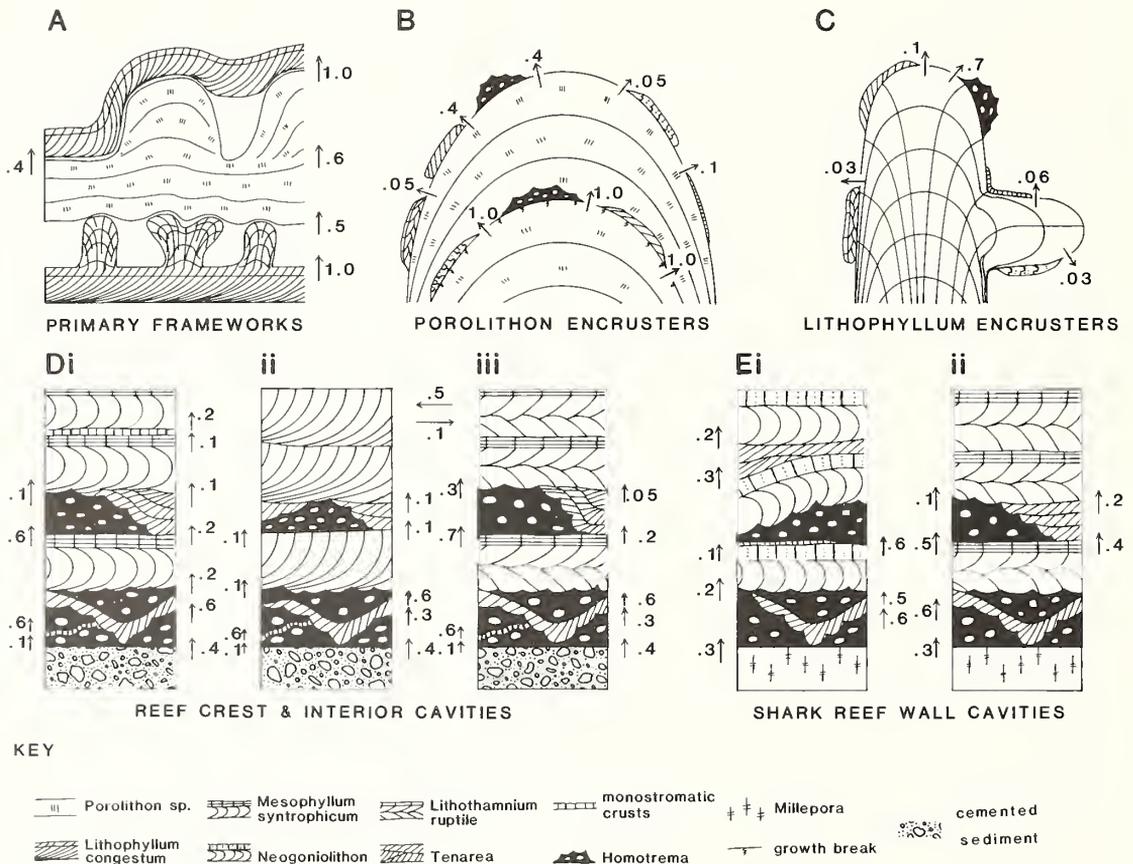
The pattern of subsequent colonization is again dominated by associations of *Lithothamnium ruptile* or laminar *Lithophyllum* or *M. syntrophicum*, all with *Tenarea* and *Homotrema*. The

succession of one of these associations by another is only occasionally found and is most commonly an alternation of laminar *Lithophyllum* and *Lithothamnium* frameworks (text-fig. 8Dii, Diii).

The Shark Reef wall overgrowth sequences are shown in text-fig. 8E. They differ from the previous overgrowths by the addition of large colonies of *Millepora* and crusts of *Neogoniolithon* (Pl. 51, fig. 5) and *Porolithon*. *Lithophyllum* and *Mesophyllum* are lacking and *Lithothamnium* is less frequent.

Discussion

The present-day succession of corallines on the St. Croix reefs has been studied by Adey and Vassar (1975). Plates placed in well-lit areas in 1–2 m of water in Boiler Bay were studied over a year. At or before 20–60 days *Leptoporpholithon* spp. dominate. *Tenarea* increases in importance up to 100 days and then *Neogoniolithon* increases at the expense of the early successional species. If grazing is heavy on plates *Leptoporpholithon* and *Tenarea* may increase. In shady reef cavities *Tenarea*, *Lithothamnium ruptile*, *Hydrolithon borgesense* occur. Adey and Vassar (1975) did not record the occurrence of *Homotrema*.



TEXT-FIG. 8. Ecological succession in coralline algal ridge frameworks. Arrows and numbers give direction and probability of the particular overgrowth illustrated; data from 352 observations of thin sections. A, succession of growth forms in *Lithophyllum* and *Porolithon* primary frameworks. B, frequency of encrusters within and on *Porolithon* frameworks. C, frequency of encrusters on *Lithophyllum* frameworks. Di–iii, succession within secondary frameworks in reef crests, interior cavities, and wall of Isaacs Reef. Ei, ii, succession in secondary frameworks within Shark Reef wall cavities.

A comparison of these successional patterns on plates with the vertical sequences described above (text-fig. 8) indicates many similarities, including the pioneer colonization by *Tenarea* and monostromatic crusts (cf. *Leptoporolithon*), and the later occurrence of *Lithothamnium ruptile* and *Tenarea* in cryptic environments. However, I additionally record later colonizations by *M. syntrophicum* and *Lithophyllum congestum* on both Isaacs and Shark reefs. *Neogoniolithon* occurs mainly in the reef wall of Shark Reef which corresponds to the positions of the settlement plates in Boiler Bay (Adey and Vassar 1975). Additional information here comes from the presence of *Lithothamnium ruptile* overgrowing fresh, branching *Lithophyllum congestum* in exposed areas. No *Lithophyllum* or *Porolithon* settled on the Boiler Bay plates but these appeared after 6 months on plates on the more exposed Fancy Algal ridge (Adey and Vassar 1975). The large degree of similarity between the results from these two investigations provides valuable evidence that ecological succession can be established with considerable accuracy from fossil material.

In a study of secondary frameworks from Recent and Pleistocene reefs in Barbados, Martindale (1976) noted no colonization succession in plates or vertical sections of crusts. However, Martindale (1976) does record a larger-scale successional change in fossil crusts over coral colonies. These represent the change from open, well-lit coralline associations (*Lithophyllum*, *Porolithon*, and *Neogoniolithon*) to cryptic associations of corallines (*Mesophyllum*, *Lithothamnium*, *Archaeolithothamnium*), bryozoans, serpulids, and foraminifers. He interprets these trends as recording the change with burial as the *Acropora palmata* thickets build up.

In reviewing ecological succession, Connel and Slatyer (1977) propose three process models to explain succession: (1) a facilitation model where successional colonizers modify the environment and make it suitable for later species, (2) a tolerance model where first arrivals are fast growing, rapid dispersers and later animals are better able to utilize resources, and (3) an inhibition model where no replacements occur until damage creates an opening which is then occupied by longer lived genera. The St. Croix data does not fit the facilitation model as colonizers in each case are encrusting a coralline substrate. Similarly, the inhibition model is inappropriate as Adey and Vassar (1975) have shown that succession returns to the pioneers after disturbance by heavy grazing. The available data best fits the tolerance model, for which Connel and Slatyer could find little supportive field evidence. Later organisms which overgrow the pioneers, are larger, more robust and longer lived than the thin, early colonizing monostromatic crusts and *Tenarea*. Grimes (1977) also suggests that vegetational successions are characterized by the replacement of small rapid dispersers, which are efficient at acquiring new space, by larger more durable and massive forms.

BIOEROSION

In both reef sections, both primary and secondary frameworks are bored to a variable degree (text-figs. 5, 6; Pl. 52). The main characteristics of these borings are similar to those described from Caribbean (Scoffin *et al.* 1980) and Bermudan (Ginsburg and Schroeder 1973; Scoffin and Garrett 1974) patch reefs with the exception of bivalve borings.

Echinoidea

Borings made by *Echinometra lucunter* are common today on the upper surfaces of both reefs (text-figs. 5, 6; Pl. 50, figs. 1, 3, 5; see also Abbott *et al.* 1974). Juveniles occupy spaces between coralline branches and as they grow specimens can be seen to have enlarged their holes by removing adjacent corallines. Borings are commonly up to 3–4 cm in diameter but may occasionally reach 6 cm. They penetrate down from the reef crest and sideways into the front wall of the reefs (text-figs. 5, 6) with sinuous J and U shapes in vertical section. Margins of occupied borings are clean, sharp, and truncated frameworks or cemented reef sediments. Stomach contents of *Echinometra* from Shark Reef contain 5–10% carbonate material by volume which is composed almost entirely of coarse sand-sized fragments of articulate corallines. Very occasional fragments of *Homotrema*, vermetids, crustose corallines, and reef rock are also found. Abbott *et al.* (1974) found that *Echinometra* grazed indiscriminately on epiphytes in Boiler Bay and record a positive correlation between occurrence of

taxa in gut contents with abundance of epiphytes on reefs. Grazing traces are common on both reef surfaces. Secondary crustose frameworks occur in both present-day and ancient *Echinometra* borings (text-fig. 6, slab SRC2; Pl. 50, fig. 5). Margins of borings may also contain smaller borings of sponges and algae.

Diadema antillarum is also a common grazer on the under surfaces of Shark Reef. Possible *Diadema* faecal pellets (cf. Hunter 1977) are found in the coarse fractions of inter-reef sediments (see below).

Lithotrya

Straight, subvertical borings by this endolithic barnacle are common on both reef crests (Pl. 52, fig. 3). They possess a distinctive oval cross-section (maximum diameters 5 and 10 mm; see Ahr and Stanton 1973). Margins to borings are sharp, smooth, and cut through both coralline framework and cemented reef sediment. Sinuosity is only seen where borers have to make a deviation around previous cavities. Borings penetrate to a maximum depth of 10 cm.

Sipunculoidea

Sipunculid worm borings are common on the upper reef surfaces (text-fig. 6). They are characterized by smooth-walled, sinuous borings which are circular in cross-section (maximum diameter 9 mm), and reach lengths of 4 cm. The borings typically have a rounded blind end within the reef.

Clionidae

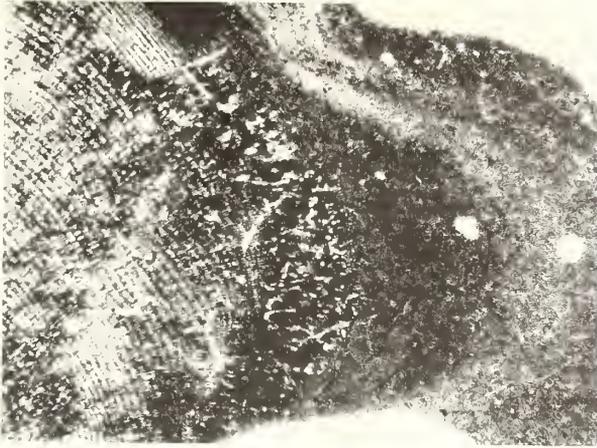
Chambers produced by clionid sponges are ubiquitous in reef slabs (text-figs. 5, 6; Pl. 52, figs. 2-4). Empty chambers account for 9 and 13.6% of the preserved blocks from Isaacs and Shark reefs, respectively. Both interior and exterior reef surfaces are bored, together with surfaces or previous larger borings. S.E.M. study reveals the characteristic sculpted surfaces of chambers and the excavated chips (Pl. 52, figs. 2-5). The chips form a significant proportion of the fine-grained intra-reef sediments (see below).

Algae

Endolithic algae are common as borers, particularly within coralline thalli. Their nature and occurrence is described above under *Lithophyllum congestum* and *Porolithon* primary frameworks.

EXPLANATION OF PLATE 52

- Fig. 1. Thin-section micrograph illustrating bored growth break in *Lithophyllum congestum*. Isaacs Reef crest (IRC1), $\times 36$.
- Fig. 2. S.E.M. micrograph of clionid sponge boring with excavated (scalloped) chip and other skeletal debris. Block SRC5 (text-fig. 6), $\times 436$.
- Fig. 3. *Lithotrya* (L) borings in reef fragment from Isaacs Reef Crest. Note characteristic smooth oval cross-section. Outer margin of specimen well-bored by clionid sponge(s), $\times 1$.
- Fig. 4. S.E.M. micrograph illustrating clionid sponge-bored coralline infilled with micrite peloids and skeletal debris with later endolithic algae. Block IRC4 (text-fig. 5), $\times 458$.
- Fig. 5. S.E.M. micrograph of fresh clionid sponge boring in micritized coralline. Note characteristic pitted surface where chips have been removed. Block IRC4 (text-fig. 5), $\times 24$.
- Fig. 6. Thin-section micrograph of cemented internal sediment illustrating abundant micrite and spar-cementing peloids, grains of *Homotrema*, and articulate coralline (lower right). Block SRF1 (text-fig. 6), $\times 100$.



1



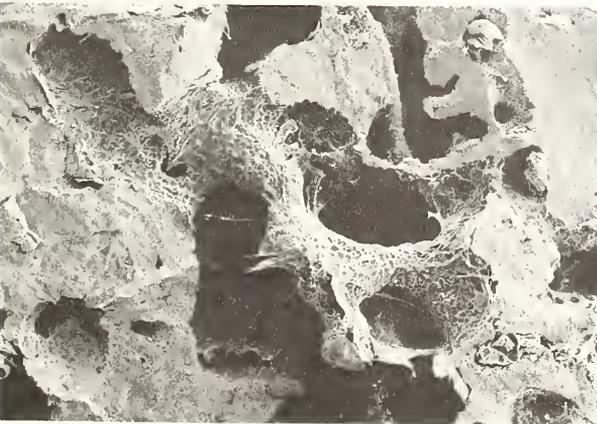
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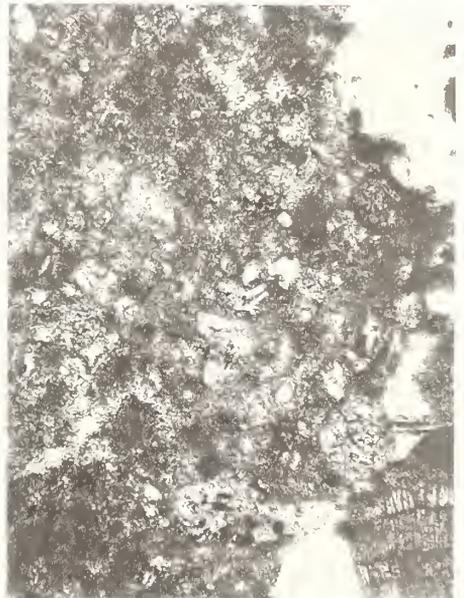
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6

BOSENCE, Coralline algal reefs

Shark Reef sediments have been divided into those from the fore and back reef areas for presentation (text-figs. 3, 9). Both areas have very coarse sand to granule-sized sediments which vary from very well to very poor sorting, the best-sorted sediments being in sand patches of the fore reef region which are being continually transported by wave currents. Small numbers of gravel-sized bioclastic grains result in grain size distributions that are coarsely to strongly skewed.

Sediment composition contrasts with that from Isaacs Reef in that *Halimeda* grains are about twice as abundant at the expense of coral grains. This is matched by an increase in cover of *Halimeda* around the patch reefs compared with Isaacs Reef. An almost pure *Halimeda* gravel forms the beach sediment behind the reefs. Also contrasting with Isaacs Reef, is an increase in abundance of coralline grains with decreasing grain size. Intraclasts, some of which resemble *Diadema* faecal pellets (Hunter 1977), are more abundant in the Shark Reef coarse-grained classes. The dominant 2ϕ modal class does not correspond with a greatly increased abundance of any particular grain type and is presumably due to hydraulic sorting.

Intra-reef sediment

Large areas of both Isaacs Reef (55%) and Shark Reef (37%) are made up of cemented internal sediment (Table 1). Cemented sediments from various parts of the reef all have very similar characteristics (text-fig. 9; Pl. 50, figs. 1, 3, 5; Pl. 52, figs. 4, 6). They are all subangular to very angular, fine to medium or medium-grained sands with a packstone texture. The dominant constituents being a brown micrite and spar cements (Pl. 52, fig. 6). Peloids are locally common (Pl. 52, fig. 4). Skeletal grains make up most of the remainder of these apparently grain-supported sediments. Foraminifers (mainly *Homotrema*) dominate (Pl. 52, fig. 6) and coralline fragments are the next most abundant. Traces of echinoid, bryozoan, serpulid, and spicule fragments also occur.

Discussion

In a simplistic view of patch reef sedimentation, a direct correlation might be expected between standing crops of carbonate secreting organisms and their abundance in inter- and intra-reef sediments. Scoffin *et al.* (1980) have investigated in detail the relationship between carbonate production and inter-reef sediments in a Barbados fringing reef. They find that sediments reflect most closely the primary frameworks of the reef. They also note that the sands are very well mixed in sediment patches across the Bellair reef. No carbonate production figures are available for Isaacs and Shark Reefs but a rough comparison can be made of abundance of grain types in inter-reef sediments with a visual impression of standing crops of producers. The only exception to this is the over-representation of *Halimeda* plates. This is well known from other regions (Garrett *et al.* 1970) and is accounted for by the rapid growth rate of this plant (Neumann and Land 1975). Evidence that bioerosion is a major source of sediment production from the reefs has been presented above. The removal of reef frameworks by sponges would be expected to result in a large proportion of coral and coralline algal grains in the silt size class of reef sediments. However, this size grade is not present as these sediments are continuously wave washed and silts are probably carried out into deeper quiet waters. This was found to be the case in similar reefs by Moore and Shedd (1977). The increased abundance of primary framework grains in the 1 to 3ϕ classes in Shark Reef (corals and coralline algae) and Isaac Reef (corals) may be accounted for by bioerosion as both *Diadema* and parrot fish produce grains of this size (Scoffin *et al.* 1980). The higher energy conditions at Isaac Reef exclude these bioeroders from the coralline ridges which may explain the decrease in abundance of corallines in the 1 to 3ϕ classes at this location. Mechanical abrasion of coralline branches and crusts could account for the greater abundance in the coarser-size classes.

Intra-reef sediments are significantly different in both texture and composition from inter-reef sediments in both localities. The consistent finer grain size of the internal reef sediments (cf. Garrett *et al.* 1970) may partly reflect the exclusion of larger particles from entering internal cavities and partly the high intra-reef production of silt-sized sponge chips (Pl. 52, figs. 2–4). Grains which are well represented both within and outside the reefs are derived from organisms constructing or living on the reefs: coralline algae, molluscs, foraminifers, and echinoids, with the addition of *Millepora* in

Shark Reef. The remaining coral and *Halimeda* grains are only common in the inter-reef areas. The exclusion of *Halimeda* and coral fragments from the internal cavities may be explained by their occurrence in the lower sea floors around the reefs and suggests that waves do not carry these grains up into the reef interstices. However, with burial of the reefs they may be expected to be deposited above the internal sediments derived from the reefs.

The earlier investigation of coralline patch reefs by Ginsburg and Schroeder (1973) allows some comparisons. External reef sediments were not studied but internal reef sediments contrast with those from St. Croix reefs. The textures of the internal sediments of the Bermuda reefs varied from silt wackestones through to coarse grainstones. The sand-sized material appears to be largely derived from the reef framework and reef encrusters with grain abundance decreasing in the following order: crustose and branching corallines, *Homotrema*, molluscs and other foraminifers, *Halimeda*, echinoid, serpulid, and ostracod. This compares well with the internal sediment grains (all sizes) identified in the Cruzan reefs (text-fig. 9). However, the silt-sized debris was found to be quite different in the Bermudan reefs being composed of fragile and encrusting reef organisms mixed with planktonic organisms. This population was not seen in either of the reefs investigated here, in thin section or under S.E.M.

Comparisons of inter-reef sediments with other Caribbean examples (mainly coral reefs) show that they are texturally similar (Milliman 1967, 1969; Scoffin *et al.* 1980). These earlier studies have also found coarsely skewed (i.e. winnowed) coarse sands and gravels forming near-reef sediments. Compositionally it might be expected that the coralline algal reef sediments would differ from coral reef sediments. However, this is not the case (see Milliman 1973 for review). Other Caribbean reef sediments are dominated by either coral, coralline, and *Halimeda* grains and often show greater proportions of coralline grains than is found in the St. Croix coralline reef sediments. This apparent anomaly might be explained firstly by the abundance of coral stands around the Cruzan algal reefs (text-figs. 2, 3) and secondly by the fact that most of the erosion of the coralline framework is considered to be in the form of silt-sized sponge chips which are not deposited in the inter-reef sediments.

COMPARISONS AND CONCLUSIONS

Comparisons

Previous studies of shallow coralline reefs have been undertaken in the Caribbean (Boyd *et al.* 1963), the Mediterranean (Thornton *et al.* 1978), and Bermuda (Ginsburg and Schroeder 1973). Each study describes subcircular patch reefs (cup reefs), which may coalesce to form a lobate ridge. In vertical section, preferential growth of the corallines is visible on the outer edge which may result in a raised rim or crest and an overhanging lip. The upper surface of the patch reefs is generally dish-shaped, with less coralline growth and greater bioerosion in the central depressed area. With the exception of Ginsburg and Schroeder (1963) none of the previous authors have described the nature of the coralline reef framework. The corallines vary with location and sample sites on the reefs: Boyd *et al.* (1963) collected samples from the reef sides and reported *Neogoniolithon* (*Goniolithon*) *solubile*, *Archaeolithothamnium episorum*, *Lithothamnium sejunctum*, *Epilithon membranaceum*. Thornton *et al.* (1978) reported a framework of thin crusts of *N. notarisii* with some *Lithophyllum* indicating a similarity to the well-known Mediterranean 'trottoirs' (Pèrès 1967; Laborel 1961). The most detailed study is by Ginsburg and Schroeder who describe frameworks of crustose corallines, *Millepora*, and vermetids. The Bermudan reefs are similar in many respects to those from St. Croix but differ in their greater height (8–12 m) and lower porosity. Coralline frameworks are constructed by laminar and columnar *Neogoniolithon* sp. with lesser *Mesophyllum syntrophicum*. They do not show the diversity of taxa or morphologies described in this paper. The complex sequences of reef growth, destruction, internal sedimentation, and cementation characteristic of patch reef formation (Schroeder and Zankl 1974; Scoffin and Garrett 1974) are common to the two examples.

Some similarities are also apparent with intertidal ledges built by crustose corallines in the Caribbean (Gessner 1970), on the Brazilian coast (Kempf and Laborel 1968), and in the

Mediterranean (Pèrès 1967; Laborel 1961). A comparison with the Pacific algal ridge systems (Emery *et al.* 1954) and deep-water coralline build-ups from the Mediterranean (Laborel 1961; Laubier 1966) is made in a recent review on coralline reef frameworks (Bosence 1983b).

Conclusions

1. The internal structure of two recent coralline reefs has been studied and nearly all the coralline algae living on the surface can be identified in thin sections from the reef interior. The occurrence of these preserved corallines can be used for palaeoenvironmental reconstruction.

2. Two main primary framebuilding coralline algae (*L. congestum* and *Porolithon pachydermum*) which today construct the intertidal algal ridge were abundant in the past in both reef sections.

3. Secondary reef frameworks occur in five associations of corallines (with *Homotrema* and vermetid gastropods) and each association is characteristic of different sub-environments on the reef and can thus be used in palaeoenvironmental reconstruction of the reef surface.

4. The occurrence of preserved primary and secondary frameworks in the slabbed reef sections permits a generalized reconstruction of past reef morphology and environment.

5. Isaacs Reef has alternated from a high- (*Porolithon* dominated) to mid-intertidal (*Lithophyllum* dominated) ridge during the last c. 2,200 years.

6. Shark Reef has had a more varied history alternating from an exposed intertidal reef to two periods of sheltered conditions during which a thick subtidal lip of secondary framework grew and the upper reef surface became reduced by bioerosion.

7. A predictable ecological succession of taxa and growth forms, and of subsidiary encrusters, is found in the primary frameworks.

8. Vertical sections through secondary frameworks illustrate predictable palaeoecological successions which equate well with previous settlement-plate experiments. Small fast-growing and presumed rapid dispersers are replaced by more massive, framework-building associations.

9. The major form of erosion on the reefs is bioerosion which is carried out mainly by clionid sponges and echinoids.

10. Inter-reef sediments are well- to poorly sorted coarse sands and gravels with symmetric to coarsely skewed distributions. Size ranges reflect the locally derived reef material and continual movement and winnowing by wave currents.

11. Compositionally, the inter-reef sediments reflect the composition of the reef frameworks, but are relatively depleted in coralline debris. Surprisingly, the sediments have a similar composition to Caribbean coral patch reefs. The relatively small amount of coralline material in the sediments is thought to be due to sponge erosion releasing silt-sized debris which is deposited in quieter waters away from the reefs.

12. Internal reef sediments are well-cemented and reflect the composition of the reef frameworks.

Acknowledgements. The assistance, advice, and previous work by Walter Adey and Bob Steneck (Smithsonian Institution) were invaluable in planning this project and I thank them also for reading an earlier version of this paper. Staff and students from the West Indies Laboratory, St. Croix, provided logistical support for fieldwork which made the study possible. Finance was provided by Goldsmiths' College Research Committee and is gratefully acknowledged. I thank Tom Easter, Owen Green, John Maddicks, and Doreen Norman at Goldsmiths' for technical and secretarial help.

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THE POSTCRANIAL SKELETON OF THE UPPER TRIASSIC SPHENODONTID *PLANOCEPHALOSAURUS ROBINSONAE*

by N. C. FRASER and G. M. WALKDEN

ABSTRACT. The postcranial skeleton of the Triassic sphenodontid, *Planocephalosaurus robinsonae*, is described from dissociated remains recovered from the type locality at Cromhall Quarry, South Gloucestershire. A full reconstruction is outlined and its relationships within the Sphenodontidae are briefly discussed. A lower Jurassic eosuchian, *Gephyrosaurus bridensis*, is shown to share a number of characteristics with *P. robinsonae*, and *Gephyrosaurus* is consequently considered to be either a member of the Sphenodontidae or an offshoot from the stem Sphenodontidae.

ABUNDANT dissociated sphenodontid and archosaurian reptile remains are known from the Triassic fissure deposits of Cromhall Quarry, South Gloucestershire (Robinson 1973; Fraser 1982; Fraser and Walkden 1983). The skull of the most common of the sphenodontids, *P. robinsonae*, was recently described by Fraser (1982) and this paper deals with the postcranial skeleton of the same species.

Whilst a number of similar-sized reptiles are represented in the deposits the much greater preponderance of *Planocephalosaurus* elements (text-fig. 1) aids in their separation from the remaining material. However, because the Cromhall sphenodontids have similar postcranial structures, it is still possible to confuse some elements with juveniles of the larger *Clevosaurus hudsoni*, particularly in the more poorly preserved fossils. To avoid such difficulties only elements from a single site, where *Clevosaurus* is rare, have been considered. At this site (fissure four, text-fig. 1) archosaurs constitute the major percentage of the non-*Planocephalosaurus* material and are readily distinguished from sphenodontid elements.

Preservation of the bone is generally excellent although few bones are absolutely complete (Pls. 53 and 54 illustrate the typical nature of the material). The numbers of bones recovered which are more than half complete are shown in the Appendix. In addition, hundreds of smaller, yet still quite readily identifiable, fragments have been sorted from the residue and examined. In order that complete bones could be illustrated, most of the reconstructions have been based on more than one specimen, but the major part of any reconstruction is represented by a single specimen which is the one referred to in the legend.

Although most of the skeleton of *Planocephalosaurus* is represented some of the more fragile elements are either incomplete or not known at all. Despite this, a reliable reconstruction has been made which shows *Planocephalosaurus* as a lizard-like animal (text-fig. 2) with a lightly built skeleton indicating agility and swift action in prey capture and predator avoidance.

From a study of its dentition (Fraser and Walkden 1983), *Planocephalosaurus* was considered to have been primarily insectivorous, although possibly capable of taking newly hatched specimens of small sphenodontids if the opportunity arose.

AXIAL SKELETON

The vertebrae are generally quite well preserved although the articulation facets for both the ribs and the adjacent vertebrae are commonly a little eroded and the neural spines are usually incomplete.

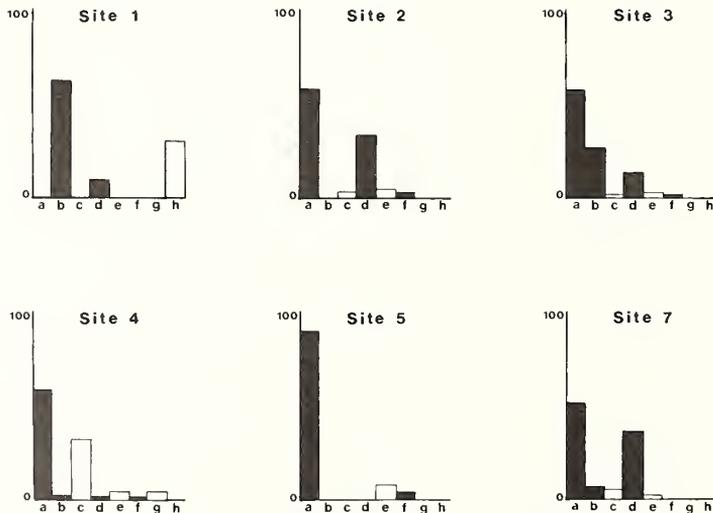
Amongst the vertebrae can be recognized the usual cervical, dorsal, sacral, and caudal elements,

but because the material is completely dissociated it is not possible to determine the exact number of vertebrae in each region. For the purposes of the reconstruction it has been assumed that there are twenty-five presacrals, two sacrals, and between thirty and thirty-six caudals corresponding to the distribution in the only extant sphenodontid, *Sphenodon*. The centrum is of the notochordal amphicoelous type throughout. There is a rudimentary zygosphenic articulation (text-fig. 9a; Pl. 53, fig. 7) with the development of a zygosphenon and zygantrium.

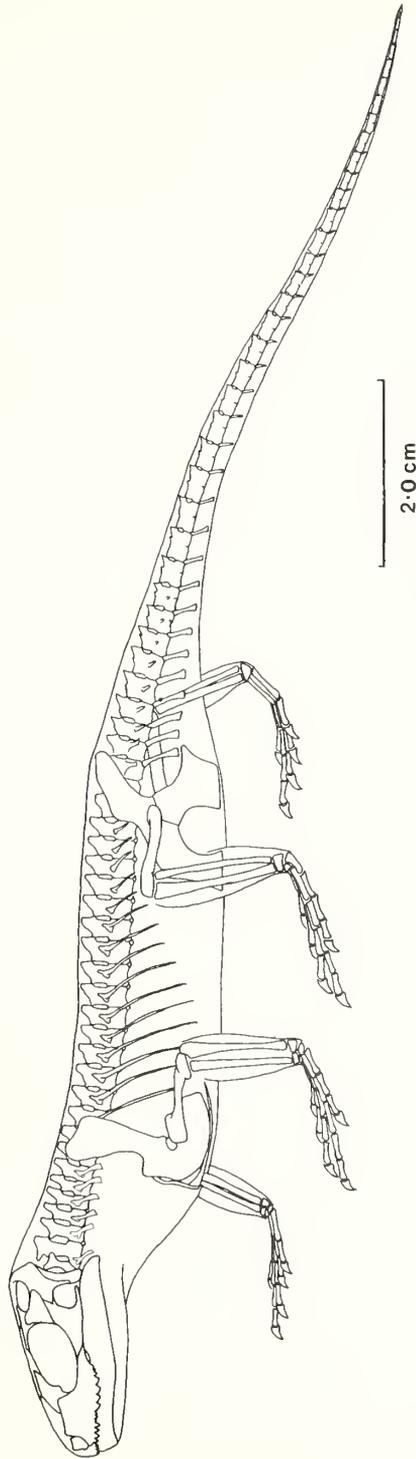
The element that was tentatively designated as the epipterygoid of *Planocephalosaurus* (Fraser 1982) is now known to be one of a pair of elements that met in the midline dorsal to the neural canal and together formed the atlas neural arch (text-fig. 3). A ventral process on each element articulated with the odontoid process medioventrally and with the atlas intercentrum ventrally. There is a postzygapophysial articulation with the axis, but the anterior process bears no facets and connective tissue probably attached it to the skull. The axis prezygapophysis takes the form of a simple circular facet that is directed dorsolaterally and overlapped by the atlas neural arch.

The odontoid process is formed by the fusion of the atlas and axis centra (text-fig. 4); a faint suture on the dorsal surface is the sole remaining evidence of their separate centres of ossification. The atlas intercentrum has not been positively identified but that of the axis has been fused to the centrum and bears a rib parapophysis on each side. The diapophyses for the axial ribs lie on the centrum.

As previously stated it is difficult to assess the precise number of cervical vertebrae; *Sphenodon* has eight, but the Jurassic sphenodontids such as *Homeosaurus* and *Kallinodon* have just seven. In the reconstruction (text-fig. 2) *Planocephalosaurus* has been shown with eight. Excluding the atlas and axis, the cervicals are typically short with widely spaced zygapophyses angled at approximately 40° (text-fig. 5; Pl. 53, fig. 3). In the first one or two elements the parapophyses are situated on the edge of the intercentrum and separate diapophyses occur along the centrum/neural arch boundary, slightly posterior to the level of the parapophyses. The corresponding cervical ribs display separate capitula and tuberculae. The diapophyses on the more posterior cervical vertebrae show a tendency to form an elliptical-shaped facet that is elongated in a posterodorsal-anteroventral direction. These



TEXT-FIG. 1. The abundance of the predominant reptile genera at each of six fossiliferous fissure deposits at Cromhall Quarry. □—sphenodontid, ◻—non-sphenodontid, a—*Planocephalosaurus*, b—*Clevo-saurus*, c—a pseudosuchian, d—a small sphenodontid, e—a primitive crocodile, f—*Sigmala*, g—*Kuehneosaurus*, h—a pseudosuchian.

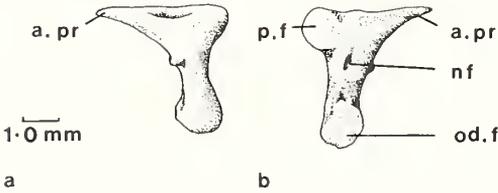


TEXT-FIG. 2. Restoration of the skeleton of *Planocephalosaurus robinsonae*.

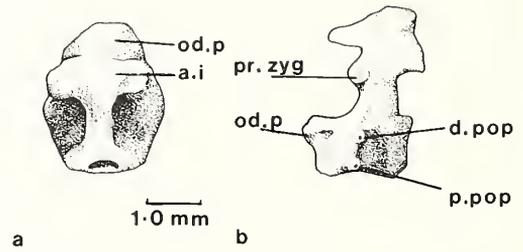
diapophyses articulated with enlarged tuberculae on the ribs but posteriorly the small capitulum soon becomes reduced until it fails to articulate with the parapophysis and both are subsequently lost. Hoffstetter and Gasc (1969) believe that in *Sphenodon* the parapophyses migrate dorsally to meet the diapophyses thereby forming elliptical-shaped synapophyses. For the posterior rib facets of *Planocephalosaurus* to be considered as true synapophyses, the diapophyses need to have enlarged at the same time as the parapophyses migrated dorsally; however, the evidence would suggest that the diapophyses enlarged to the exclusion of the parapophyses without any fusion of the two facets. In this way *Planocephalosaurus* apparently differs from *Sphenodon* in the formation of the elliptical-shaped dorsal rib facets.

Where the exact transition between cervical and dorsal vertebrae takes place is unknown, but the dorsal vertebrae are generally longer, with the elliptical facets for the rib articulation situated more dorsally on the neural arch (text-fig. 6). However, these rib facets become progressively smaller in the posterior members of the dorsal series (text-fig. 7). In comparison with the cervical vertebrae the zygosphenic articulation on the dorsals is slightly more pronounced.

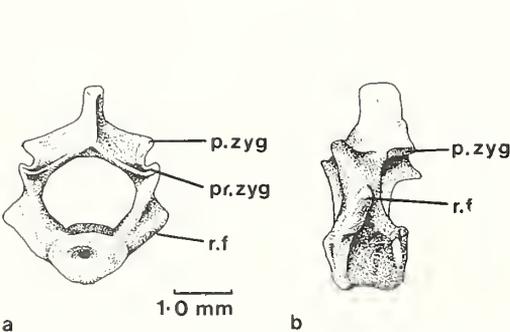
The two sacral vertebrae (Pl. 53, figs. 9, 10) have not been recovered in the fused condition. However, a clear distinction can be made between them (text-fig. 8). In both instances the very stout ribs are fused to the vertebrae with no trace of a suture, but in the first sacral these ribs are directed slightly ventrally, whereas in the second sacral each rib extends laterally and also bifurcates distally.



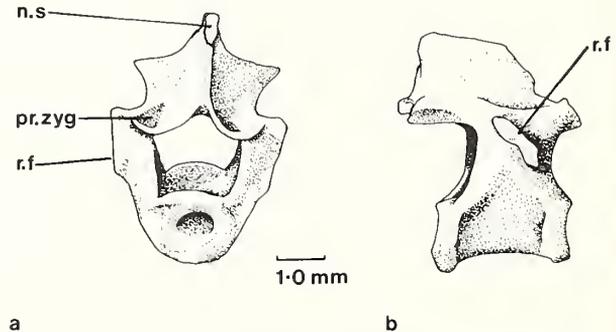
TEXT-FIG. 3. *Planocephalosaurus robinsonae*. Atlas neural arch. AUP No. 11136. *a*, lateral view and *b*, mesial view. See list of Abbreviations used in Text-figures, pp. 594-5.



TEXT-FIG. 4. *Planocephalosaurus robinsonae*. Reconstruction of the atlas/axis complex from AUP No. 11137. *a*, ventral and *b*, lateral aspects.

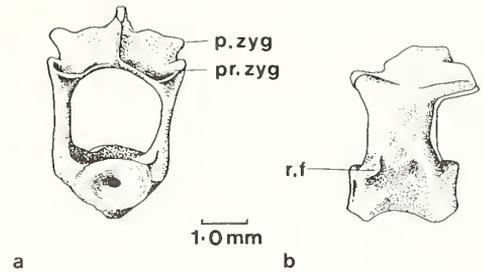


TEXT-FIG. 5. *Planocephalosaurus robinsonae*. Reconstruction of a cervical vertebra from AUP No. 11138. *a*, anterior and *b*, lateral aspects.



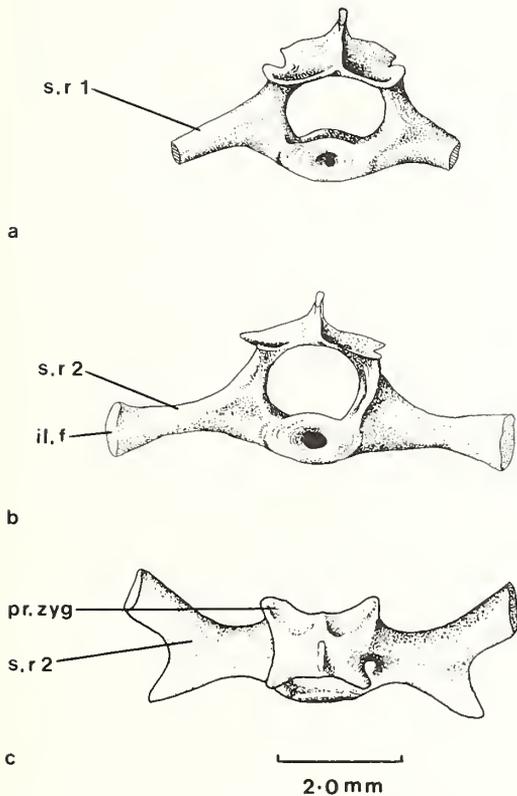
TEXT-FIG. 6. *Planocephalosaurus robinsonae*. Reconstruction of a mid-dorsal vertebra from AUP No. 11139. *a*, anterior and *b*, lateral aspects.

TEXT-FIG. 7. *Planocephalosaurus robinsonae*. Reconstruction of a posterior dorsal vertebra from AUP No. 11096. *a*, anterior and *b*, lateral views.

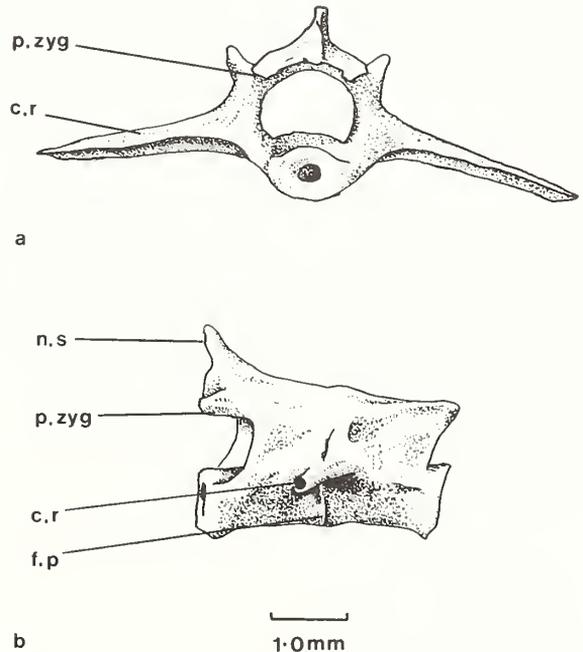


An anterior process extends both towards the rib of the first sacral and laterally to an articulation with the ilium. The posterior process bears no articulation facets and was presumably solely for muscle attachment. Such bifurcation of the second sacral ribs is also observed in the three Jurassic sphenodontid genera: *Homeosaurus*, *Kallimodon*, and *Sapheosaurus* (Hoffstetter and Gasc 1969), as well as in *Clevosaurus* (Swinton 1939).

The anterior caudal vertebrae are approximately equal in length to the posterior dorsals and they bear dorsoventrally compressed ribs projecting at right angles to the spinal cord (text-fig. 9*a*; Pl. 53, fig. 12). These ribs are fused to the neural arch and possess shallow ventral grooves. The neural spines



TEXT-FIG. 8. *Planocephalosaurus robinsonae*. Reconstructions of the sacral vertebrae. *a*, anterior view of the first sacral from AUP No. 11097. The second sacral in *b*, anterior view and *c*, dorsal view from AUP Nos. 11098 and 11099.



TEXT-FIG. 9. *Planocephalosaurus robinsonae*. Reconstructions of caudal vertebrae. *a*, posterior view of an anterior caudal from AUP No. 11100 and *b*, lateral view of a mid-caudal from AUP No. 11101.

are less elongated than in the dorsal series. Posteriorly the vertebrae become more elongate whilst the transverse processes become progressively shorter, more circular in cross-section, and directed posterolaterally rather than laterally (text-fig. 9*b*). They are eventually lost altogether (Pl. 53, figs. 13, 14). In the same way the neural spines become smaller and the zygapophyses converge until they form nothing more than rudimentary contact points. Fracture planes are present and these appear in the anterior members of the caudal series where the vertebrae are relatively short and still bear small transverse processes (text-fig. 9*b*): at an estimate between caudal 5 and caudal 10.

With the exception of the fused atlas and axis there are small anteroventral and posteroventral facets on all the centra of the vertebral column which testify to the presence of intercentra throughout. Probably as a result of their small size and delicate nature none has been positively identified from the cervical region and only a few have been recovered representing the dorsal region. These dorsal intercentra are simple crescent-shaped bands of bone (text-fig. 10*c*), but the caudal intercentra take the form of chevron bones which possess a triangular fossa to allow for the passage of the caudal nerves and blood-vessels (text-fig. 10*a*). Below this fossa a medial ventrally directed process separated the muscle blocks on either side of the tail. The anterior chevron bones have a basal transverse bar at the point of attachment to the vertebral column, but in the posterior chevrons this bar is reduced so that the chevron is borne on two separate pedicels (text-fig. 10*b*; Pl. 53, fig. 18).

As already mentioned, the ribs were typically of the holocephalous type, the capitulum having been lost and the tuberculum expanded. However, in the first two or three cervical vertebrae there are small parapophyses and correspondingly the first three or four cervical ribs also possessed rudimentary capitula (text-fig. 11*a*). These may not necessarily have articulated with the parapophyses since ligaments could have completed the attachment where the capitula were reduced to mere protruberances. The posterior cervical ribs possess a short shaft that is expanded distally (text-fig. 11*b*; Pl. 53, fig. 17) whilst in the dorsal ribs the shaft is generally narrow and longer—particularly in the anterior dorsals (text-fig. 11*c*).

PECTORAL GIRDLE

In total, five elements contribute to the pectoral girdle: one interclavicle, two clavicles, and two scapulocoracoids. There is no suture visible separating the scapula from the coracoid.

The interclavicle is a T-shaped bone with a slender anterior crossbar that supported the clavicles (text-fig. 12*a*; Pl. 53, fig. 16). This crossbar curves dorsally at its distal extremities. The facets for the clavicles are situated on the anteroventral edge of the bone and take the form of confluent grooves allowing the paired clavicles to meet at the midline.

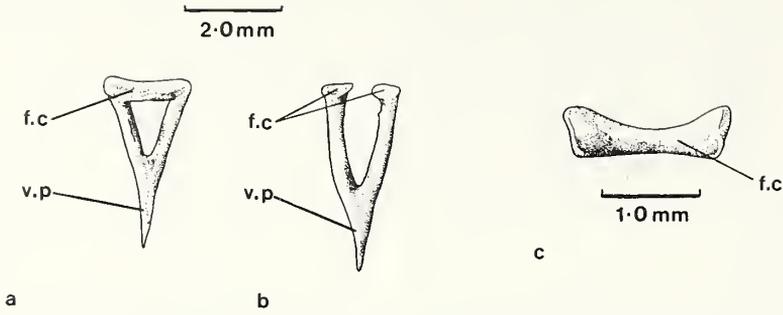
The clavicles are slender rod-like elements that curve dorsoventrally from their articulation with the interclavicle (text-fig. 12*b, c, d*). A long slender depression on the posteroventral surface represents the facet for the interclavicle and there is a small notch at the distal end where it makes contact with the scapulocoracoid. However, the posterolateral border of the clavicle possibly abutted against a cartilagenous zone of the scapulocoracoid for a short distance ventral to this notch.

EXPLANATION OF PLATE 53

Figs. 1-19. *Planocephalosaurus robinsonae*. 1, AUP No. 11093, atlas/axis complex, right lateral view, $\times 8$. 2, AUP No. 11123, atlas/axis complex, anterior view, $\times 9$. 3, AUP No. 11094, cervical vertebra, anterior view, $\times 9$. 4, AUP No. 11094, cervical vertebra in anterior, left lateral, and posterior views, $\times 6.5$. 8, AUP No. 11096, posterior dorsal vertebra, anterior view, $\times 10$. 9, AUP No. 11097, 1st sacral vertebra, anterior view, $\times 8.5$. 10, AUP No. 11098, 2nd sacral vertebra, anterior view, $\times 7$. 11, AUP No. 11098, 2nd sacral vertebra, dorsal view, $\times 7$. 12, AUP No. 11124, anterior caudal vertebra, anterior view, $\times 8$. 13, AUP No. 11125, mid-caudal vertebra, left lateral aspect, $\times 10$. 14, AUP No. 11126, caudal vertebra, left lateral aspect, $\times 7$. 15, AUP No. 11110, right scapulocoracoid, posterolateral view, $\times 5.5$. 16, AUP No. 11108, interclavicle, ventral aspect, $\times 8$. 17, AUP No. 11127 and 11106, cervical ribs, $\times 6$. 18, AUP No. 11104, chevron bone, $\times 8$. 19, AUP No. 11109, right clavicle, $\times 6.5$.

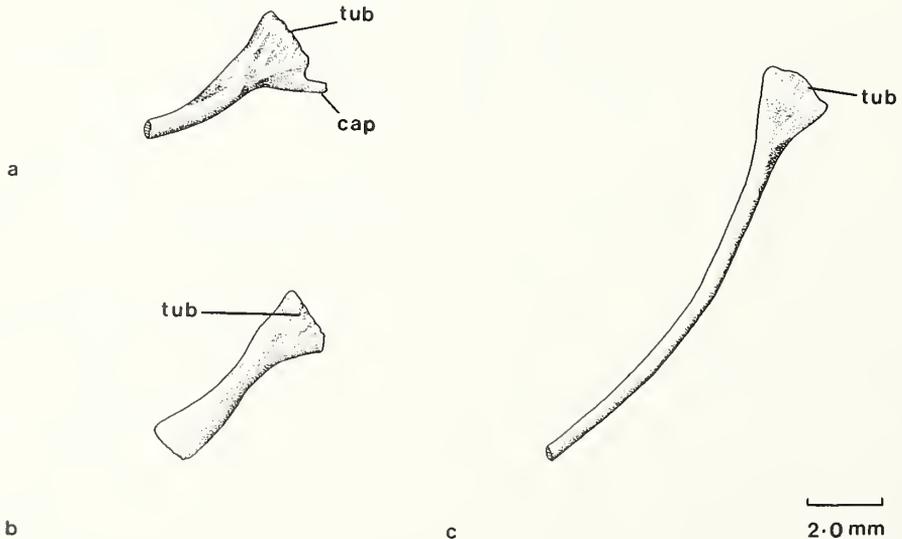


FRASER and WALKDEN, Upper Triassic sphenodontid

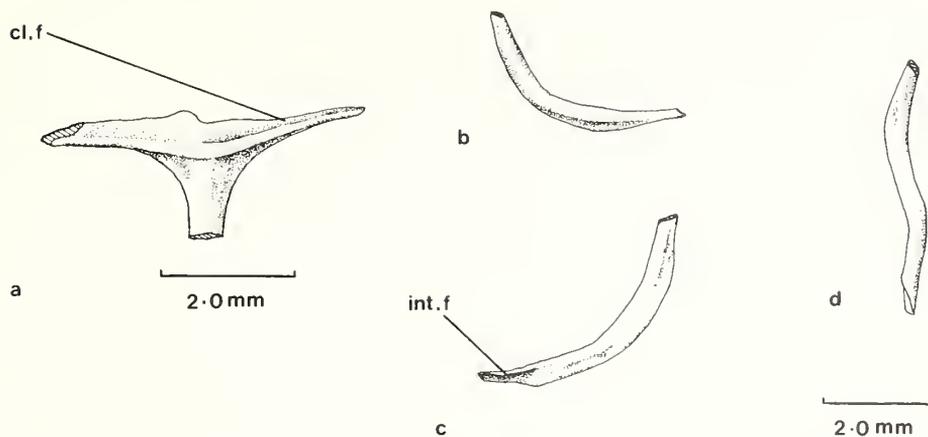


TEXT-FIG. 10. *Planocephalosaurus robinsonae*. Intercentra. *a*, anterior chevron bone, AUP No. 11103, in anterior view. *b*, posterior chevron, AUP No. 11104, anterior view. *c*, dorsal intercentrum, AUP No. 11102, dorsal view.

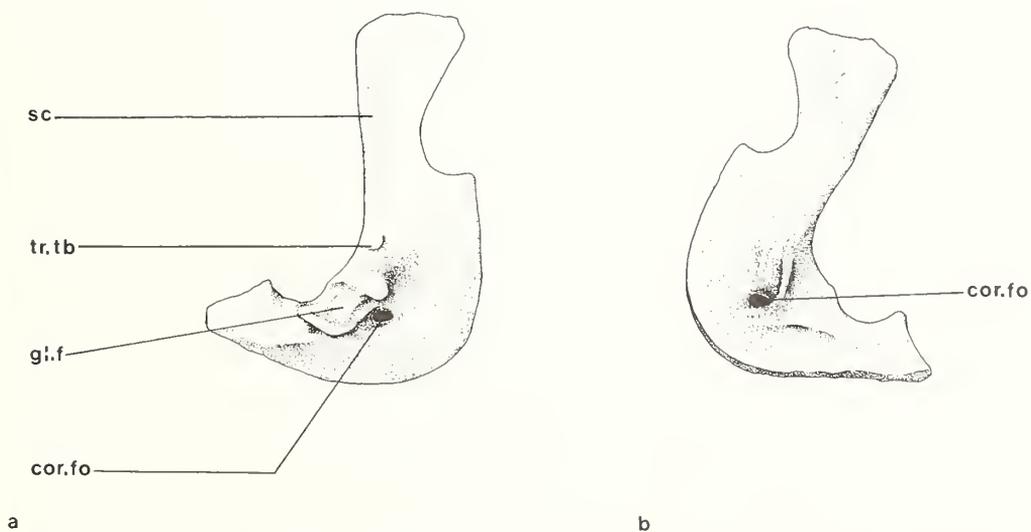
The scapulocoracoid is generally rather poorly preserved, but there are one or two almost complete specimens (text-fig. 13; Pl. 53, fig. 15). The glenoid fossa is the most robust part of the bone and consequently is more frequently preserved. It bears well-developed buttresses to support the proximal head of the humerus. Anterior to the glenoid is the supracoracoid foramen which carried the supracoracoid nerve and associated blood-vessels. Along the posterior margin of the bone, immediately dorsal to the glenoid, is a small tubercle to which the triceps tendon was attached. The element extends dorsally and there is a single fenestration entering into the anterior margin of the scapula blade which, as in the Lacertilia, probably related to the origin of the limb musculature (Romer 1956).



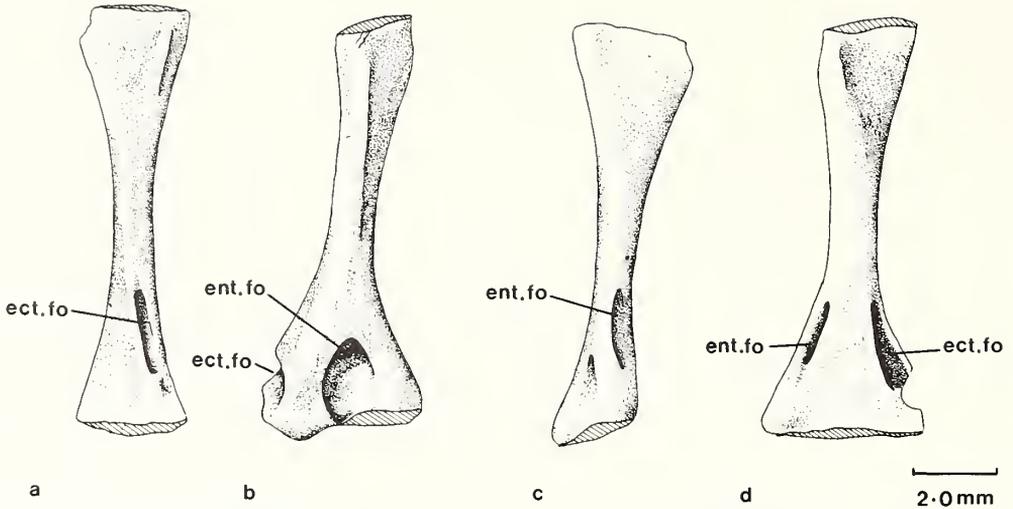
TEXT-FIG. 11. *Planocephalosaurus robinsonae*. Ribs. *a*, anterior cervical, AUP No. 11105. *b*, posterior cervical, AUP No. 11106. *c*, anterior dorsal, AUP No. 11107.



TEXT-FIG. 12. *Planocephalosaurus robinsonae*. Dermal elements of the pectoral girdle. *a*, an interclavicle, AUP No. 11108, in ventral aspect. Right clavicle, AUP No. 11109, in *b*, anterior view, *c*, posterior view, and *d*, dorsal view.



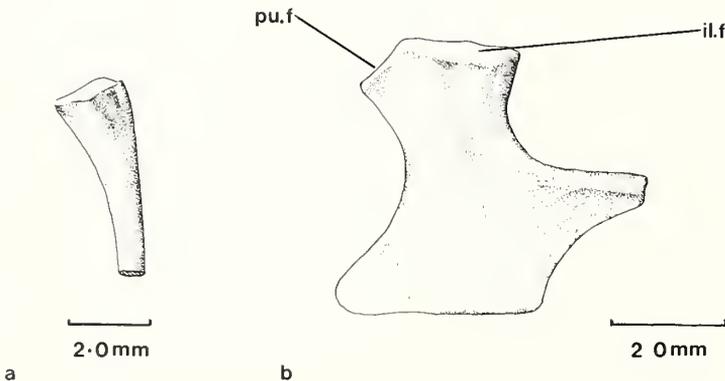
TEXT-FIG. 13. *Planocephalosaurus robinsonae*. Reconstruction of a right scapulocoracoid from AUP Nos. 11110 and 11111. *a*, lateral and *b*, mesial aspects.



TEXT-FIG. 14. *Planocephalosaurus robinsonae*. Partial reconstruction of the humerus from AUP Nos. 11112 and 11113. *a*, anterior, *b*, ventral, *c*, posterior, and *d*, dorsal aspects.

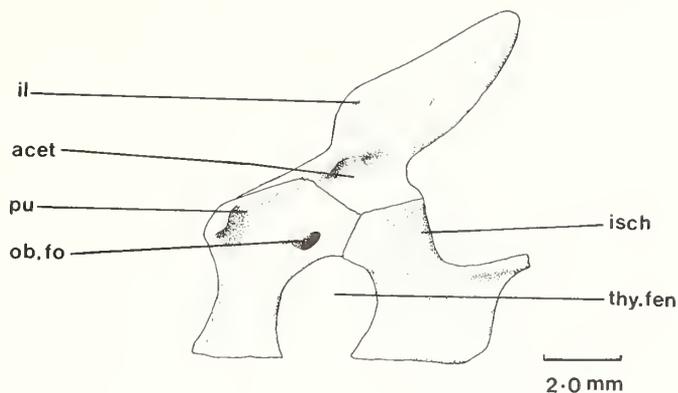
FORELIMB

The humerus (Pl. 54, figs. 1-4) is a slender element bearing expanded and compressed proximal and distal heads with an axial twist of the shaft so that the planes of the two heads are approaching 90° to each other (text-fig. 14). The proximal head is flattened anteroposteriorly with a ridge on the anteroventral edge marking the insertion of the latissimus dorsi muscle (text-fig. 14*a*). A similar ridge on the posteroventral edge was for the insertion of the deltopectoralis muscle (text-fig. 14*b*). The distal head is dorsoventrally compressed with the entepicondyle expanded slightly more than the ectepicondyle. The entepicondyle is perforated by a foramen (text-fig. 14*c*) which opens into a deep depression on the ventral surface (text-fig. 14*b*). The ectepicondyle foramen (text-fig. 14*d*), which allows for the passage of the radial nerve and blood-vessels, generally appears more as a groove than a foramen since the bone bridging across the canal is thin and membranous and thus prone to fragmentation. The articular surfaces on both proximal and distal heads have not been preserved in any of the specimens recovered.



TEXT-FIG. 15. *Planocephalosaurus robinsonae*. *a*, proximal head of an ulna, AUP No. 11114. *b*, lateral aspect of a left ischium, AUP No. 11115.

TEXT-FIG. 16. *Planocephalosaurus robinsonae*. Composite reconstruction of a left pelvic girdle in lateral aspect.

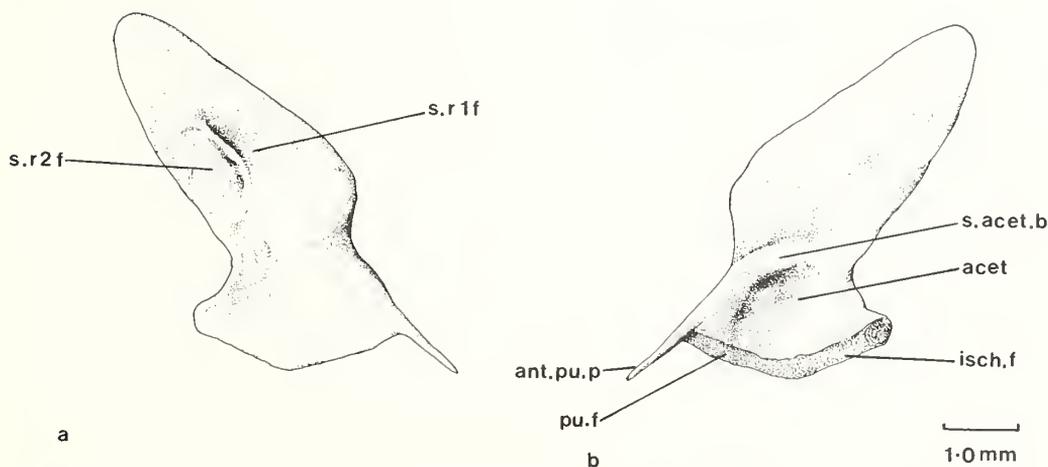


The epipodials are not as well represented being more slender and consequently rather more vulnerable to breakage. Only the proximal end of the ulna is completely known (text-fig. 15a). The expanded head is flattened anteroposteriorly and in all probability bore an olecranon epiphysis which is missing in all the recognizable specimens. There is a shallow depression on the posterior surface of the head outlining an area for muscle attachment. The shaft is narrow and circular in cross-section.

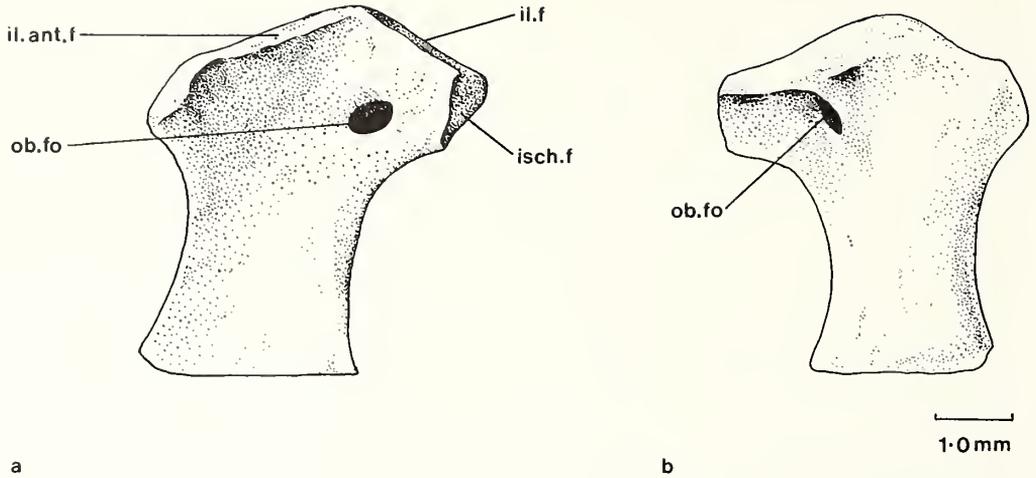
PELVIC GIRDLE

All three elements of the pelvic girdle are well represented in the deposits and a complete reconstruction is possible (text-fig. 16).

The ilium (Pl. 54, fig. 5) consists of a posterodorsally directed iliac blade which medially bears articular surfaces for the two sacral ribs (text-fig. 17a). The bone expands ventrally to form the major part of the acetabulum which is bounded dorsally by a well-defined supracetabular buttress (text-fig. 17b). On the anterior edge of the element, just dorsal to the buttress, is a small tuberosity for the attachment of the iliotibialis muscle. There are broad ventral contacts with the pubis and ischium and in addition an anterior process sheathed the anterior edge of the pubis thereby lending rigidity to the structure of the girdle.



TEXT-FIG. 17. *Planocephalosaurus robinsonae*. Reconstruction of left ilium from AUP No. 11116. a, mesial and b, lateral aspects.



TEXT-FIG. 18. *Planocephalosaurus robinsonae*. Left pubis, AUP No. 11117. *a*, lateral and *b*, mesial aspects.

The pubis (text-fig. 18*a*; Pl. 54, fig. 6) bears a dorsal facet for the ilium and a shorter posterior facet for the ischium. An obturator foramen is situated just anterior to the latter facet. The ventral plate of the bone is emarginated posteriorly by the thyroid fenestra which separates the pubis from the ischium ventrally.

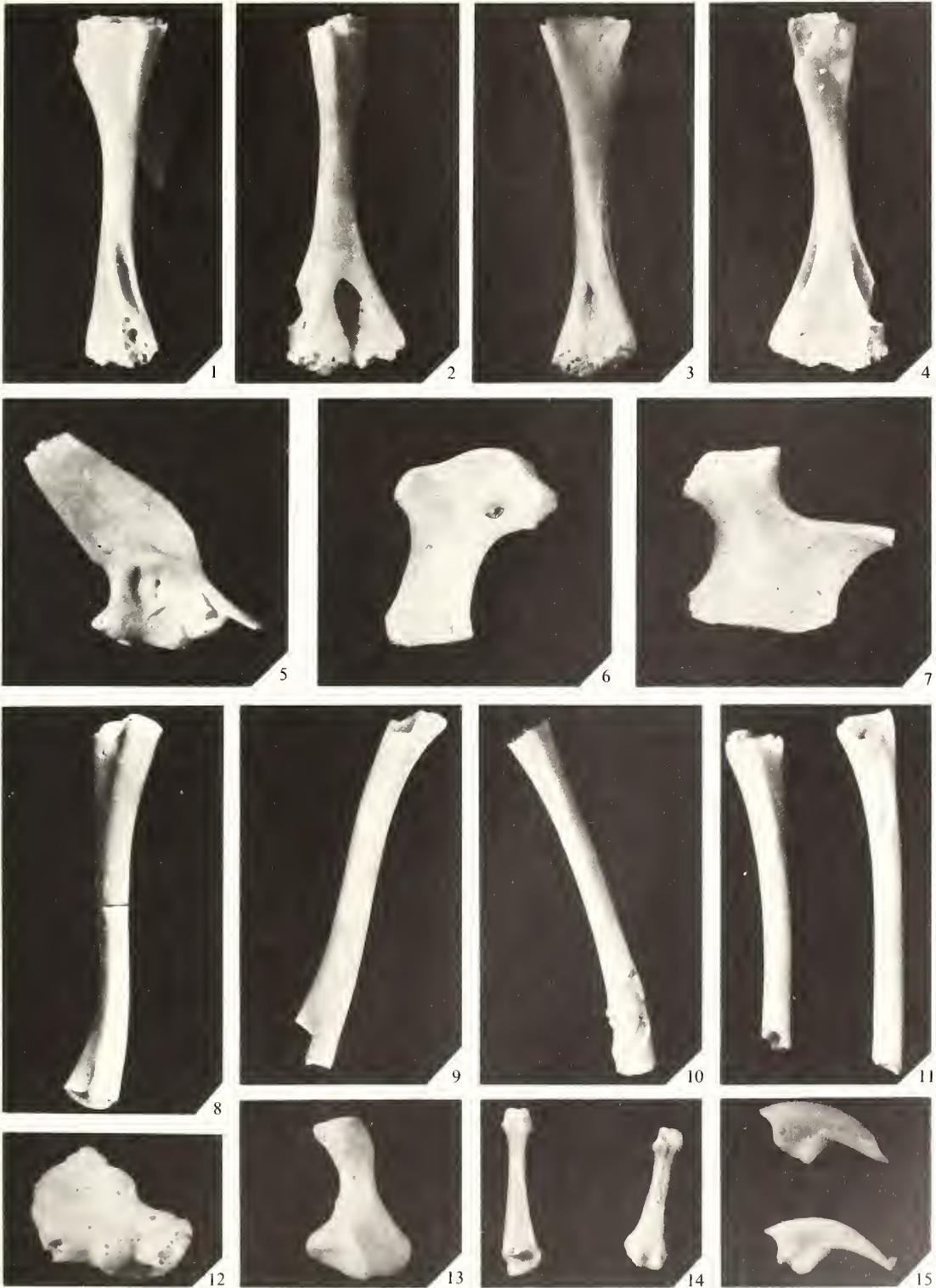
The ischium (text-fig. 15*b*; Pl. 54, fig. 7) formed the posterior half of the puboischial plate. The anterior edge has a short facet for the pubis and ventral to this there is a concave margin marking the posterior boundary of the thyroid fenestra. The posterior margin of the bone is extended backwards into a prominent tubercle for the attachment of ligaments and tendons of the tail musculature.

HINDLIMB

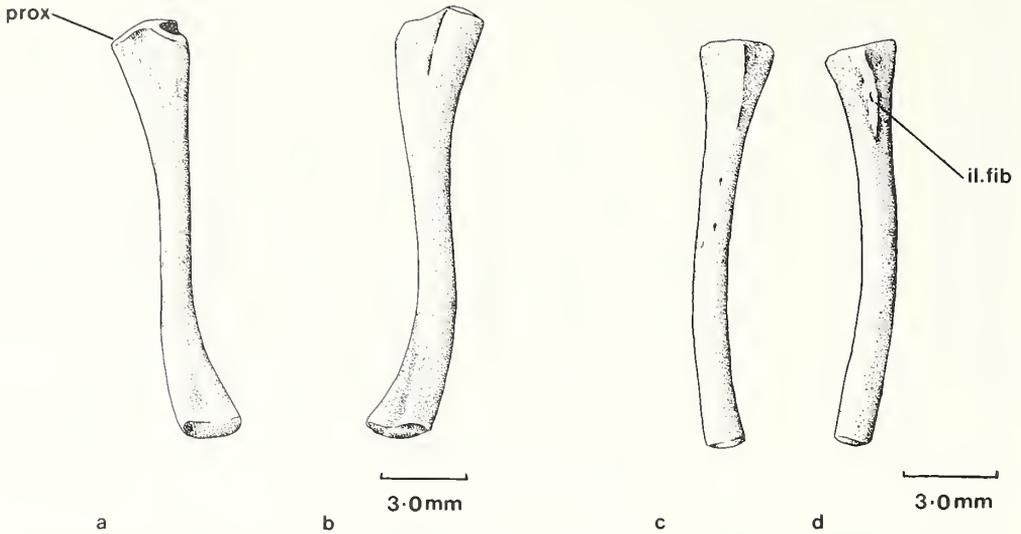
The femur (Pl. 54, figs. 8, 9) is a long slender bone with a sigmoid flexure along the length of the shaft (text-fig. 19*a, b*). The proximal expansion bears a well-developed internal trochanter situated ventral to the articulation head. Lying on the anterior surface, positioned between the internal trochanter and the head, is an area for the attachment of the puboischiofemoralis internus. Unfortunately, the epiphyses of the element are missing in all instances and thus other details of muscle attachment are unknown.

EXPLANATION OF PLATE 54

Figs. 1–15. *Planocephalosaurus robinsonae*. 1–4, AUP No. 11112, humerus in anterior, ventral, posterior, and dorsal aspects, $\times 5.5$. 5, AUP No. 11132, right ilium, lateral aspect, $\times 5.5$. 6, AUP No. 11117, left pubis, lateral view, $\times 5.5$. 7, AUP No. 11115, left ischium, lateral view, $\times 5.5$. 8, AUP No. 11118, femur, $\times 4$. 9, AUP No. 11128, femur, $\times 4.5$. 10, AUP No. 11119, fibia, $\times 4$. 11, AUP No. 11129, two tibias, $\times 4$. 12, AUP No. 11120, astragalocalcaneum, $\times 9.5$. 13, AUP No. 11121, tarsometatarsal, $\times 10$. 14, AUP No. 11130, phalanges, dorsal, and planar views, $\times 10$. 15, AUP No. 11131, ungual phalanges, $\times 9.5$.



FRASER and WALKDEN, Upper Triassic sphenodontid



TEXT-FIG. 19. *Planocephalosaurus robinsonae*. Reconstruction of a femur from AUP No. 11118. *a*, anterior and *b*, posterior aspects. Reconstruction of a tibia from AUP No. 11119, *c*, anterior and *d*, posterior aspects.

Of the two epipodials only the tibia (text-fig. 19*c, d*; Pl. 54, figs. 10, 11) has been confidently identified, but again the articulation surfaces themselves have been poorly preserved. It is a long slender bone that is concave towards the fibula. The posterior surface of the proximal head bears a slight ridge and rugosity for insertion of the iliofibularis musculature.

MANUS AND PES

A variety of small carpals, tarsals, and metapodials have been recovered from the residues at all the sites, but these have proved difficult to separate into distinct forms and it is likely that the structures of the manus and pes are quite uniform in all the Triassic sphenodontids; varying only in size.

The manus and pes of *Planocephalosaurus* are described from elements recovered solely from site four, but the following comments also serve as an outline for the generalized sphenodontid structure.

The small bones of the carpus are difficult to determine since many of their distinguishing characteristics are obscured by erosion and polishing. The astragalus and calcaneum are fused into an astragalocalcaneum with no trace of sutures (text-fig. 20*a*; Pl. 54, fig. 12). It is a relatively flat bone-bearing articulation facets on its dorsomedial surface for the tibia and fibula, and a well-defined concavity for the fourth distal tarsal. The distal tarsals themselves are unknown.

With the exception of the fifth metatarsal, the metapodials are all similar, varying only in size and slight details of the proximal head. Each metapodial has a long slender shaft with the proximal head slightly expanded and usually bearing small tuberosities for the attachment of the digital extensor and flexor muscles. The fifth metatarsal (text-fig. 20*c, d*), which should more accurately be termed the fifth tarsometatarsal, since it is a fusion of the fifth distal tarsal with the fifth metatarsal, is easily recognized as a small robust bone that is clearly 'hooked' and very similar to that observed in *Sphenodon*. The proximal head has a broad facet for the fourth distal tarsal, and tuberosities on the

plantar surface were for the attachment of flexor muscles such as the gastrocnemius. Robinson (1975) discussed the role of the hooked fifth metatarsal in the functioning of the hind limb and concluded that it was of major importance in allowing for the opposition of the first digit to the fifth, and thereby increasing the gripping powers of the foot. It also had a role to play in bringing the crus and pes musculature to bear in the locomotor effect of the hind limb.

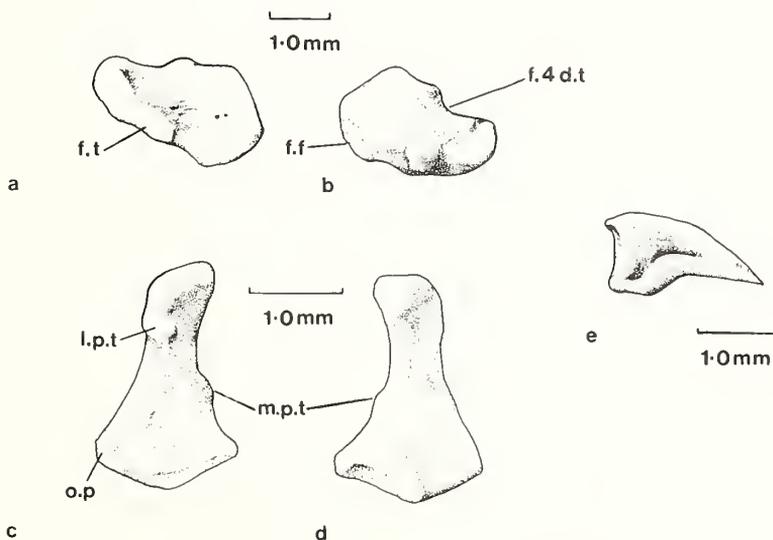
The phalanges (Pl. 54, fig. 14) bear deeply concave proximal articulation surfaces whilst the distal head is convex. There is some variation in the shape of the shaft—some have an almost circular cross-section whereas others exhibit a degree of dorsoventral compression and also on occasions possess a shallow ventral ridge. The latter were probably the most proximal in position (Evans 1981). A number of ungual phalanges are known which are mediolaterally compressed (text-fig. 20e; Pl. 54, fig. 15). These phalanges possess medial and lateral grooves which may have borne ducts supplying secretory glands.

As a consequence of the material being completely dissociated the phalangeal formula is unknown, but it may have been the same as *Sphenodon*, namely:

Hand 2, 3, 4, 5, 3
Foot 2, 3, 4, 5, 4

RECONSTRUCTION OF THE SKELETON

There is a complete absence of articulated material from which direct measurements of *Planocephalosaurus* could be taken. Thus to deduce the relative proportions of the body the mean sizes of the available completely ossified elements must be calculated. There are, however, only a few complete limb bones which do not provide satisfactory sample sizes from which to calculate means. To rectify this deficiency the full lengths of a number of incomplete bones were extrapolated by direct



TEXT-FIG. 20. *Planocephalosaurus robinsonae*. Reconstruction of a left astragalocalcaneum from AUP No. 11120. *a*, anterior and *b*, posterior views. Right tarsometatarsal, AUP No. 11121, in *c*, plantar and *d*, dorsal views. *e*, Ungual phalanx, AUP No. 11122, in lateral view.

comparison with intact representatives of each of the four relevant limb elements, and the following mean lengths were obtained:

Forelimb:	Humerus	11 mm	}	20 mm
	Ulna	9 mm		
Hindlimb:	Femur	16 mm	}	29 mm
	Tibia	13 mm		

With respect to the vertebrae, their numbers more than their individual sizes govern the relative proportions of the axial skeleton. With dissociated material it is very difficult to estimate the exact numbers of vertebrae in the column, but the relative abundance of each of the four vertebral types within the deposits (Table 1) suggests that it is perfectly acceptable to reconstruct *Planocephalosaurus* with the same vertebral count as *Sphenodon*.

TABLE 1. Relative abundances of the four major vertebral types of *Planocephalosaurus robinsonae* expressed as a percentage of the total vertebral count from two different strata at Site 4. The percentages for *Sphenodon* are obtained from data given by Hoffstetter and Gasc (1969) where *Sphenodon* is assumed to possess twenty-five presacrals, two sacrals, and between twenty-nine and thirty-six caudals.

	<i>P. robinsonae</i> . Level k, site 4	<i>P. robinsonae</i> . Level m, site 4	<i>P. robinsonae</i> . Total numbers at site 4	<i>Sphenodon</i> <i>punctatus</i>
Per cent cervical vertebrae	13.3	12.8	12.5	12.7-14.3
Per cent dorsal vertebrae	25.7	26.5	26.2	27.0-30.4
Per cent sacral vertebrae	2.8	3.2	2.9	3.2-3.6
Per cent caudal vertebrae	58.7	57.7	58.0	57.2-51.8
Total number of vertebrae in the sample	218	189	646	

The full reconstruction shows *Planocephalosaurus* having a snout-vent length of approximately 7.5 cm with an additional 7.0-8.5 cm of tail. The forelimb/hindlimb ratio is 69.6%, but this disparity is in common with other eosuchians and is not as great as that generally seen in bipedal reptiles such as *Malerisaurus*, *Saltosuchus*, *Basiliscus*, etc. (Ewer 1965; Chatterjee 1980). In addition, the vertebral numbers suggest that the trunk of *Planocephalosaurus* was not reduced in length; the combined tibia and femur length being approximately 45% that of the trunk. In bipeds, on the other hand, the latter ratio is much higher: 75% for *Malerisaurus* and 100% in *Basiliscus* (Chatterjee 1980). The small limb disparity in quadrupedal eosuchians, such as *Planocephalosaurus*, may permit better acceleration and the ability to change direction quickly. This, coupled with opposable first and fifth digits would have enabled *Planocephalosaurus* to negotiate quite rough terrain at speed in its attempts to avoid danger and capture elusive prey.

DISCUSSION

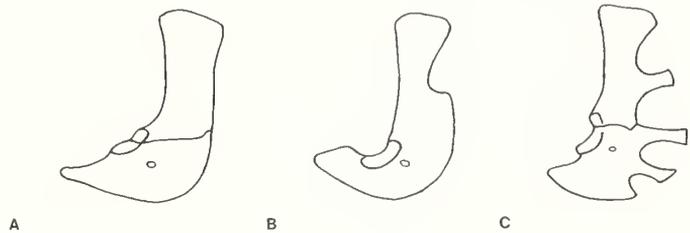
Following Evans (1980), the family Sphenodontidae is considered to lie within the infraclass Eosuchia. The following discussion concentrates on the affinities of *Planocephalosaurus* with a second eosuchian, *Gephyrosaurus*, and assesses the possibility of including the latter within the Sphenodontidae.

The rudimentary zygosphenic articulation of *Planocephalosaurus* (text-fig. 9a) is a character not reported amongst other fossil eosuchians with the exception of *Saurosternon* and *Gephyrosaurus*.

However, Evans (1981) points out the difficulties of observing such a feature in articulated skeletons and suggests that it might be more widespread than reported. Together with *Gephyrosaurus*, *Homeosaurus*, and *Sphenodon* strong fracture planes occur in the caudal vertebrae of *Planocephalosaurus*. These are absent in many other eosuchian genera. Evans (1981) suggests this may be the result of the functional importance of the tail in other groups (e.g. for swimming or as a counterbalance) and may not have any bearing on ancestral relationships.

In a similar fashion to *Sphenodon* the scapula and coracoid of *Planocephalosaurus* have fused into a single unit and the same is also true of *Gephyrosaurus*. But unlike *Sphenodon*, other sphenodontids, and *Gephyrosaurus*, *Planocephalosaurus* does possess a fenestrated scapulocoracoid. Compared with the lacertilians this fenestration is rudimentary as only one fenestra occurs in the scapula region of the bone compared to two in *Iguana* (text-fig. 21). *Iguana* also possesses two fenestra in the coracoid section of the bone whilst in *Planocephalosaurus* this region is unfenestrated. Evans (1981) believed that such fenestration is a uniquely lacertilian character, but the present evidence would suggest otherwise and further support is provided by Carroll (1975) who reported a similar condition in *Saurosteruon*. Thus with regard to the pectoral girdle *Planocephalosaurus* would appear quite advanced, but with respect to the humerus it conforms to the pattern observed in *Sphenodon* and *Gephyrosaurus*, possessing both ent- and ectepicondylar foramina.

TEXT-FIG. 21. The scapulocoracoid ossification of A, *Sphenodon*, B, *Planocephalosaurus*, and C, *Iguana*.



The pelvic girdle of *Planocephalosaurus* is very similar to that of *Sphenodon* and *Homeosaurus* having a puboischiadic plate perforated by a well-developed thyroid fenestra. This condition is also seen in other advanced eosuchians such as *Kuehneosaurus* and *Gephyrosaurus*. The iliac blade of *Planocephalosaurus* is not as elongated as that of *Sphenodon* and resembles more closely that of *Gephyrosaurus*.

Thus the postcranial skeleton of *Planocephalosaurus* does not depart noticeably from the general sphenodontid structure. The main difference is in the structure of the scapulocoracoid where that of *Planocephalosaurus* exhibits fenestration, but this is atypical of the family. In all other respects, including the cranial morphology (Fraser 1982), *Planocephalosaurus* is a typical sphenodontid. At the same time it can be said that there are a number of similarities between *Planocephalosaurus* and *Gephyrosaurus*. However, *Gephyrosaurus* was assigned by Evans (1980) to a new family within the Eosuchia, the Gephyrosauridae. There is therefore reason to believe that there are some affinities between the Sphenodontidae and Gephyrosauridae and a brief résumé of cranial morphology would seem to strengthen the argument.

Evans (1980) commented on the fusion of both frontals and parietals in *Gephyrosaurus* and considered this to be unusual within the Eosuchia; however, *Planocephalosaurus* also shows this characteristic. The sphenodontids generally do not possess a lachrymal and whilst this element is present in *Gephyrosaurus* it is quite rudimentary. The incomplete lower temporal bar of *Gephyrosaurus* is a characteristic that also occurs in some members of the Sphenodontidae—including *Planocephalosaurus* and *Clevosaurus* (Robinson 1973). The quadriradiate shape of the squamosal is a feature shared with the sphenodontids and Evans herself (1980) noted the similarity of the quadrate–quadratojugal arrangement but concluded that it must be a result of convergence.

Turning to the palate, the possession of an enlarged row of teeth on the palatine of *Gephyrosaurus* is another characteristic of the sphenodontids. Whilst there is a general tendency in *Clevosaurus* and *Sphenodon* to show a reduction in the number of small teeth scattered across the palatal elements, *Planocephalosaurus*, in common with *Gephyrosaurus*, retains a number of small palatal teeth.

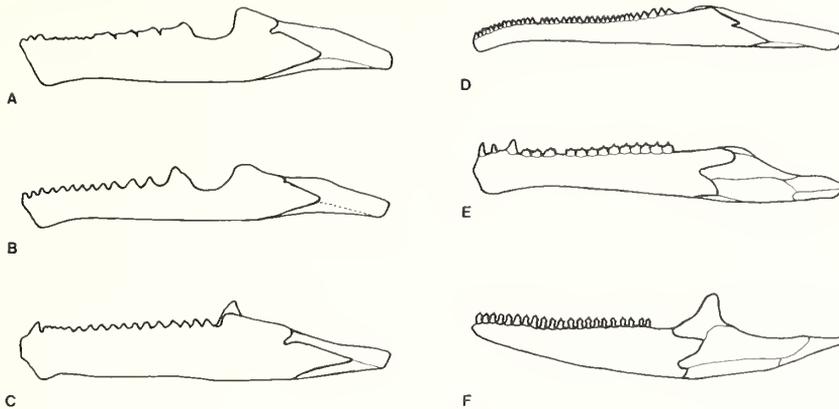
The posterior process of the dentary of *Sphenodon* meets the articular complex and braces the lower jaw (text-fig. 22). Such a process is not seen in other eosuchian genera such as *Youngina*, *Tanystropheus*, and *Kuehneosaurus*, but it is known in other sphenodontids such as *Planocephalosaurus* and *Clevosaurus* and is also seen in *Gephyrosaurus*. Evans (1980) notes the overall similarity of the *Gephyrosaurus* lower jaw to that of the sphenodontids, including the lack of a splenial, but again concludes that this must be the result of convergence.

The number of characteristics shared by *Gephyrosaurus* and the Sphenodontidae suggest a close relationship between the two (Table 2), the only obvious difference so far noted being the existence of a rudimentary lachrymal in *Gephyrosaurus*, and it is quite easy to see how this element could have been lost in the sphenodontids. However, one major difference does exist and that is the attachment of the marginal dentition. Whereas *Gephyrosaurus* has a pleurodont attachment the sphenodontids typically display an acrodont dentition. This difference does not necessarily rule out a close relationship between the two, however, since within the Lacertilia both acrodont and pleurodont forms are recognized.

TABLE 2. A comparison of sphenodontids and some other eosuchians.

	<i>Sphenodon</i>	<i>Clevosaurus</i>	<i>Planocephalosaurus</i>	<i>Homoosaurus</i>	<i>Kuehneosaurus</i>	<i>Tanystropheus</i>	<i>Gephyrosaurus</i>	Rhynchosaurs	<i>Youngina</i>	<i>Prolacerta</i>	<i>Macrocnemus</i>	<i>Palaeagama</i>	<i>Askeptosaurus</i>
Fusion of the frontals	o	o	x	o	o	o	x	o	o	o	o	o	o
Fusion of the parietals	x	o	x	o	o	x	x	x	o	o	o	o	o
Lachrymal small or absent	x	x	x	x	o	x	x	o	o	o	x	-	o
Lower temporal arcade incomplete	o	x/o	x/o	o	x	x	x	o	o	x	x	-	o
Enlarged palatine tooth row	x	x	x	x	o	o	x	o	o	o	o	-	o
Dentary with pronounced posterior process	x	x	x	x	o	o	x	o	o	x	o	-	o
Splenial absent	x	x	x	-	o	x	x	o	o	o	o	-	o
Acrodont dentition	x	x	x	x	o	o	o	o	o	o	o	o	o
Zygosphene/zygantrum	x	x	x	-	o	o	x	o	o	o	o	o	o
Caudal fracture planes	x	x	x	x	o	x	x	o	o	o	o	o	o
Most presacrals with single headed ribs	x	x	x	x	o	o	x	o	o	x	o	o	o
Vertebrae amphicoelous and notochordal	x	x	x	x	o	o	x	o	x	x	x	x	x
Scapulocoracoid a single bone	x	x	x	x	o	o	x	x	o	x	o	o	o
Scapulo coracoid fenestrated	o	o	x	o	o	o	o	o	o	o	o	o	o
Humerus with two distal foramina	x	x	x	x	o	x	x	o	x	o	o	x	o
Thyroid fenestra	x	x	x	x	x	x	x	o	o	o	x	o	x
Hooked fifth tarsometatarsal	x	x	x	x	o	x	x	x	o	x	x	o	o

x—character present. o—character absent.



TEXT-FIG. 22. Lateral aspects of the dentaries of A, *Clevosaurus*, B, *Planocephalosaurus*, C, *Sphenodon*, D, *Gephyrosaurus*, E, *Tanystropheus*, and F, *Iguana*. (C after Robinson (1976), D after Evans (1980), E after Wild (1980), and F after Romer (1956)).

It might be postulated that intermediate forms would exist between sphenodontids and their eosuchian ancestors in which the marginal dentition displayed some degree of pleurodony. The evidence presented suggests that *Gephyrosaurus* may be such an intermediate form. If it is not considered to be a 'true' sphenodontid then it probably represents an early offshoot from the stem Sphenodontidae.

It is also postulated that accompanying this trend towards a firmer anchorage of the marginal dentition, there is a tendency within the Sphenodontidae for a reduction in tooth numbers. Thus it is likely that within the Sphenodontidae and their ancestors there is a spectrum of forms ranging from small, relatively delicate individuals with numerous pleurodont teeth to more robust species possessing firm acrodont teeth with a marked decrease in their absolute numbers (Table 3). Such

TABLE 3. Tooth arrangement and insertion in three Triassic eosuchians indicating a probable trend towards acrodonity and a reduction of numbers in the Sphenodontidae.

	<i>Gephyrosaurus bridensis</i>	<i>Planocephalosaurus robinsonae</i>	<i>Clevosaurus hudsoni</i>
Palatal Dentition	Numerous teeth scattered across palatines, pterygoids, and vomers. Ordered into an enlarged tooth row on the palatine	Numerous teeth on palatines, pterygoids, and vomers. Predominantly arranged in rows with two enlarged tooth rows on the palatine	Reduction in palatal dentition. Teeth arranged in two rows on the pterygoids. A single enlarged tooth row on the palatine. Occasionally a few vomerine teeth
Insertion of marginal dentition	Pleurodont	Acrodont	Acrodont
Number of functional marginal teeth in the mature individual:			
(a) premaxilla	8-10	4	2-3
(b) maxilla	35-40	12-14	5-6
(c) dentary	30-40	13-14	5-6
			Juvenile teeth worn away to the bone anteriorly

ditional modifications are obviously associated with altered dietary habit, with the skull also becoming generally more robust and consequently capable of withstanding the greater stresses imposed upon it by more demanding diets.

Another species that occurs in the Cromhall fauna which is expected to substantiate the evolutionary trends outlined above, is presently being described by D. I. Whiteside (in prep.) from abundant remains occurring in Triassic fissure deposits at Tytherington Quarry (ST 660 890).

Acknowledgements. We thank the N.E.R.C. for continued financial support of the work on late Triassic reptile-bearing palaeokarstic phenomena. We are grateful to Mr. Hodges of the Amey Roadstone Corporation Ltd. who allowed us to work in Cromhall Quarry at all times and we also thank the British Museum for providing access to their collections of *Clevosaurus* and *Kuehneosaurus* material.

APPENDIX

Total number of each postcranial element of *Planocephalosaurus robinsonae* recovered from fissure four, Cromhall Quarry.

Element	at.ar.	at/ax.	ce.v.	d.v.	1st s.	2nd s.	caud.	ch.	int.c.	ce.r.	d.v.	cl.
Numbers	17	12	69	169	8	11	377	147	87	61	150	13
Element	int.cl.	sc.	hum.	rad.	il.	isch.	pu.	fem.	tib.	5th met.	ast.	
Numbers	9	12	36	14	27	21	13	26	23	26	3	

ABBREVIATIONS

at.ar.	atlas arch	int.c.	intercentrum	il.	ilium
at./ax.	atlas/axis	ce.v.	cervical rib	isch.	ischium
ce.v.	cervical vertebra	d.r.	dorsal rib	pu.	pubis
d.v.	dorsal vertebra	cl.	clavicle	fem.	femur
1st s.	1st sacral vertebra	int.cl.	interclavicle	tib.	tibia
2nd s.	2nd sacral vertebra	sc.	scapulocoracoid	5th met.	5th tarsometatarsal
caud.	caudal vertebra	hum.	humerus	ast.	astragalocalcaneum
ch.	chevron bones	rad.	radius		

ABBREVIATIONS USED IN TEXT-FIGURES

acet.	acetabulum	f.t.	tibia facet
a.i.	axis intercentrum	f.4 d.t.	facet for 4th distal tarsal
ant.pu.p.	anterior pubis process	gl.f.	glenoid fossa
a.pr.	anterior process	il.	ilium
cap.	capitulum	il.ant.f.	anterior facet for ilium
cl.f.	clavicle facet	illf.	facet for ilium
cor.fo.	coracoid foramen	il.fib.	insertion for iliofibularis muscle
c.r.	caudal rib	int.f.	facet for interclavicle
d.pop.	diapophysis	isch.	ischium
ect.fo.	ectepicondylar foramen	isch.f.	facet for ischium
ent.fo.	entepicondylar foramen	l.p.t.	lateral plantar tubercle
f.c.	facet for centrum	m.p.t.	median plantar tubercle
f.f.	fibula facet	n.f.	nutrient foramen
f.p.	fracture plane	n.s.	neural spine

Abbreviations used in text-figs. (cont.)

ob.fo.	oburator foramen	r.f.	rib facet
od.f.	odontoid facet	s.acet.b.	supracetabular buttress
od.p.	odontoid process	sc.	scapula blade
o.p.	outer process	s.r.1	sacral rib 1
p.pop.	parapophysis	s.r.2	sacral rib 2
p.f.	posterior facet	s.r.1f.	facet for 1st sacral rib
prox.	proximal head	s.r.2f.	facet for 2nd sacral rib
pr.zyg.	prezygapophysis	thy.fen.	thyroid fenestra
pu.	pubis	tr.tb.	tubercle for triceps attachment
pu.f.	facet for pubis	tub.	tuberculum
p.zyg.	postzygapophysis	v.p.	ventral process

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OSTEOLOGY OF THE PALAEOCENE TELEOST *ESOX TIEMANI*

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ABSTRACT. The Palaeocene pike *Esox tiemani* combines many typically esocid features such as an elongate body, depressible and canine teeth, elongate snout and jaws, almost straight preopercle, small second and third hypurals separated by a gap, large ethmoid process on the ectopterygoid, and anteriorly lobed scales with other features in which it is intermediate between Recent umbrids and esocids. Branchiostegal rays are almost equally divided between the ceratohyal and epihyal, while in Recent umbrids they are more numerous on the ceratohyal and in Recent esocids they are more numerous on the epihyal. The opercle of *E. tiemani* has a prominent dorsolateral flange that probably covered part of the insertion of the levator operculi muscle. The flange is larger in umbrids and virtually absent in Recent esocids, in which much of the insertion for the levator operculi is on the dorsolateral surface of the opercle.

WE now know that the pikes (genus *Esox*, family Esocidae) have lived in North America apparently continuously since the Palaeocene, sixty million years ago. Fossils of *Esox* have been reported from the Pleistocene of the Yukon and Ontario (Crossman and Harington 1970) and of Florida (Cavender *et al.* 1970), the Miocene of Oregon (Cavender *et al.* 1970), the Oligocene of Montana (Cavender 1977), the Eocene of Ellesmere Island (Estes and Hutchinson 1980) and Colorado (Wilson 1981), and the Palaeocene of Alberta and Saskatchewan (Wilson 1980).

The Palaeocene esocid *E. tiemani* Wilson (1980), from the Paskapoo Formation of Alberta, is known from several articulated specimens including the holotype, a complete fish, and from numerous disarticulated bony elements at several sites within the same formation.

The osteology of *E. tiemani* is of special interest because it is the oldest-known esocid, and yet clearly possesses many of the unique specializations of the living pikes. The oldest Eurasian esocoids, which are also of Palaeocene age, belong to the Palaeoesocidae (Sytchevskaya 1976, 1982) and represent rather different skeletal adaptations.

The purpose of this paper is to present a detailed account of the osteology of *E. tiemani*, based on additional preparations of the holotype specimen, in addition to information obtained from the numerous disarticulated bones collected from the type locality and other sites in the Paskapoo Formation. In addition, a skeletal reconstruction and comments on the phylogenetic relationships of the species are presented.

MATERIALS AND METHODS

The holotype specimen (UAVP 15002) was briefly described by Wilson (1980). The specimen is complete except for the distal portions of the dorsal fin and the dorsal lobe of the caudal fin. The skull was preserved in part and counterpart and, since the original description, has been prepared by transfer methods. The right side of the skull in the counterpart (text-fig. 1) was embedded in bioplastic and the opposite (left) side prepared (text-fig. 2). This face is referred to in the present paper as UAVP 15002B.

The other material which was part of the original collection (UAVP 15005, a skull, and 15006, 15070, 15071, and 15072, four small partial fish) has been supplemented by additional disarticulated bones collected at the type locality in 1979 and prepared more recently. These consist of two dentaries (UAVP 17685 and 17686), an angular (UAVP 17670), a parasphenoid (UAVP 17678), an opercle

(UAVP 17676), and a group of scales possibly representing a coprolite (UAVP 17677). In addition to these, a great many *Esox* fossils continue to be recovered from other sites in the Paskapoo Formation. The most notable of these is a series of partial fish, primarily skulls, from the Lovettville Creek site (Wilson 1980, fig. 1, site 4), with catalogue numbers UAVP 15024, 15027-15031, and 17259.

Description of the skeleton of *E. tiemani* involved a detailed comparison of the skeletal elements of the fossil species with skeletons of Recent esocoids, primarily *E. lucius*, *E. masquinongy*, *Novumbra lubbsi*, *Dallia pectoralis*, *Umbrina krameri*, *U. pygmaea*, and *U. linnii*. Osteological features of the Umbridae were summarized by Wilson and Veilleux (1982). Those of esocids have not recently been described in detail, but the descriptions of Sytchevskaya (1976) were supplemented by observations on Recent skeletal material in the University of Alberta Museum of Zoology. For catalogue numbers of the Recent osteological material available for comparative purposes in this study, see Wilson and Veilleux (1982).

In almost all features the fossil species was found to be much more similar to the Recent esocids than to the Recent umbrids. Where information on particular parts of the skeleton was lacking in the fossils from the type locality, the reconstruction was prepared by using additional data, first from other fossil specimens from the Paskapoo Formation, and secondly from Recent esocids.

The following is a list of the abbreviations used in the figures:

AA	angulo-articular	HS	haemal spine	PP	pelvic plate
BH	basihyal (glossohyal)	HU	hypural	PR	pteroic
BR	branchiostegal	IO	infraorbital	PS	parasphenoid
CH	ceratohyal	LA	lachrymal	PT	post-temporal
CL	cleithrum	LE	lateral ethmoid	PU	preural centrum
CT	canine or fixed teeth	MS	mesopterygoid	QU	quadrate
DE	dentary	MT	metapterygoid	SC	supracleithrum
DT	depressible teeth	MX	maxilla	SM	supramaxilla
EC	ectopterygoid	OP	opercle	SN	supraneural
EH	epihyal	PA	palatine	SO	subopercle
ES	extrascapular	PC	postcleithrum	UC	ural centrum
EU	epural	PE	proethmoid	UH	urohyal
FR	frontal	PH	parhypural	UN	uroneural
HH	hypohyal	PM	premaxilla	VO	vomer
HM	hyomandibula	PO	preopercle		

OSTEOLOGY

The skull roof of *E. tiemani* closely resembles that of the Recent species *E. lucius* and *E. masquinongy*. Frontals are elongate and narrow anteriorly, rounded posteriorly, and have a prominent supraorbital sensory canal, enclosed in bone, as in the Recent species (text-fig. 1). Nasals are not preserved in any specimen. UAVP 15005 has a pair of small supraorbitals. Parietals are separated by the supraoccipital and extend laterally to the pterotics. A canal-bearing extrascapular is present in the holotype (text-fig. 1).

Proethmoids are elongate and tapered posteriorly, broader and diverging anteriorly. Lateral ethmoids are seen in UAVP 15002B where they have a conical shape, convex anterolaterally (text-fig. 2A). Pterotics, also visible in this specimen, are elongate anteroposteriorly as in *E. lucius*. Infraorbitals and lachrymal are only poorly preserved in UAVP 15002B, where they appear to be similar to those in Recent *Esox* (text-fig. 2).

The parasphenoid is preserved in UAVP 15002B and 17678. It is narrow and elongate, as in Recent *Esox*. The vomer is broad and truncate anteriorly (text-fig. 1), narrower and tapered posteriorly, and possesses depressible teeth along its ventral surface. There are no fixed or canine teeth on the vomer such as are found at the anterior end of the vomer in *E. masquinongy* (Cavender *et al.* 1970).

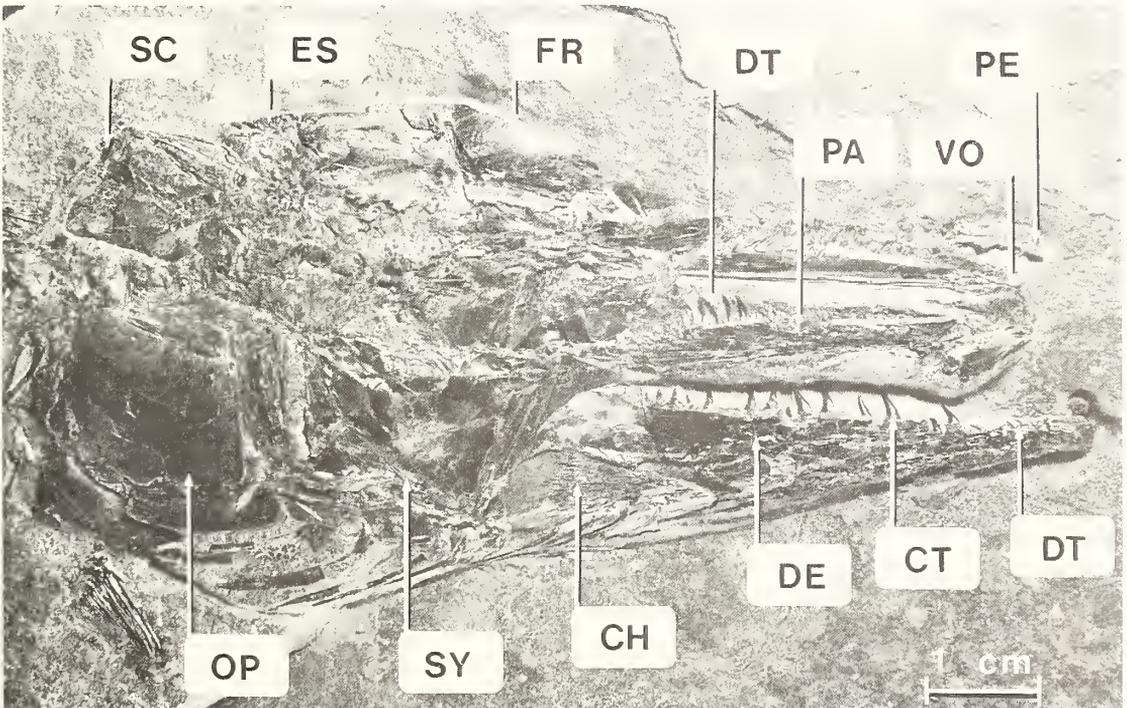
Premaxilla, maxilla, and supramaxilla are preserved best in UAVP 15002B (text-fig. 2). The premaxilla bears a series of small depressible teeth along its oral margin. Anteriorly the bone is

triangular and posteriorly a narrow extension underlies the anterior portion of the maxilla. The maxilla is markedly curved medially at its anterior end, where it articulates with the palatine. Posteriorly it is narrow and gently curved. A single elongate supramaxilla extends just beyond the posterior end of the maxilla, as in Recent *Esox*.

The dentary and angulo-articular are preserved in UAVP 15002, 15002B, 15005, 17670, 17685, and 17686. Dentaries are among the most common *Esox* fossils at other localities. The mandible is more elongate than in other early Tertiary *Esox* described by Sytchevskaya (1976), having an 'articular angle' of about 50 degrees (text-figs. 1, 2). The dentary is slender anteriorly and bears the mandibular sensory canal in a bone-enclosed tube near its ventral margin. Fixed or canine teeth are borne posteriorly and depressible teeth anteriorly. About ten canine teeth are present per ramus, from a point ventral to the anterior end of the maxilla, to a point just anterior to the coronoid process. The largest canine teeth are at the mid-point of the series. For a fish of comparable size, the canine row appears to have slightly more teeth and to extend slightly further anteriorly than in *E. lucius*.

Palatines are like those of *E. lucius*: elongate bones with numerous depressible teeth which grade in size from largest anteromedially to smallest posteriorly and along the posterolateral margin (text-figs. 1, 2). The largest anterior teeth (text-fig. 2) have the characteristic truncated bases of depressible teeth (Wilson, 1980, fig. 2h, i), unlike anterior palatine teeth of *E. masquinongy* which are of the canine type (Cavender *et al.* 1970).

The ectopterygoid is robust and angled, with a prominent ethmoid process as in Recent *Esox* (text-fig. 2). The mesopterygoid is small, the metapterygoid is large, and the quadrate robust with a prominent anterodorsal strut that supports the ectopterygoid, as in Recent *Esox*. The symplectic is nearly straight, as in *Esox*, *Novumbra*, and *Dallia*, but not *Umbra* (Wilson and Veilleux 1982).



TEXT-FIG. 1. Skull of *Esox tiemani* holotype, UAVP 15002, in dorsolateral view.

The shapes of the hyoid arch bones can be seen in UAVP 15002B (text-fig. 2) and 15005, where they are very similar to the corresponding bones in *E. lucius*. The hyomandibula has a long, posteroventrally directed opercular arm, a prominent laterally directed preopercular strut, a thin anteroventral flange lying against the metapterygoid, and a shaft directed slightly anteroventrally, forming a right angle with the opercular arm and about one and a half times as long as the latter. The epihyal is elongate, tapered posteriorly, and with a gently curved ventral margin as in Recent esocids but not umbrids. The ceratohyal is also elongate and hourglass shaped, very similar to that of Recent *Esox*. Ventral hypohyals are small conical bones with slightly projecting ventral tips (text-fig. 2). Branchiostegals are acinaciform and in the holotype number eleven on the right side and twelve on the left, where six attach to the medial and posteroventral surfaces of the ceratohyal, and six to the ventrolateral surface of the epihyal (text-fig. 2). The total number of branchiostegals is low for known Esocidae (Crossman 1960, Sytchevskaya 1976), agreeing only with some specimens of *E. americanus*, but differing in the distribution of branchiostegals between the epihyal and ceratohyal. Also in the holotype (text-fig. 2), the urohyal is seen to be a long, slender bone, tapered anteriorly, somewhat expanded dorsoventrally at its posterior end, and slightly wider than deep at its anterior end. Branchial-arch bones are not preserved, except for the dermal tooth-plate of the basihyal (glossohyal). In UAVP 15002B and in 15005 it is seen to be thin and broad, tapering gradually from its truncated anterior end, as in Recent esocids.

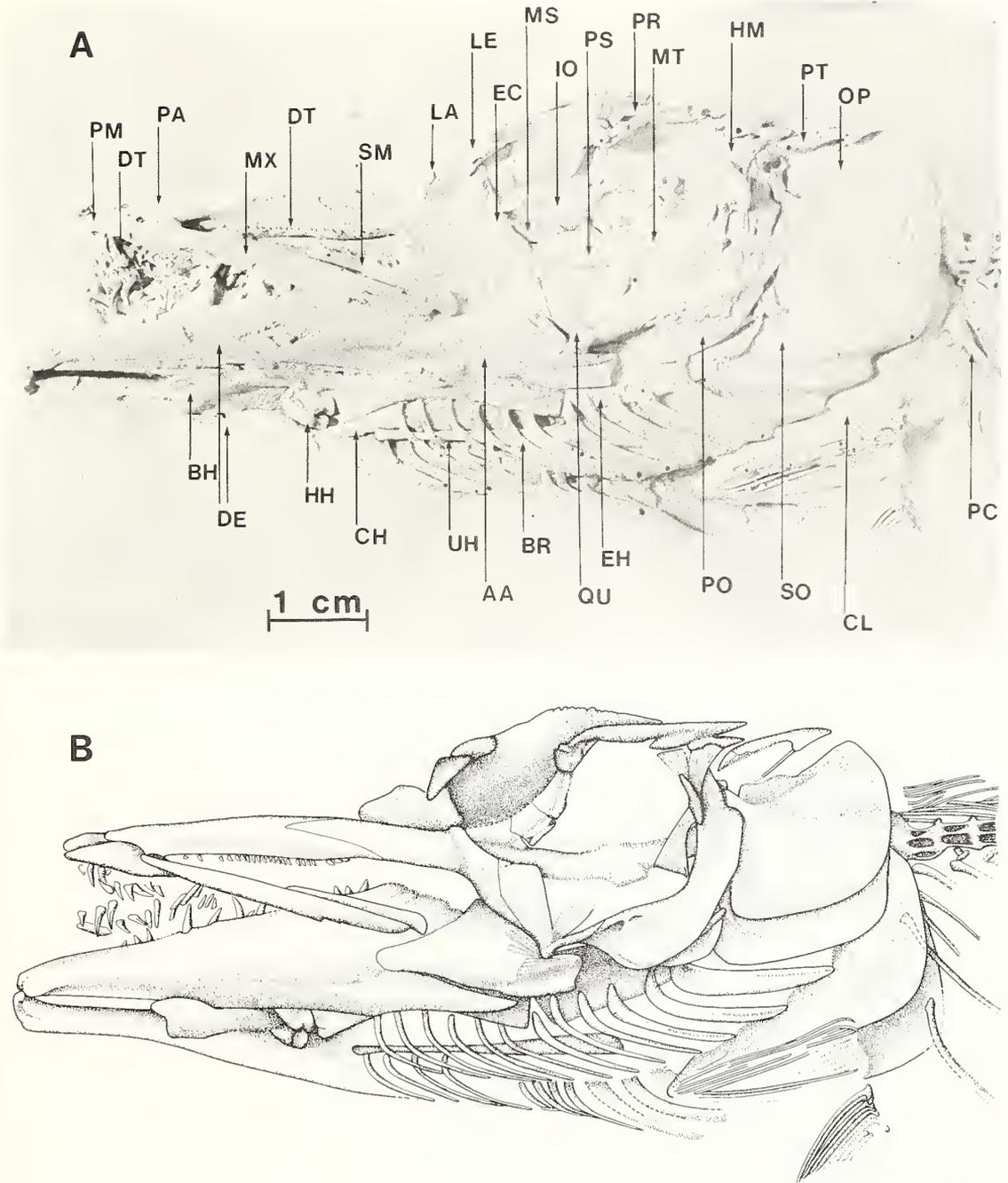
The preopercular is like that of Recent *Esox* but appears stouter. It is slightly bent at the angle (text-fig. 2), with a bone-enclosed sensory canal running the entire length of the bone and an anteromedial flange somewhat larger than the one in Recent *Esox* and reminiscent of that in *Novumbra*. Details of the interopercle are not visible but the subopercle (text-fig. 2) is only slightly curved, has roughly parallel dorsal and ventral margins, and has a prominent vertically directed articular process at its anterodorsal corner, as in Recent *Esox*. It differs from subopercles of the latter in being somewhat less elongate for its depth.

One of the most striking differences between *E. tiemani* and all other esocids, including Eurasian fossil forms (Sytchevskaya 1976), is the shape of the opercle (text-figs. 1, 2). Like those of Recent *Esox* the opercle has vertical anterior and posterior margins, but the ventral and posteroventral margins are more rounded, the articular process at the anterodorsal corner is more slender, and in overall proportions the bone is deeper relative to its length than in the modern species. In addition, the dorsal margin near the articular process bears a thin, plate-like dorsal extension which is continuous with the lateral surface of the body of the opercle, except for a shallow groove. On the medial surface a ridge, corresponding to the dorsal margin of the bone in other esocids, extends from the articular process to the posterolateral corner of the bone, and is separated from the dorsal extension by a narrow fossa, seen best in UAVP 15029 where it is filled with sediment. The fossa extends about two-thirds the distance from the articular process to the posterodorsal corner.

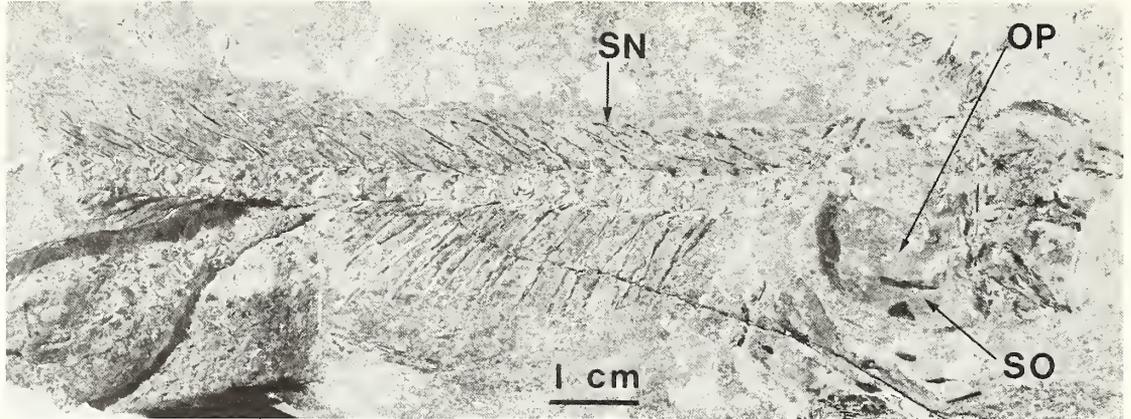
Few significant differences are seen between the pectoral girdle of *E. tiemani* and modern esocids. The cleithrum has a greatly elongated ventral arm, seen in UAVP 15071, and a slender postcleithrum extends posteroventrally from the angle, which is located just behind the posterior end of the subopercle. The supraclithrum, visible in the holotype (text-fig. 1) and in UAVP 15006 (text-fig. 3), bears a canal along its posterodorsal border. The post-temporal is forked, but whereas in modern esocids this bone is thin and plate-like, it appears in the holotype to be more strut-like (text-fig. 2). Pectoral rays number fourteen on the right side of the holotype.

Pelvic plates are virtually the same as those of modern esocids and umbrids other than *Dallia* (Wilson and Veilleux 1982): elongate pubic processes anteriorly, flanked medially by thin pubic plates, with rounded iliac plates posteriorly upon which the fin rays are borne in an anterolateral to posteromedial oblique row. Pelvic rays consist of a splint and approximately eleven rays, as counted in UAVP 15070 (text-fig. 4).

The vertebral column consists of nineteen caudal and approximately forty precaudal vertebrae, including ural centra. The first caudal vertebra, taken to be the first vertebra with an expanded haemal arch, is above the middle of the anal pterygiophore series, and below the middle of the dorsal pterygiophore series. Precaudal vertebrae bear slender ribs which do not appear to have autogenous



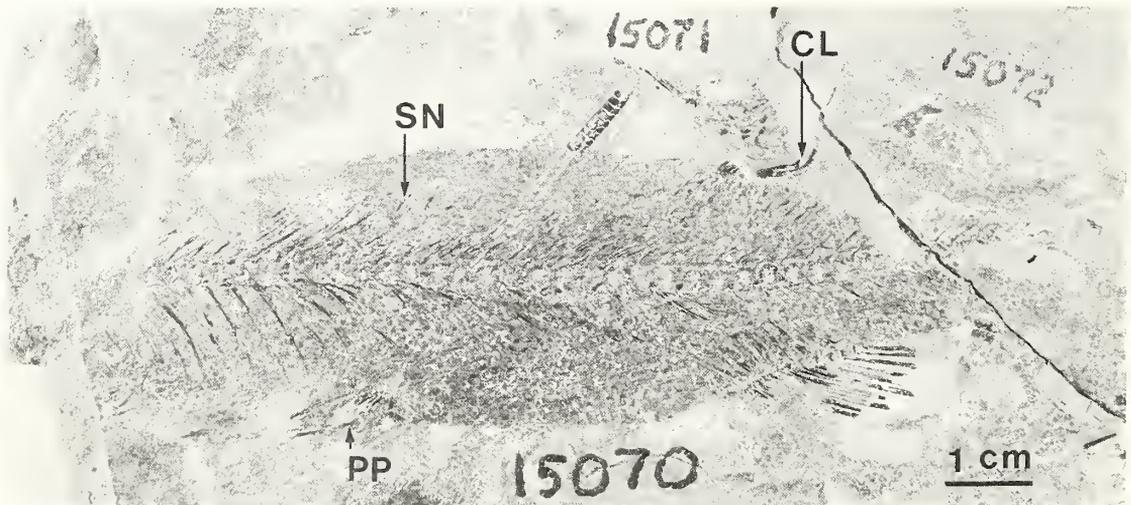
TEXT-FIG. 2. Skull of *Esox tiemani* holotype, UAVP 15002B, in ventrolateral view. A, ammonium-chloride-coated cast of the specimen. B, Drawing of the same specimen.



TEXT-FIG. 3. Trunk and posterior portion of skull of *Esox tiemani*, UAVP 15006, a specimen with estimated standard length of 215 mm.

parapophyses. Neural spines are also slender, but neural arches are expanded somewhat, especially on anterior vertebrae. Epineurals are present on all precaudal and the first few caudal vertebrae. Epipleurals or epihaemals are present on the last few precaudal and the first few caudal vertebrae. A series of slender, S-shaped supraneurals, seen best in UAVP 15006 (text-fig. 3) and 15070 (text-fig. 4), extends from just behind the pectoral girdle to just in front of the dorsal fin origin.

The dorsal and anal fins are situated far posteriorly (text-fig. 5) as in other esocoids. Dorsal rays number approximately fifteen or sixteen, preceded by several shorter unbranched rays, and are supported by sixteen long, slender pterygiophores (proximal radials) in the holotype and by fifteen in UAVP 15070, counting the anteriormost-forked pterygiophore as one. The anal fin originates about the length of two vertebrae more posteriorly than the dorsal fin (text-figs. 4, 5), and consists of twelve



TEXT-FIG. 4. Trunk and anterior caudal region of UAVP 15070, estimated standard length 150 mm; ventrolateral portion of skull and portions of trunk of UAVP 15071, estimated standard length 70 mm; and portions of the trunk and caudal region of UAVP 15072, estimated standard length 70 mm.



TEXT-FIG. 5. Complete specimen of *Esox tiemani*, holotype, UAVP 15002, ammonium-chloride-dusted cast of original specimen.

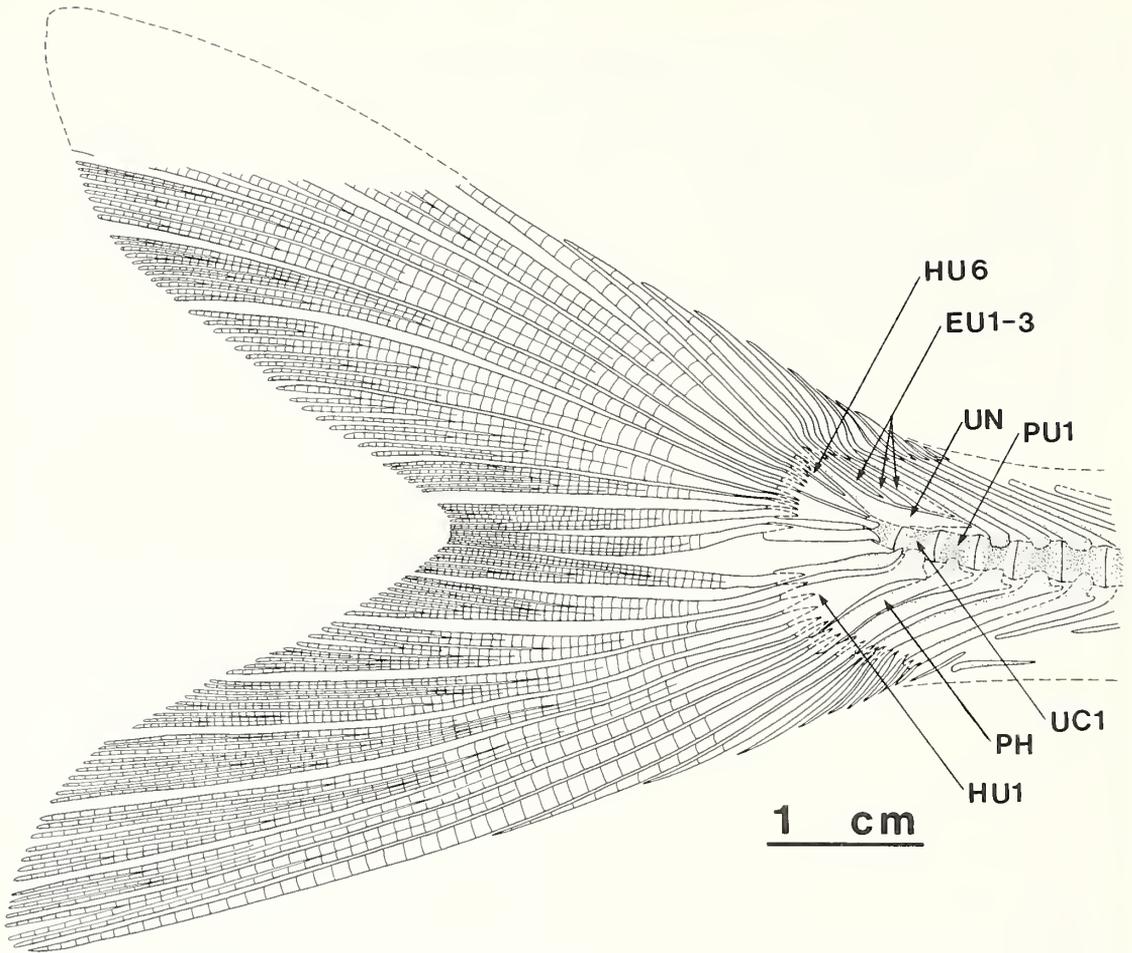
principal rays, preceded by several shorter unbranched rays. Anal pterygiophores number thirteen in UAVP 15070 and fifteen in the holotype. The margin of the anal fin is rounded, as in other esocoids. Ossified middle and distal radials cannot be distinguished in either the holotype or in UAVP 15070, so it is possible that they remain unossified as they do in some umbrids (Wilson and Veilleux 1982).

The caudal skeleton is preserved well in the holotype (text-fig. 6), in which it has two ural centra, two lower and four upper hypurals, a single uroneural, and three very slender epurals. The most posterior neural arch and spine is that on the second preural centrum. A distinct gap separates hypurals 2 and 3, which are less broad dorsoventrally than hypurals 1 and 4, as in *Novumbra* and other species of *Esox* (Wilson and Veilleux 1982). The first hypural, the parhypural, and the last few haemal spines bear anteriorly directed processes near their bases. The caudal fin consists of nineteen principal rays, with nine branched rays above and eight below the mid-line. Dorsal procurrent rays number approximately ten, and are decidedly S-shaped and anteroposteriorly expanded near the middle of the series. Ventral procurrent rays number eleven, and are more uniform in shape, except that the anteriormost procurrent ray seems larger and oriented more anteroposteriorly than its neighbours.

The articulated specimens display only the exposed portions of their scales. These are circular to slightly elongate, with fine, closely spaced, concentric circuli. No trace of cardioid scales (Scott and Crossman 1973) was seen on any specimen. Extrapolating from the presence of eight scale lengths within the length of three vertebrae on UAVP 15070, the species has a total of approximately 144 lateral-line scales, making it comparable to *E. masquinongy* in this respect. Entire scales are preserved in UAVP 17677, in which they can be seen to have the typical features of modern species of *Esox*: focus about two-thirds the length of the scale from the anterior margin, scale broadly oval to almost rectangular, anterior field deeply cleft by one to three (usually two) radii which produce a lobed anterior edge to the scale. Scales like these have also been reported from the Eocene of Colorado (Wilson 1981).

RECONSTRUCTION AND COMPARISONS

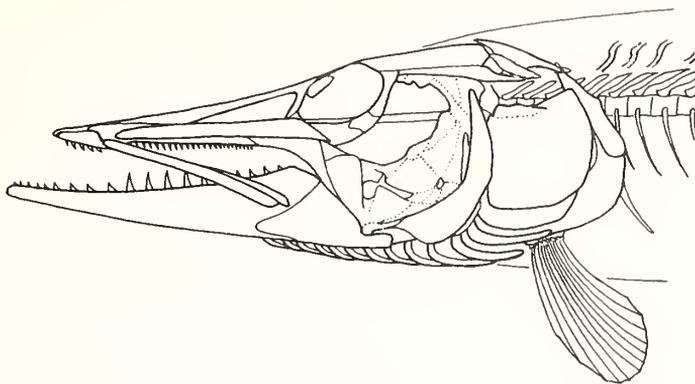
E. tiemani is reconstructed in lateral view in text-figs. 7 and 8. The skull is restored with an elongate lower jaw projecting anterior to the snout, and with the quadrate lower jaw articulation ventral to the posterior margin of the orbit. These features are essentially as preserved in the holotype. The lacrymal, although not well preserved in any specimen, is reconstructed as extending anteriorly



TEXT-FIG. 6. Drawing of caudal region of *Esox tiemani*, holotype, UAVP 15002.

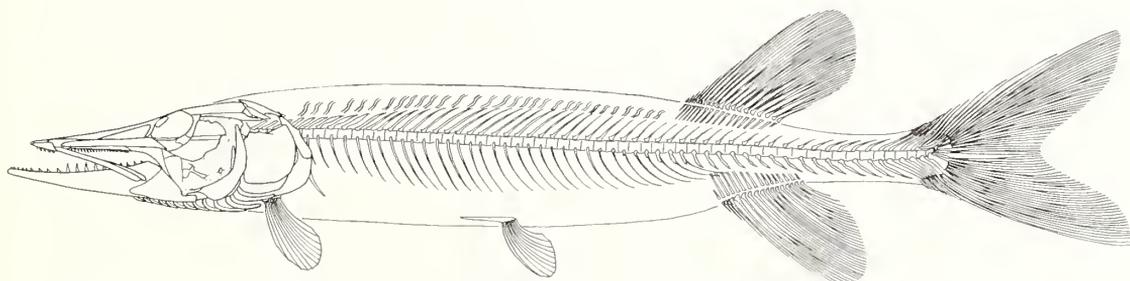
on to the snout as in Recent *Esox* (text-fig. 7). Sytchevskaya (1976) has used the ratio of snout length to postorbital head length to distinguish certain species of *Esox*. The ratio for *E. tiemani* is approximately 1.1, somewhat lower than values for *E. masquinongy*, higher than values for *E. americanus*, *E. borealis*, and *E. lepidotus*, and about the same as values for *E. lucius*, *E. reicherti*, and *E. niger*.

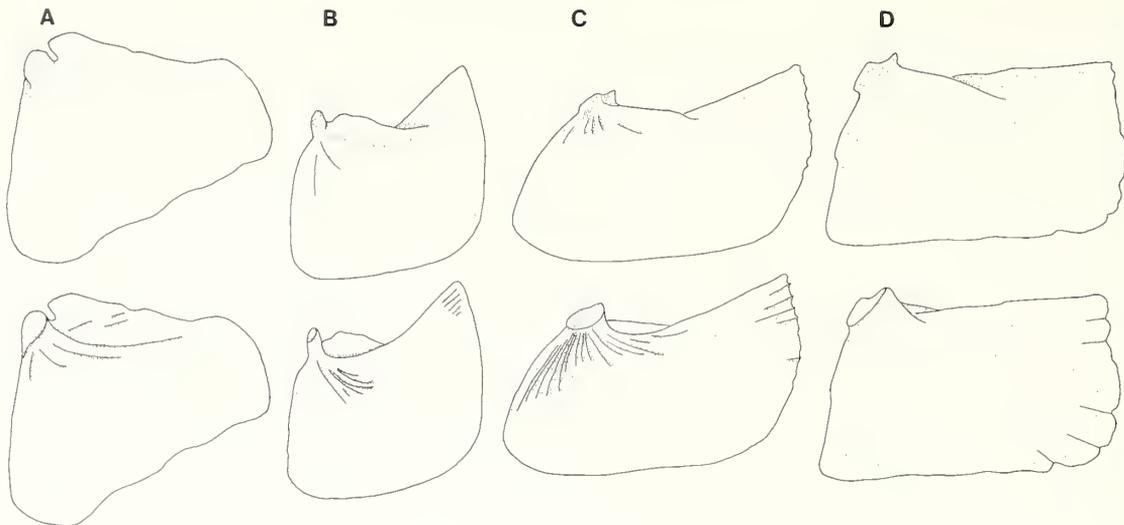
The number of branchiostegals is lower than for Recent esocids. Some specimens of *E. americanus* and rarely *E. lucius* have a similar total number. However, in the great majority of specimens of all Recent esocids (Crossman 1960) the number of branchiostegals on the epihyal exceeds that on the ceratohyal by two or three, whereas in *E. tiemani* the branchiostegals are distributed almost equally between the two bones. The situation is reversed in Recent umbrids (Wilson and Veilleux 1982), where more branchiostegals are found on the ceratohyal. The presence, in the fossil, of more branchiostegals on the left ceratohyal than on the right is the usual situation for modern esocids (Crossman 1960), in which the left branchiostegal membrane usually overlaps the right.

TEXT-FIG. 7. Reconstruction of skull of *Esox tiemani* in lateral view.

The opercular region is shorter anteroposteriorly than in Recent esocids, and the prominent anterodorsal flange (text-fig. 9B) on the opercle distinguishes the species from all other esocids. In young specimens of *E. lucius* the dorsal opercular margin is in two sections, a lateral ridge extending posteriorly and slightly ventrally from the articular process across about two-thirds of the width of the bone, and the posterodorsal margin, which runs from the posterodorsal corner of the bone, anteriorly and slightly ventrally along the dorsomedial edge to a point about one-third the width of the bone from the articular process. Where the two ridges overlap, in the middle third of the bone, there is a shallow groove (text-fig. 9D). The levator operculi muscle (Winterbottom 1974) inserts along the lateral ridge and on the lateral face of the opercle posterodorsal to it, as well as on the dorsal edge and dorsomedial surface of the bone. The situation in young specimens of *E. masquinongy* is similar (text-fig. 9C), except that the lateral ridge forms a flange, like that in *E. tiemani* but much smaller in extent. As well the overlap between the ridges and the groove between them is scarcely present.

The opercle of the Palaeocene to Eocene palaeoesocid *Boltyschia* has what might be interpreted as an incipient or remnant anterodorsal flange, and a ridge on the medial surface of the bone running posteriorly from the articular process (Sytchevskaya 1976, pl. i, figs. 3-4). In most umbrids, the opercle is not as rectangular as it is in esocids or even *Boltyschia*, and all three extant genera have a plate-like extension dorsal to a line joining the articular process with the posterodorsal corner of the bone. Opercles of *Novumbra* are most similar to those of *Boltyschia*. In *Novumbra* (text-fig. 9A) there is a medial ridge running posteriorly from the articular process, and the dorsal flange is broadest anteriorly. The levator operculi inserts entirely on the medial surface of the opercle, dorsal to the ridge.

TEXT-FIG. 8. Reconstruction of *Esox tiemani* in lateral view, intermuscular bones and scales omitted.



TEXT-FIG. 9. Comparison of opercles in lateral view (upper drawings) and medial view (lower drawings). A, *Novumbra hubbsi*, UAMZ 3713. B, *Esox tiemani*, UAVP 15029. C, *E. masquinongy*, UAMZ 3744. D, *E. lucius*, UAMZ 4876.

The articular process of the opercle is also longer in *E. tiemani* than in Recent species. In overall shape the opercle of *E. tiemani* is somewhat intermediate between those of *Boltyschia* and *Novumbra* on the one hand, and extant species of *Esox* on the other, because it is more rectangular than the former but less rectangular and less elongated than the latter. One can visualize a transformation series from a *Novumbra*-like opercle, through *Boltyschia*, *E. tiemani*, and *E. masquinongy*, to the condition in *E. lucius* (text-fig. 9). The majority of the dorsal margin of the opercle of Recent esocids is thus probably homologous with the medial ridge of umbrids. The dorsal opercular flange of umbrids is the homologue of the anterodorsal and lateral ridge in esocids. The opercle of the Oligocene species *E. dispar* differs further from these in having an elongate yet rounded opercle (Sytchevskaya 1976).

In overall body form (text-fig. 8) *E. tiemani* is a long, slender fish. Postcranially the skeleton is comparable to that of Recent North American esocids with the exception of meristic differences. A meristic comparison of relevant features of *E. tiemani* with other fossil and Recent species is given in Table 1.

DISCUSSION

Esox tiemani is anatomically the best-known fossil esocid, thanks mostly to the excellent preservation of the holotype. There is no doubt that it represents a distinct species because of the mosaic of meristic differences between the fossil and other known esocids (Table 1). In one of these, the branchiostegal ray distribution, the fossil is intermediate between Recent umbrids and esocids. In addition to the meristic characters, there is a unique combination of proportional and shape features of the skull which serve to distinguish this species from others. The most striking of these is the shape of the opercle, as described above. Others include the somewhat stouter, slightly bent preopercle with well-developed anteromedial flange, and the elongate lower jaw with perhaps a greater ratio of fixed or canine teeth to depressible teeth along the oral margin of the dentary.

TABLE 1. Comparison of meristic features of *Esox tiemani* with other Recent and fossil species of *Esox*. Data for other esocids from Sytchevskaya (1976). BR—branchiostegal rays, P—pectoral fin rays, V—pelvic fin rays, D—total dorsal fin rays, A—total anal fin rays, CS—supplementary caudal rays, TV—total vertebrae, CV—caudal vertebrae.

	BR	P	V	D	A	CS	TV	CV
<i>E. lucius</i>	11-20	11-18	8-13	17-26	14-21	20	56-65	21-22
<i>E. masquinongy</i>	16-19	14	11	21-24	20-22	27	63-67	21-22
<i>E. reicherti</i>	13-14	12	9-12	17-22	15-18	27	64-65	21-22
<i>E. americanus americanus</i>	11-16	13-17	8-10	15-19	14-17	?	44-51	19
<i>E. a. vermiculatus</i>	9-14	14-15	9-10	17-21	15-19	26	42-49	18
<i>E. niger</i>	12-16	15	10-11	20-21	16-19	22-28	49-54	20-21
<i>E. borealis</i>	13-15	12-13	9-11	18-19	?	?	56-58	21-23
<i>E. papyraceus</i>	?	13?	10?	17	15	13	48	20
<i>E. lepidotus</i>	14	15	13	19-21	19	17-18	52-60	18
<i>E. dispar</i>	?	13	11	19	?	?	61	18
<i>E. tiemani</i>	11-12	14	11	19	15	21	59	19

The question of the phylogenetic relationships of the Palaeocene species is more difficult to answer, because the position of the esocids within the fossil and Recent esocoid families is poorly understood, as are the relationships among esocid species.

Nelson (1972) proposed a division of Recent *Esox* species between two subgenera: *Esox*, including *E. lucius*, *E. reicherti*, and *E. masquinongy*; *Kenoza*, including *E. americanus* and *E. niger*. Unfortunately, the features of the cephalic sensory canals used by Nelson to separate the subgenera are not clearly visible on the available specimens of *E. tiemani*. Nelson did, however, suggest that the number of total vertebrae seen in *Kenoza* (42-54) was primitive for the genus as a whole, and that the greater number seen in the subgenus *Esox* (56-67) was a derived condition. Nelson's hypothesis would suggest that the vertebral number in *E. tiemani* (59) is indicative of a closer relationship to the subgenus *Esox*.

On the other hand, the low branchiostegal number and the distribution of branchiostegals between ceratohyal and epihyal, as discussed above, together with the opercular structure, are all features in which *E. tiemani* is intermediate between Recent umbrids and esocids. These features therefore indicate that the Recent subgenera of *Esox* are more closely related to each other than either is to *E. tiemani*. The evidence bearing on this question is admittedly slim, and a more reliable estimate of relationships must await further study.

With respect to the question of the position of the esocids within the Esocoidei, *E. tiemani* demonstrates that a large number of fundamental esocoid features (including posteriorly situated dorsal and anal fin, S-shaped supraneurals, and toothless maxillae) and esocid features (depressible and canine teeth, elongate snout, jaws, and trunk, elongate vomer and palatines, ethmoid process on ectopterygoid, nearly straight preopercle, squared opercle, small second and third hypurals separated by a gap, and anteriorly lobed scales) are geologically much older than was previously known.

The significance of this is that in the absence of *E. tiemani*, the fossil record of esocoids appeared to show a tendency for the older esocoids (*Boltyschia*, *Palaeoesox*) to be anatomically more like umbrids than like modern esocids (Sytchevskaya 1976). Eurasian fossil esocids, similarly, tended to have such features as less elongate jaws and fewer vertebrae compared with some modern esocids. Whether these features are indeed primitive for esocids remains to be seen. But the apparent correlation with greater geologic age must be rejected in view of the structure of *E. tiemani*, which suggests that such esocid features as elongate bodies and jaws and depressible teeth were completely evolved before features such as branchiostegal ray numbers and opercular structure, in which *E. tiemani* is still intermediate between Recent umbrids and esocids.

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A NEW FRESHWATER LIMULOID FROM THE MIDDLE TRIASSIC OF NEW SOUTH WALES

by J. W. PICKETT

ABSTRACT. *Dubbolimulus peetae* gen. et sp. nov. is described from freshwater strata of middle Triassic age near Dubbo, New South Wales, and is referred to the new family Dubbolimulidae. Previous reports of xiphosurans from Australia are reviewed; *Pincombella belmontensis* Chapman, 1932 and *Hemiaspis tunnecliffei* Chapman, 1932 are shown to be respectively an insect and a trilobite.

REPORTS of merostomes from Australia are contained in only eight publications. Three of these (McCoy 1899; Gill 1951; Caster and Kjellesvig-Waering 1953) deal with eurypterids, and are not further mentioned in this article. A fourth (Quilty 1972) reports an unnamed Cambrian aglaspid from Tasmania. The remaining four (Chapman 1932; Riek 1955, 1968*b*; Riek and Gill 1971) are concerned with xiphosurans, and are summarized briefly.

AUSTRALIAN XIPHOSURANS

Chapman (1932) established the taxa *P. belmontensis* from the insect beds (?Boolaroo Sub-group, late Permian) near Belmont, New South Wales, and *H. tunnecliffei* from the late Silurian Dargile Formation at Studley Park, Kew, Victoria. Much better preserved than either of these is the magnificent specimen of the rather anomalous *Austrolimulus fletcheri* from the Beacon Hill shale lens in the middle Triassic Hawkesbury Sandstone of the Sydney district (Riek 1955, 1968*b*). The youngest xiphosuran so far known from the Australian continent is *Victalimulus mcqueeni* Riek and Gill, 1971 from the early Cretaceous fish bed (Strzelecki Group) near Koonwarra in Victoria (Waldman 1971).

Three of these papers are based on careful examination of available material. On the other hand, neither of the two species described by Chapman (1932) is xiphosuran. The holotype specimen of *P. belmontensis* (Pl. 56, fig. 2) is clearly the wingless and, for the most part, legless body of a hemipteran with a small scutellum and distinct pronotal lobes. Riek (1968*a*) lists sixty-two species of Hemiptera from the horizon yielding *P. belmontensis*. These are based on generally incomplete animals, either wings, heads, or thoraxes; since so few are known in all aspects of their morphology, no attempt is made here to reconcile *P. belmontensis* with any of the described forms. Chapman's figures (1932, pl. 14, figs. 1-3) are difficult to interpret in relation to the specimen. He appears to have taken some irregularity in the matrix to be the anterior border of his figs. 2 and 3 ('Anterior border . . . marked out by a definite rust-stained impression') and the real anterior margin to mark the edge of 'opercular plates'. Chapman considered that he was examining the specimen in ventral aspect, whereas it represents the back of the insect from which the wings have been torn. This, together with its distorted position, may have led him to interpret the only preserved, jointed leg as a dorsally attached telson. Chapman's fig. 2 was reproduced by Størmer (1955, fig. 13.6), who, for reasons now apparent, could not place *Pincombella* within any of the defined subdivisions of the suborder Limulina, listing it (p. P23) under 'Superfamily and Family uncertain'. For similar reasons it was referred to 'incertae sedis' by Bergström (1975).

The true affinities of the other species described by Chapman, *H. tunnecliffei*, are not immediately so clear. It is certain that Chapman's reconstruction (1932, pl. 14, fig. 5) bears no resemblance to the actual specimen. The broad anterior border with radiate markings is a conchoidal fracture lying outside the true area of the specimen, which is marked by dark colouration; there is no suggestion of pleural spines, rather the lateral profile is fairly straight; there is no hint of a telson. The

specimen (MUGD 1201, not 1801 as quoted by Chapman, refigured here as Pl. 56, fig. 5) consists for the greater part of the thoracic area of a trilobite with relatively wide axis (13.5 mm) and narrow pleurae (6.3 mm). The pygidium is entirely missing and the fragmentary cephalon shows no detail at all. It is probably a poorly preserved homalonotid trilobite (pers. com. K. S. W. Campbell and P. A. Jell). One such species, *Trimerus harrisoni* (McCoy, 1876), has been described from the Dargile Formation in the Melbourne area. Chapman's damaged specimen has been compared alongside the holotype of *T. harrisoni*, NMV P7503. The axis of Chapman's specimen is more clearly demarcated than in the holotype of *T. harrisoni*, but the latter has suffered very little distortion compared with the former. The clearer delineation of the axis of '*H. tunnecliffei*' is taken to be a result of the distortion. It is highly probable that the name *H. tunnecliffei* is a junior synonym of *Homalonotus harrisoni* McCoy (reassigned to *Trimerus* by Gill 1949).

SYSTEMATIC PALAEOLOGY

Repositories. The repositories of specimens quoted are denoted by the following abbreviations: MM, Geological and Mining Museum, Sydney; MUGD, Department of Geology, University of Melbourne; NMV, National Museum of Victoria, Melbourne.

Superfamily LIMULOIDEA Zittel, 1885

- 1885 Limulidae Zittel, p. 643.
- 1944 Limulacea Zittel; Raymond, p. 504.
- 1952 Limulacea Zittel; Størmer, p. 636.
- 1955 Limulacea Zittel; Størmer, p. P21.
- 1975 Limulacea Zittel; Bergström, p. 303.

Discussion. The suffix of the superfamilial name has been changed in conformity with Recommendation 29A of ICZN. Størmer (1952, 1955) included three families in the Limuloidea: Paleolimulidae Raymond, 1944; Mesolimulidae Størmer, 1952; and Limulidae Zittel, 1885. The family Limulidae was redefined by Riek and Gill (1971) to include those genera previously referred to the Mesolimulidae, thus comprising the genera *Limulus*, *Tachypleus*, *Carcinoscorpius*, *Mesolimulus*, *Psammolimulus*, and their new genus *Victalimulus*. They excluded the genus *Limulitella* Størmer, 1952, placing it with the Paleolimulidae and regarding it as a probable synonym of *Paleolimulus*. The type species of *Limulitella*, *Limulus bronni* Schimper, 1850, is in need of re-examination to establish the status of the genus. A fourth family name, Austrolimulidae, was established by Riek (1955) for the highly individual *Austrolimulus*; no other genus has yet been referred to this family. Via Boada and Villalta (1966) established a new family Heterolimulidae for their genus *Heterolimulus* from the Triassic of Spain. Bergström (1975) summarized the classification up to this point. More recently Romero and Via Boada (1977) described the genus *Tarracolinulus* from the same horizon as *Heterolimulus*, and included the latter without comment in the family Limulidae, a conclusion with which I agree.

Dubbolimulus gen. nov. has features which differentiate it from each family (although, if *Limulitella* is set aside because of its doubtful status, two of the families contain but a single genus), so that it would be possible to establish a separate family for it. *Dubbolimulus* can be separated from the Austrolimulidae by the absence of exaggerated genal spines and of 'free posterior segments' on the opisthosoma. It is distinguished from the Paleolimulidae by the fact that the ophthalmic ridges do not meet in front of the cardiac lobe, by the absence of distinct annulation of the axis of the opisthosoma, and by the absence of movable lateral spines on the opisthosoma. This last feature represents a point of similarity with the Austrolimulidae; *Austrolimulus* is the only other limuloid genus which lacks movable spines on the opisthosoma. A characteristic peculiar to the Austrolimulidae is the fact that the anterior margin of the opisthosoma, at its junction with the prosoma, extends well beyond the area bounded by the ophthalmic lobes (Riek 1968b, fig. 1), whereas there is a clear correlation between these two features in other genera.

Features which distinguish *Dubbolimulus* from genera of the Limulidae are: (a) absence of movable

spines, (b) apparent absence of free lobes on the anterior part of the opisthosoma, (c) the greatly unequal prosoma and opisthosoma, and (d) genal angles which are distant from the lateral margins of the opisthosoma. Setting aside (c) and (d) as being possibly of lesser significance phylogenetically, the other two characters could be either features which no antecedent of *Dubbolimulus* ever possessed, or ones which have been secondarily lost. Movable spines are unknown in Palaeozoic Limulina until the Permian *Paleolimulus avitus*, in which both the movable spines ('stylets') and the free lobe are specifically mentioned by both Dunbar (1923) and Raymond (1944). According to Ivanov (1933, fig. 54) the movable spines originate as the distal tips of the somites of the opisthosoma, which separate and move posteriorly during development of the embryo, being already present in the first larval stage. In view of the complexity of such a development it seems reasonable to regard all those forms in which it is expressed as belonging to a single lineage. The same applies to the sharing of somite VI, between the prosoma and opisthosoma, which appears to be connected with the production of the free lobes of the opisthosoma. These two features are fairly general among Limuloidea. Bergström (1975, p. 295) regards the sharing of somites VI and VII between prosoma and opisthosoma as distinctive of the suborder Limulina.

While the gross characters of *Dubbolimulus* link it to genera of Limulidae and Paleolimulidae, it is considered likely that the apparent absence of the free lobe on the opisthosoma is due rather to a masking of the characteristic by general simplification of morphological features of the opisthosoma, and that the absence of movable spines is another expression of the same trend. Phylogenetically, this means that *Dubbolimulus* is an offshoot of the main lineage of Limuloidea, rather than an independent derivative of a lineage closer to either Belinuroidea or Euprooidea. This conclusion notwithstanding, *Dubbolimulus* cannot be assigned to either of the subfamilies of Limulidae, which are distinguished on the basis of characters entirely lacking in *D. peetae*. Although it shares the absence of movable spines with *Austrolimulus* and is of approximately the same age, the extraordinary genal spines and the 'free posterior segments' of the opisthosoma of *A. fletcheri* preclude consideration of any close relationship between *Austrolimulus* and *Dubbolimulus*. It is therefore appropriate to establish a new family for the latter. Raymond's original diagnosis of the superfamily (1944, p. 504) included movable lateral spines as a criterion. Their absence in *Dubbolimulus* and *Austrolimulus* excludes this as a suprafamilial character.

An alternative phylogeny for xiphosurans has been presented by Fisher (1981, 1982), based on cladistic principles. This focuses on the nature of the prosoma/opisthosoma articulation, and varies from earlier suggestions (e.g. Bergström 1975) in deriving the Limuloidea and Euprooidea independently from the Belinuroidea. Both the younger groups are characterized by fusion of the opisthosomal segments, and Fisher uses the declination of the occipital band of the prosoma to determine polarity of various conditions of it with respect to the primitive (unfused) condition of the opisthosoma. Fisher (1977) has argued in favour of a ventral enrolment in *Euproops*, affording protection of the underparts. The articulation in *Limulus*, however, serves to achieve strong flexuring in the dorsal direction (Richter 1964), associated with righting strategies; the remarkable ophthalmic spines of *Euproops* absolutely preclude any similar dorsal flexuring, even had the structure of the occipital band allowed it. It seems to me that the morphological differences in the occipital band discussed by Fisher (1981) reflect these differences in function, which are in all probability generally characteristic of each superfamily.

The free segments reported at the rear of the opisthosoma in *Paleolimulus* (one segment) and *Austrolimulus* (three segments) support a derivation of Limuloidea from Belinuroidea. However, there appears to be some doubt about the nature of these structures. The most recent reconstruction of *Paleolimulus* by Fisher (1981, fig. 3b) excludes such a segment, and Raymond (1944, p. 50) seems to have had some reservation concerning it. I have examined the holotype of *A. fletcheri* with specific reference to this point. Certainly there are indistinct features suggesting transverse structures at the rear of the opisthosoma, but the 'segments' are definitely fused and were incapable of any independent movement. More significantly, they are confined to the area of the opisthosomal doublure, and thus had no appendages corresponding to them. Separation of the counterparts of the holotype has resulted in a transverse fracture of the exoskeleton anterior to these 'segments', so that

the posteriormost part of the opisthosoma is held on the dorsal counterpart. Consequently, although only dorsal features can be observed for most of the skeleton, the rear of the opisthosoma and the telson can only be observed in ventral view. While the possibility remains that the poorly expressed transverse features represent true segmentation, the absence of any trace of appendages tends to belie such an interpretation. In the absence of material, other than the holotype specimen, with which to check this feature, it seems wiser not to regard the transverse structures as reflecting a true segmentation, and it should not be considered a primitive character in either *Paleolimulus* or *Austrolimulus*.

A comprehensive phylogeny of xiphosurans is presented by Fisher (1982, text-fig. 1). The nature of the text of his article implies that this phylogeny was arrived at by cladistic analysis. However, no discussion of the parameters used in achieving the result is presented, which makes it difficult to compare *Dubbolimulus* on the same basis. It is difficult to understand his close placement of *A. fletcheri* with *Psamminimulus gottlingensis* and *Limulitella bronui*. *Austrolimulus*, with its reduced opisthosoma, exaggerated genal spines, absence of movable spines, and absence of posterolateral facets, is the most aberrant of all limuloids known so far; none of these features is characteristic of either of the other two genera on this branch of Fisher's proposed phylogeny. I regard both *Austrolimulus* and *Dubbolimulus* as being derived independently from the mainstream of Limuloidea.

Some of the remarks made by Fisher (1981) relating to the function of certain features of the limuloid carapace are of interest in the present context: in particular, (a) reduction of prosomal spines, reducing drag during swimming, (b) the significance of the free lobes in maintaining channels for respiratory currents during shallow burial, and (c) the function of movable spines as sensors against the substrate. All three of these features are reduced in both *Austrolimulus* and *Dubbolimulus* and, in the light of Fisher's observations, allow comment on the autecology of these genera. Fisher (1981, p. 57) predicts an association between development of free lobes and the importance of burrowing and burial in the activities of limuloids. This is an attractive suggestion which, coupled with the reduction in drag during swimming because of the absence of spines, suggests that swimming heavily outweighed burrowing in the relative significance of the activities of *Dubbolimulus*. Further support for this suggestion comes from Fisher's (1975) analysis of degree of vaulting of the prosoma in *Limulus* (strongly vaulted) and *Mesolimulus* (much flatter), in which he concludes that the two shapes are better suited to burrowing and swimming respectively. As the prosoma of *Dubbolimulus* was probably much flatter than that of *Limulus*, this strengthens the suggestion that burrowing was not an important activity of *D. peetae*.

The movable lateral spines, which occur in all limuloid genera except *Austrolimulus* and *Dubbolimulus*, serve to transmit information from the substrate, allowing precise orientation. The extended genal spines of *Austrolimulus*, coupled with the long telson, provide a refined mechanism of maintaining orientation (in both longitudinal and lateral senses) probably more critical than that provided by the movable spines; this could account for the obsolescence of movable spines in that genus. *Dubbolimulus*, however, does not show any features which could take over this function of the movable spines, so their absence in that genus remains unexplained.

Family DUBBOLIMULIDAE fam. nov.

Type genus. *Dubbolimulus* gen. nov.

Diagnosis. Limuloidea without dorsal or lateral spines, except for the genal angles of the prosoma and the posterolateral terminations of the opisthosoma adjacent to the telson joint; opisthosoma fused, much smaller than the prosoma; genal angles distant from lateral margins of opisthosoma.

Genus *Dubbolimulus* gen. nov.

Type species. *D. peetae* sp. nov.

Diagnosis. Prosoma semicircular, smooth; posterior margin lying near 90° to axis and bearing posteromarginal facet; opisthosoma with smoothly curved lateral margin without lateral spines;

scarcely wider than the distance between the ophthalmic ridges of the prosoma; free lobes not apparent on dorsal surface of opisthosoma.

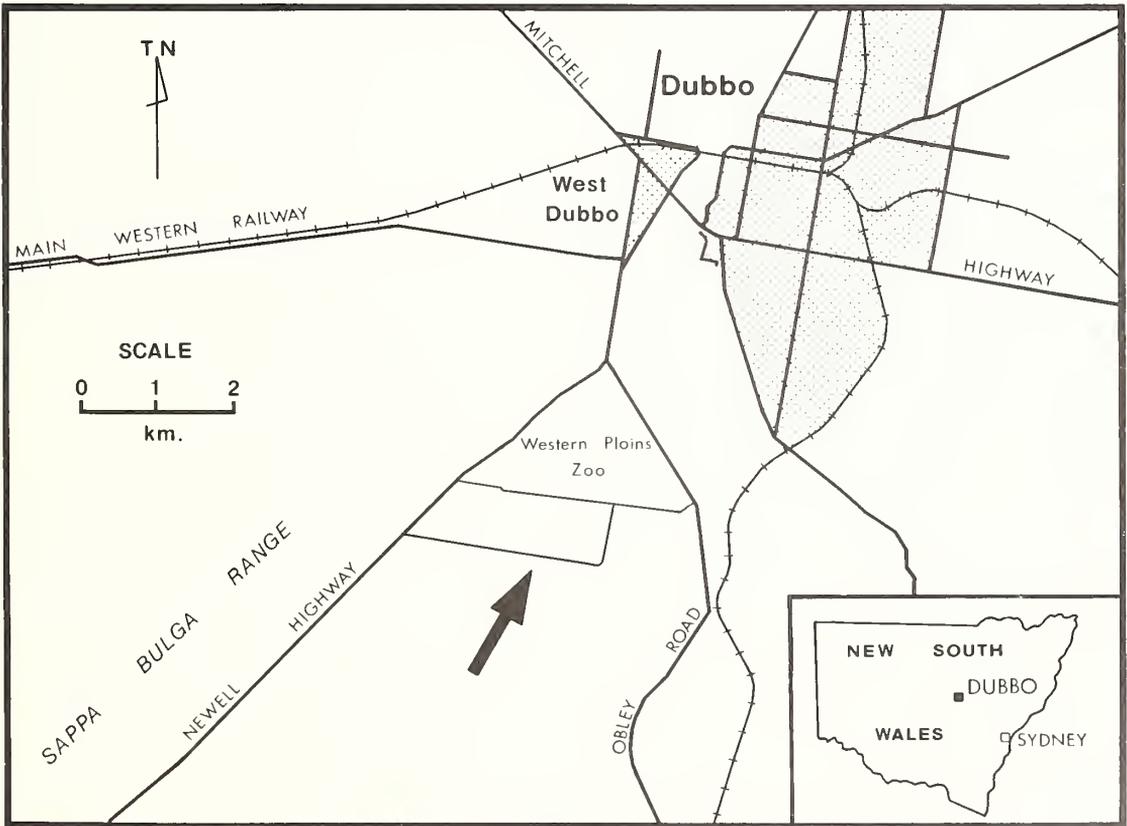
Derivation of name. From the type locality near Dubbo, New South Wales, Australia.

Dubbolimulus pectae sp. nov.

Plate 55; Plate 56, figs. 3, 4

Diagnosis. As for genus.

Material. Holotype and only specimen preserved as counterparts MM F27693 (dorsal) and MM F27694 (ventral). The specimen is preserved in a red-brown, iron-rich, slightly micaceous shale with common plant remains, most conspicuously *Dicroidium odontopteroides* var. *moltenense* Retallack. The specimen was recovered south of Western Plains Zoo, Dubbo, at approximate grid reference 151004 (yards), Dubbo 1:250,000 geological sheet (SI/55-4), 148° 37' E, 32° 19' S (text-fig. 1). Plant fossils are abundant at the locality, including many species illustrated in a recent paper by Holmes (1982) which deals with the flora of a locality 15 km to the south. This flora was considered middle Triassic by Holmes.



TEXT-FIG. 1. Map of the district around Dubbo, New South Wales, showing the type locality of *Dubbolimulus pectae* gen. et sp. nov. arrowed.

Description. The specimen consists of the flattened prosoma and opisthosoma, still in juxtaposition. The telson is lacking. Traces of some of the appendages have been impressed through the carapace. Separation has occurred in the dorsal exoskeleton, as there is little difference between dorsal and ventral counterparts (Pl. 55, figs. 1, 2); traces of the appendages are clearer in the ventral counterpart. The specimen may have been lying in a slight depression before burial, as compression has depressed the inner parts of the prosoma below both the prosomal margin and the opisthosoma.

The outline of the flattened prosoma approximates closely to a semicircle. It is 27.8 mm wide immediately in front of the genal angles and 14.0 mm long. The dorsal surface is marked by ophthalmic ridges which begin near the posterior margin at a point midway between axis and lateral margin. The compound eyes begin *c.* 1.0 mm anterior of this point, and are probably just under 2.0 mm long. The visual surface of the eye is not adequately preserved, but its position is marked by an outward inflection in the ophthalmic ridge. In front of the eye the ridge curves gently inward and runs forward again to a point 6.5 mm from the posterior margin and 5.5 mm from the axis, where it is inflected axially. The ophthalmic ridge is not continuous across the front of the prosoma, but terminates at a point 3.5 mm from the axis and 3.0 mm from the anterior margin. The left ophthalmic ridge is not as well preserved. The cardiac lobe is trapezoidal, 4.0 mm wide posteriorly, 2.3 mm wide at the front, and 7.0 mm long. The axial furrows are now the highest points on the flattened specimen, presumably corresponding to a greater amount of cuticular material beneath (apodemes, ventral exoskeleton, appendages). The axis is depressed and is marked by a crack (without separation) which reaches to within 3.0 mm of the anterior margin. It is not possible to count the number of apodemes, though there were certainly not less than four. The genal angles are produced into short (1.5 mm), blunt, genal spines which project posterolaterally. There may have been a narrow border (*c.* 0.2 mm wide) similar to that in *Limulus*, but details of this are obscured by flattening, possible concentric fracturing near the margin, and the fact that the doublure, apparently markedly angulated like that of *Limulus*, is impressed through the dorsal skeleton. The trace of this angulation disappears 3.0 mm from the posterior margin, suggesting that the angulation fades out, as in *Limulus*. In *Limulus* the angulation defines a triangular widening of the doublure in front of the mouth; this preoral area is present in *Dubbolimulus*, but is semicircular and clearly impressed through the carapace. There is a slight indication of a pair of median ocelli 7.0 mm from the anterior margin, where an increase in height of the ridge produced by the longitudinal axial crack suggests the original presence of a short, axially aligned, ocellar ridge. Alternatively, a median structure represented by an anteriorly convex curve 1.5 mm wide and 2.1 mm from the anterior margin may represent the trace of an ocellar tubercle forming the anterior edge of the interophthalmic region (Pl. 56, fig. 4, arrows). The posterior margin of the prosoma is rather straight, deflected posteriorly only at the genal angles. Between the posterior margin and the rounded anterior portion of the prosoma are triangular areas, here termed posteromarginal facets (after Meischner 1962, p. 185, 'hintere Randfacette'); they are defined by the inner edge of the genal spine, the posterior edge of the cardiac lobe, and the posterior end of the ophthalmic ridge. The anterior margins of the posteromarginal facets are formed by an angulation along which the dorsal surface of the prosoma is deflected ventrally. Crushing of the facets during compression has obscured details of morphology along most of the posterior margin of the prosoma.

The opisthosoma is conspicuously smaller than the prosoma, measuring 12.0 mm across its greatest width near the junction with the prosoma, and 7.5 mm from the anterior margin to the lobes on either side of the telson attachment; this makes it about equal in size to the area within the ophthalmic ridge of the prosoma. The lateral margins run parallel for 2.0 mm before turning axially, so that the opisthosoma tapers markedly to a minimum width of 4.2 mm, 1.5 mm from the posterior margin, which has a shallow re-entrant *c.* 1.0 mm deep for the telson attachment. The lateral margins bear no trace of either fixed or movable spines. As on the prosoma, the cardiac lobe is defined by the most raised part of the specimen, bounding a trapezoidal area 4.0 mm wide anteriorly and 2.5 mm wide at the rear. These ridges show traces of probably six apodemes. The area between the ridges is rather depressed. The lateral margins show a narrow border not more than 0.5 mm wide, which may correspond to the ventral doublure. If this is the case, the doublure is relatively narrower than in *Limulus*, possibly reflecting the absence of lateral spines. There is no indication of anterolateral free lobes on the opisthosoma; rather, the

EXPLANATION OF PLATE 55

Figs. 1, 2. *Dubbolimulus peetae* gen. et sp. nov. Holotype specimen. Ballimore Formation, middle Triassic, Dubbo, New South Wales, $\times 4$. 1, MM F27693, upper counterpart, showing the impression of the doublure, the posterolateral facets, and suggestions of apodemes on the opisthosoma. 2, MM F27694, lower counterpart, low angle lighting showing the appendages.



1



2

PICKETT, *Dubbolimulus*

doublure continues around the anterolateral corner, whereas in *Limulus*, with its well-developed free lobes, the morphology is quite complex in this area.

Some prosomal appendages have been impressed through the carapace (Pl. 55, fig. 2). Traces of five appendages are evident on the right side. Assuming that appendage I (the chelicera) would not be apparent and that the first ridge represents appendage II (by analogy with *Limulus*), a group of four legs (appendages II-V) is succeeded by a gap (in which there are two smaller, unidentified impressions) and another long, laterally directed leg, corresponding to the posteriorly directed appendage VI of *Limulus*. None of the legs projects beyond the rim of the carapace, but legs V and VI almost reach it. No joints in the legs are discernible. They are almost straight, with a slight anterior curve. On the left there are less regular impressions of possibly five legs reaching almost to the margin, but except for appendage VI these are less easily identifiable.

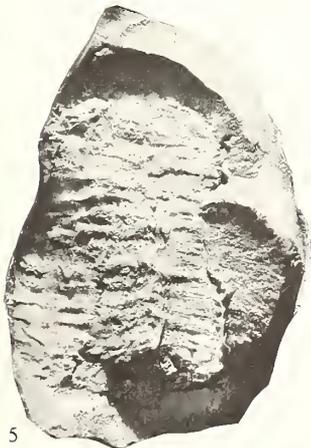
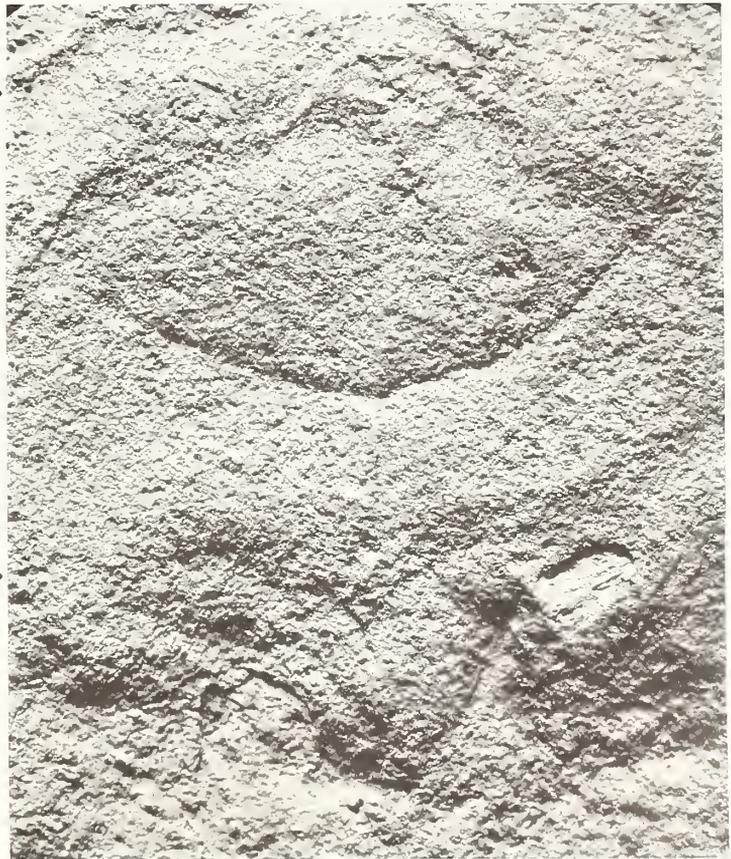
A possible reconstruction of *D. peetae* gen. et sp. nov. is shown in text-fig. 2.

Discussion. The specimen has been much flattened during compaction of the sediment. This is most obviously expressed as (a) the impression of legs, doublure, and apodemes through the carapace, (b) the presence of an axial crack and some damage in the region of the left ophthalmic ridge, and (c) wrinkles on the outer part of the prosoma. This latter point particularly may reflect the fact that the exoskeleton was not strongly mineralized. The wide angle between the rear margin of the prosoma and the lateral edges of the opisthosoma is an unusual feature in limuloids, and was originally attributed to anterolateral movement of the genal angles during compaction.

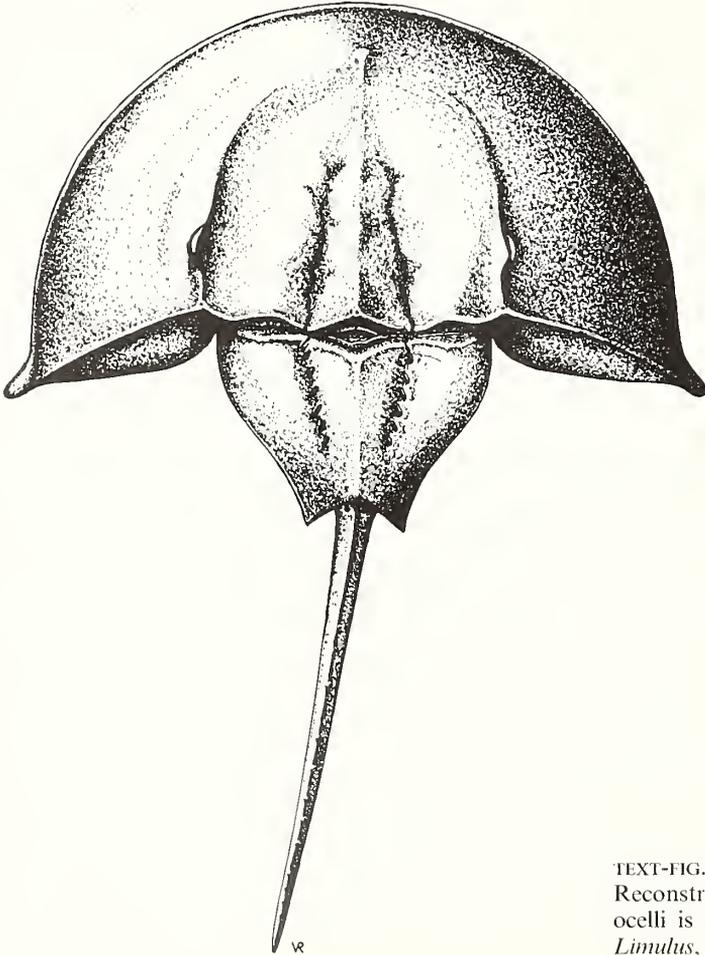
To examine the effects of compression on limuloids, four juvenile specimens of *Limulus polyphemus* were embedded in clay and subjected to considerable pressure applied by means of screw clamps. Some lateral spread occurred in all cases, the least amount occurring in the specimen illustrated in Pl. 56, fig. 1, in which the maximum width of the prosoma increased by 1.4%. The length of the prosoma, however, was reduced by over 10%. In no case was there any change which suggested that the condition observed in *Dubbolimulus* could have resulted from the spreading of an original configuration of genal angles similar to that in *Limulus*. The prosoma outside the ophthalmic ridges has suffered the greatest damage, being compressed into a number of concertina-like folds roughly concentric with the margin. It is apparent that the dorsal spines greatly reinforce the exoskeleton (thicker at these points), as the areas around them have suffered little crushing. Probably for this reason there is no development of a longitudinal axial crack as in the holotype of *D. peetae*, since young *L. polyphemus* have six axial spines, three on the prosoma and three on the opisthosoma. Insufficient pressure was achieved to impress the appendages through the dorsal exoskeleton. By contrast, a specimen flattened between numerous sheets of paper in a hydraulic press suffered considerable anterolateral movement of the genal angles, and the spines on the ophthalmic ridges were flattened sideways.

EXPLANATION OF PLATE 56

- Fig. 1. *Limulus polyphemus*. Epoxy resin cast of juvenile specimen compressed in deformation experiment. Note the concentric folds of the exoskeleton outside the ophthalmic ridges, and the proximity of the genal spines to the lateral margins of the opisthosoma, $\times 0.95$.
- Fig. 2. *Pincombella behuontensis* Chapman. NMV P13646, latex cast of holotype, Boolaroo Sub-group, late Permian, Belmont, New South Wales, $\times 7.5$.
- Figs. 3, 4. *Dubbolimulus peetae* gen. et sp. nov. MM F27693, holotype, Ballimore Formation, middle Triassic, Dubbo, New South Wales. 3, upper counterpart, $\times 1$. 4, detail of upper counterpart showing median area of prosoma in ocellar region, $\times 14$; the arcuate structure is the rear edge of the doublure; arrows indicate the levels of structures which may be interpreted as ocelli.
- Fig. 5. *Trimerus harrisoni* (McCoy). MUGD 1201, latex cast of '*Hemiaspis*' *tunnecliffei* Chapman, Dargile Formation, late Silurian, Studley Park, Melbourne, Victoria. The area in shadow near the top of the figure lies outside the real margin of the specimen, but is what was interpreted as a wide border with radiate markings by Chapman (1932, pl. 14, fig. 5). Thoracic pleurae are visible on the right, but only the posterior pleurae are preserved on the left, $\times 1$.



It is apparent that the hydraulic conditions of compression under geological circumstances hinder lateral spreading of strongly profiled organisms, as established by Walton (1936) and Rex and Chaloner (1983) for plant compressions. I thus conclude that the outline of *Dubbolimulus* as preserved is very close to the original. Having determined this, there is some support for the undisturbed rear margin of the prosoma from other aspects of the morphology. If the prosoma was moderately arched (as it must have been to create room for the appendages, their musculature and the digestive organs), the possibility emerges, with an outline like that of *Dubbolimulus*, that the arched posterior margins beyond the edges of the opisthosoma left a wide gape, exposing the underparts of the prosoma. Such a morphology would be out of character with the general style of limuloids, which are close to their substrate on all sides so that their ventral surface is well protected. The rear margin of the prosoma of *Dubbolimulus* bears a triangular area on either side of the interophthalmic region which is interpreted as a ventrally deflected posteromarginal facet, thus largely closing the gape at the rear of the prosoma. This structure occurs in *Psammodimulus* (Meischner, 1962) and *Vicialimulus*, though not described in the latter. It is also present in the oldest member of the group, *Paleolimulus*, being clearly indicated in Dunbar's (1923) figures, in '*Limulus*' *woodwardi* Watson, 1909, and in *Mesolimulus walchi*, in which it has a somewhat exaggerated development.



TEXT-FIG. 2. *Dubbolimulus pectae* gen. et sp. nov. Reconstruction by Vivien Reid. The position of the ocelli is not certain, and the telson is based on *Limulus*, $\times 3$.

Ivanov (1933, fig. 63) figured a specimen of *M. walchi* and remarked (1933, p. 295) that, on the underside of the prosoma, there is an obvious furrow corresponding to the pleural part of the anterior border of the sixth segment. He equated this with a ridge in the same position on the dorsal surface of other specimens. This structure may be one taken up by Störmer as a primitive feature (1952, p. 630: 'A furrow along the inner margin of the genal angles may also be a primitive character'). It is possible that the angulation at the anterior border of the posteromarginal facet corresponds to the boundary between segments V and VI but, as it appears to have a function in protecting the ventral surface of the prosoma, this is not necessarily so.

Habitat. *Dubbolimulus* was recovered from strata which are undoubtedly of freshwater origin. No marine Triassic rocks are known in New South Wales, the nearest being 800 km distant near Gympie in Queensland (Fleming 1966; Runnegar 1969). The Ballimore Formation is the basal unit of the Great Artesian Basin in the Dubbo area, and lies unconformably on folded strata of Ordovician to Devonian age. The oldest marine strata in the New South Wales portion of the Great Artesian Basin are early Cretaceous (Aptian) in age (Scheibnerová 1976; Morgan 1980); the marine succession in this basin is the result of a north to south transgression. To the east there was an area of high land, just as there is today. Thus the locality was probably as remote from the ocean in Triassic times as it is at present, and any possibility of marine influence can be ruled out. The general area abounds in plant fossils (e.g. Holmes 1982), indicating a limnic situation, and the specimen of *Dubbolimulus* was recovered while collecting plant fossils. Riek and Gill (1971) suggested that their specimen of *Victalimulus*, also from freshwater strata, may have migrated there for breeding purposes. In view of the distance of the type locality from any areas of marine sedimentation, such a possibility seems remote for *Dubbolimulus*.

There has been a certain reluctance on the part of palaeontologists to attribute a freshwater habitat to fossil limuloids (Riek and Gill 1971; Holland *et al.* 1975). None the less, in addition to the species described by those authors (*V. mcqueeni* and *Casterolimulus kletti*), there are others which have been recovered from non-marine strata: *A. fletcheri* (Riek, 1955), *Psammolimulus gottlingensis* (Meischner, 1962). On the other hand, species of undoubted marine origin are *M. walchi* (Störmer 1952; Barthel 1974), *Heterolimulus gadeai* and *Tarracolimulus riei* (Via Boada *et al.* 1977), '*Limulus*' *woodwardi* (Watson, 1909) and '*L.*' *syriacus* (Woodward, 1879). Species referred to *Limulitella* appear to belong to both groups, e.g. *L. bromii* (Bill, 1914) and *L. liasokeuperinus* (Braun, 1860) appear to be from non-marine strata, whereas *L. vicensis* (Bleicher, 1897) is marine.

Colleagues have been strongly influenced by the marine nature of modern limulids, and by the rare reports of some species in fresh waters. However, Annandale (1909, p. 295) claimed that *Carcinoscorpius rotundicauda* is 'mainly if not entirely estuarine' and indicated that it occurs almost 150 km from the mouth of the Hooghly River. The remoteness of *Dubbolimulus* from any marine areas suggests strongly that its whole life cycle was spent in fresh water. Riek and Gill (1971, p. 207) have suggested that *Victalimulus* migrated to fresh water for breeding. If one accepts a migration between marine and limnic environments for *V. mcqueeni*, it seems more likely, in view of the basically marine nature of extant forms, that the breeding phase would have been marine, as, for instance, in many Recent terrestrial crabs.

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RAMSEYOCCRINUS AND RISTNACRINUS FROM THE ORDOVICIAN OF BRITAIN

by STEPHEN K. DONOVAN

ABSTRACT. *Ramseyocrinus* Bates, 1968, has hitherto been included in the family Eustenocrinidae Ulrich, 1925, but it differs from all other members of this family in having only four radials, an anal X which is supported by two radials (rather than two or three superradials, or a brachial and superradial), a cup which is about as wide as high, and a column which is tetrameric proximally and tetragonal holomeric distally. A new family, Ramseyocrinidae, is erected for this genus. Of the true eustenocrinids, *Ristnacrinus* Öpik, 1934 is recognized from the British Ordovician for the first time, based upon the occurrence of its distinctive columnals with synarthrial articulating ridges. *Ristnacrinus* columnals are known from four localities of Cautleyan-Rawtheyan (?Hirnantian) age and comparison with similar columnals from the Swedish Boda Limestone (Ashgill) suggests that more than one species may be present in Britain.

ONLY about thirty crinoid species have been described from the British Ordovician (Ramsbottom 1961; Bates 1965, 1968; Brower 1974; Donovan 1983). However, dissociated skeletal elements of crinoids, especially columnals, are common particularly in the Caradoc and Ashgill. Only highly distinctive columnals are of practical use in taxonomy, as homeomorphs between distantly related taxa are probably common (Broadhead and Strimple 1977). However, it is possible to make a generic identification of at least some columnals (Donovan 1983). One of the most distinctive of all columnals found in the Ordovician is that of the dististele of *Ristnacrinus* Öpik, 1934, which has been recognized by a number of subsequent authors (Chauvel and Le Menn 1972, 1979; Chauvel *et al.* 1975; Briskeby 1981; Wright 1983).

The radial plates of the dorsal crinoid cup are defined as those ossicles which are radial in position. Basal plates have an interrarial orientation. Some inadunate crinoids possess two radial plates in some or all rays of the cup. Such a compound radial is composed of an inferradial (supported by the basal plates) and a superradial (supported by the associated inferradial). *Ristnacrinus* belongs to the family Eustenocrinidae, whose members possess five compound radials. Re-examination of a second British Ordovician crinoid which was thought to belong to this family, *Ramseyocrinus cambriensis* (Hicks) (Bates 1968), reveals that, despite similarities, it is certainly not a eustenocrinid. This species is therefore included here in a new crinoid family, the Ramseyocrinidae.

Terminology used in this paper follows Moore *et al.* (1968), Ubaghs (1978), and Webster (1974).

SYSTEMATIC PALAEOLOGY

Class CRINOIDEA J. S. Miller, 1821

Subclass INADUNATA Wachsmuth and Springer, 1881

Order DISPARIDA Moore and Laudon, 1943

Family RAMSEYOCCRINIDAE NOV.

Diagnosis. Monocyclic crinoids with a low, cylindrical cup, as wide as the proximal column. Four radials, with an anal X supported by two radials. Basals concealed or absent. Four arms, isotomously branched. Anal X bears at least three further plates in the anal series. Proximal stem quadripartite; distal stem holomeric, tetragonal.

Discussion. Bates (1968) assigned *R. cambriensis* to the Eustenocrinidae but it differs from other members of this family by having only four non-compound radials, an anal X which is supported by two radials (rather than two or three superradials, or a brachianal and superradial) and a column which is tetrameric proximally while retaining tetragonal symmetry throughout. Differences of the cup plate arrangements are illustrated by text-fig. 1.

In *Eustenocrinus* five basals are apparent and are offset from the radials, all of which are compound (text-fig. 1A). The anal series is supported by the superradials of the B-, C-, and D-rays. The first circlet of primibrachs are fixed to the cup. Only four arms are present. *Ristnacrinus* has basals which are either hidden or absent (text-fig. 1B). The five radials are all compound, each superradial supporting an arm. Ossicles of the anal series are small and are supported by the C- and D-ray superradials, to the left of the C-ray brachial. *Peniculocrinus* (text-fig. 1E) is similar to *Eustenocrinus* but the anal series is supported by a large brachianal in the C-ray (i.e. five arms are present) and the D-ray superradial. The first two circlets of brachials are fixed.

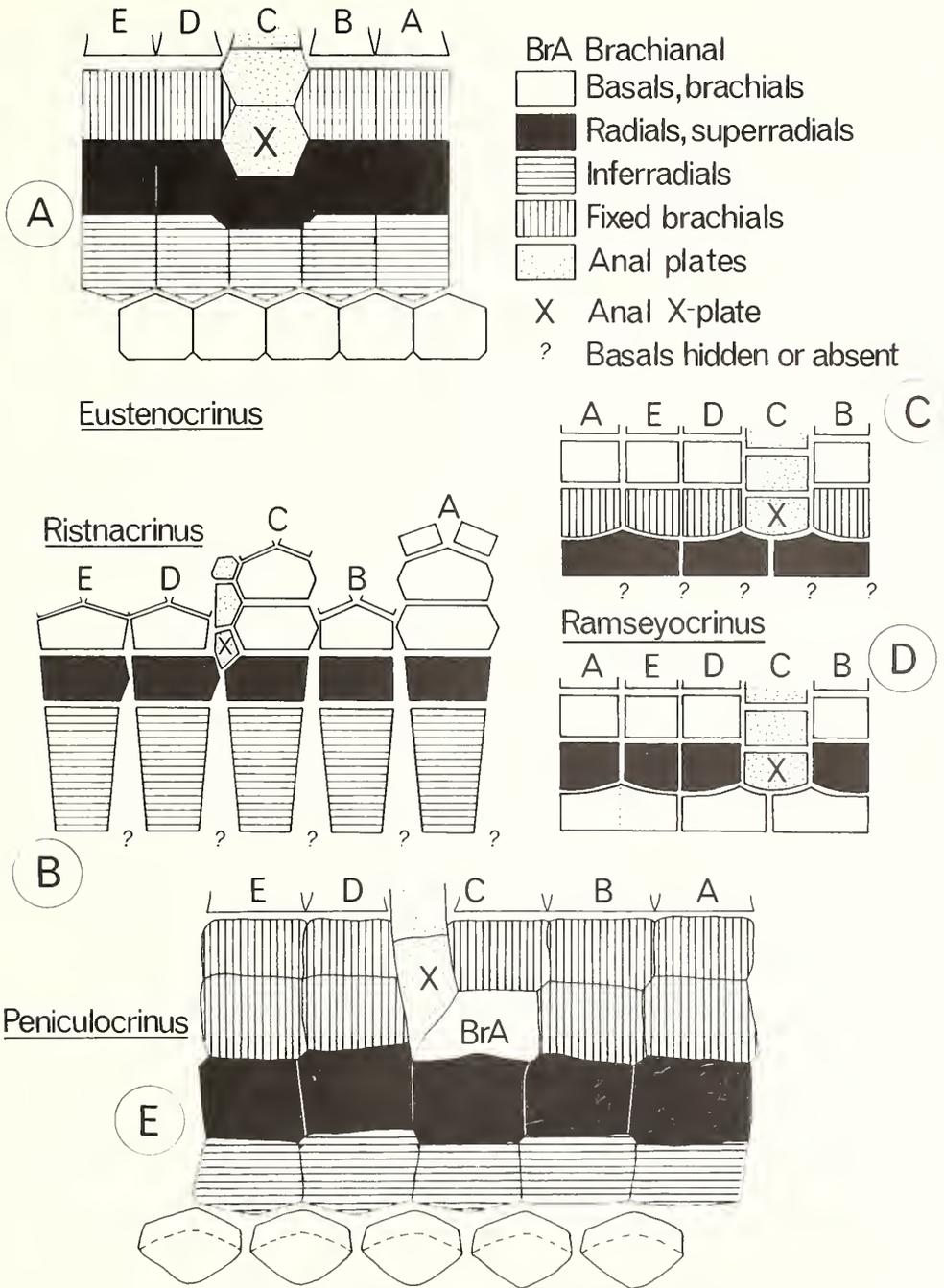
In order to contrast these eustenocrinid genera with *Ramseyocrinus* it is first necessary to define the plates of the cup in the latter. Two alternative interpretations are shown (text-fig. 1C, D). Text-fig. 1D is based mainly upon the interpretation of Bates (1968, p. 407), although his inferradial is labelled as an anal X. In this plating scheme basals are three in number, the large basal in the A- and E-rays apparently being fused from two smaller plates. Radials are not offset from basals but are directly supported by them. This is unsatisfactory because the 'basals' are radial in orientation. The four arms are directly supported by the radials. The anal X is supported by the two smaller basals.

The interpretation preferred in this paper is shown in text-fig. 1C. Basals are either hidden or absent. The cup is composed of four radials, surmounted by a circlet of four fixed brachials (the ramseyocrinid *Entrochus primus* does not have this circlet of fixed brachials; R. J. Prokop, pers. comm.). The radials in the A- and E-rays are fused. The four arms arise directly from the radials. The anal X is supported by the two smaller radials. This interpretation (text-fig. 1C) is preferred because of the obvious similarities of the cup plating to that of crinoids such as *Eustenocrinus* (although *Ramseyocrinus* does not have split radials, merely radials surmounted by fixed brachials). Radials may be defined as the most proximal plates in each ray (Moore *et al.* 1952, p. 608). It is apparent that the most proximal plates in each ray of *Ramseyocrinus* are those called basals by Bates (1968) (text-fig. 1D). It is therefore correct to regard his 'basals' as radials. Moore *et al.* (1978, p. T554) propose that both basals and split radials are present, i.e. the most proximal circlet of free brachials in text-fig. 1C are incorporated in the cup as superradials, the fixed brachials (this paper) are inferradials and the lowest plate circlet are basals. The first two plates of the anal series are regarded as a compound radial. Similar arguments to those stated above can be applied to show that the lowest plate circlet in the cup is not composed of basals. The lowest free brachial circlet (text-fig. 1C) does not appear to be fixed.

If present, and it is emphasized that this cannot be proved, the basals must be extremely small and are probably concealed by the lobes of the stem. Many articulate crinoids have a hidden circlet of infrabasal plates (cryptocyclic) (Rasmussen 1978). However, these infrabasals are concealed by relatively broad, circular, or pentagonal columnals. The lobes of the proxistele in *R. cambriensis* are narrow and separated.

The anal tube can be recognized in two specimens of *R. cambriensis* (NMW 29.308.G296 and Manchester Museum L12360). It is also seen in *Entrochus primus* (R. J. Prokop, pers. comm.). In both species the tube is formed of a column of about four plates.

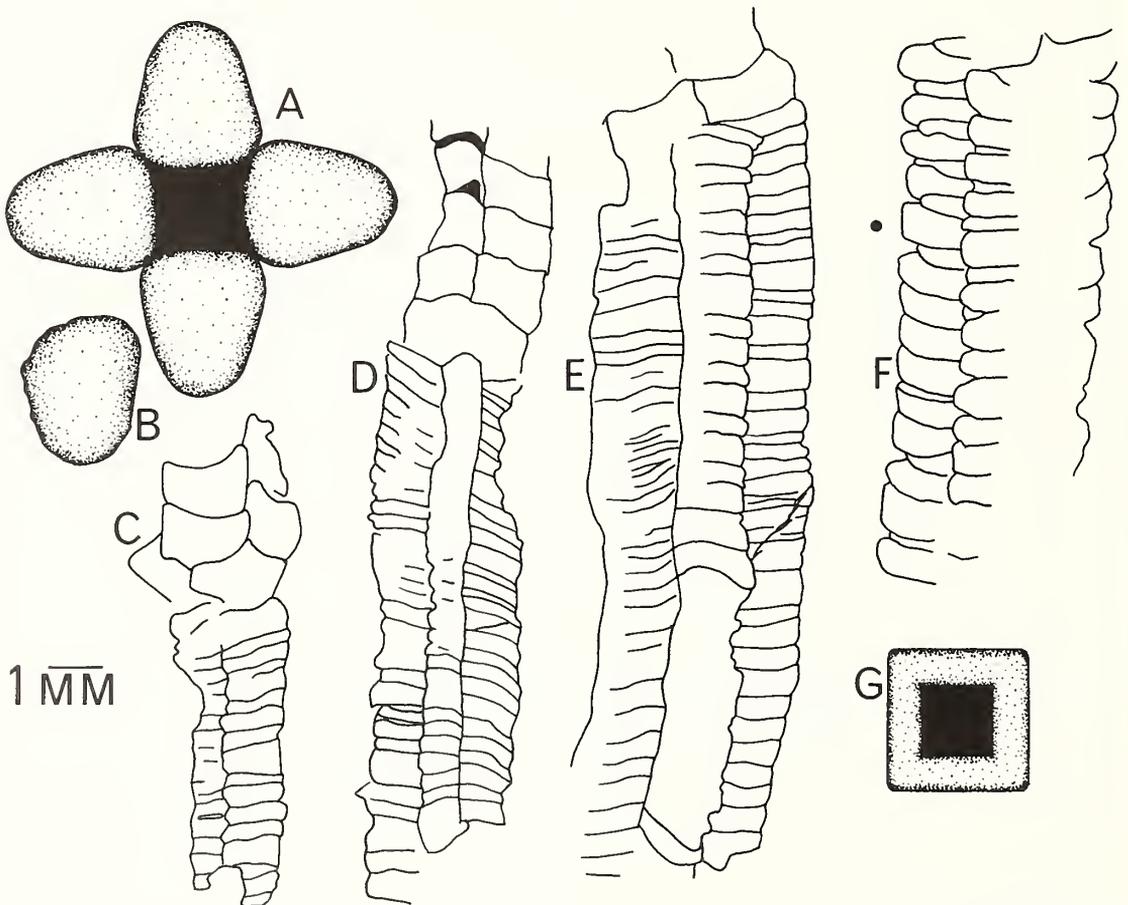
If this new interpretation is now compared with *Eustenocrinus*, *Ristnacrinus*, and *Peniculocrinus*, a number of differences are apparent. Each of the eustenocrinid genera has five compound radials, whereas *Ramseyocrinus* has only four radials, none of which is compound. The cups of eustenocrinids are tall, sometimes incorporating brachials. The cup of *Ramseyocrinus* is about as wide as high, including a circlet of fixed brachials. The anal series of *Ramseyocrinus* is supported by two radials, whereas that in eustenocrinids is supported by three superradials (*Eustenocrinus*), two superradials (*Ristnacrinus*), or a superradial and a fixed brachianal (*Peniculocrinus*). This last point is particularly



TEXT-FIG. 1. Cup plating diagrams for: A, *Eustenocrinus* (after Ulrich 1925; Moore 1962); B, *Ristnacrinus* (after Öpik 1934); C, D, *Ramseyocrinus*. Two interpretations of the cup are shown, both based on NMW 29.308.G296 and G318 (counterparts). In C the basals are hidden or absent, radials and a circlet of fixed brachials are present, and the anal X is supported by two radials (this paper). In D basals and radials are present, two basals supporting the anal X (based on the description of Bates 1968). E, *Peniculocrinus* (after Moore 1962).

important, although it is apparent that minimal reduction of the superradials in the C- and D-rays of *Ristnacrinus* could lead to the anal X being supported by two inferradials.

The stem of *Ramseyocrinus* is also radically different from that of eustenocrinids. The unusual column of *Ristnacrinus* is discussed in detail below but it is sufficient to note here that most columnals are holomeric (i.e. composed of a single ossicle) and circular, with a central synarthrial ridge. *Peniculocrinus* has a subpentagonal column (Moore *et al.* 1978, p. T554), with what appear to be lenticular columnals (cp. Moore *et al.* 1978, text-fig. 347.2e, p. T555, with Taylor 1983, text-fig. 41, p. 61). The stem of *Eustenocrinus* is circular and apparently pentameric (Ulrich 1925, p. 99). The column of *Ramseyocrinus* differs from all these by showing fourfold symmetry (text-figs. 2, 3). The proxistele of *R. cambriensis* is tetralobate and quadripartite. Distally the column is square but holomeric.



TEXT-FIG. 2. *Ramseyocrinus cambriensis* (Hicks). Columns and columnals. A, reconstruction of the articular facet of a proximal columnal (Donovan 1983, text-fig. 2c). B, NMW 29.308.G220, dissociated mere. C, D, NMW 29.308.G296 and G318 (counterparts), proxistele beneath cup. E, F, BM(NH) E3, proxistele immediately beneath cup (E) and slightly more distal (F, in which the columnal marked by a dot is 36 mm below the base of the cup). G, tentative reconstruction of the articular facet of a distal columnal. Lumen shape, size, and orientation conjectural. All camera lucida drawings of latex casts, except A and G.

Genus RAMSEYOOCRINUS Bates, 1968

Type species. Dendrocrinus cambriensis Hicks, 1873, designated by Bates (1968).

Diagnosis. As for the family Ramseyocrinidae, with the first circling of brachials fixed.

Discussion. The first primibrach circling of the only other Ramseyocrinid known, *Entrochus primus*, is free above the radials (R. J. Prokop, pers. comm.).

Ramseyocrinus cambriensis (Hicks), 1873

Text-figs. 1C, D, 2, 3

1873 *Dendrocrinus cambriensis* Hicks, p. 51, pl. 4, figs. 17–20.

1960 *Iocrinus? cambriensis* (Hicks) Ramsbottom, pp. 5, 6, pl. 3, figs. 9–11.

1968 *Ramseyocrinus cambriensis* (Hicks) Bates, pp. 406–409, pl. 76, figs. 1–5.

Diagnosis. Radials fused in the A- and E-rays; arms branched isotomously at least four times.

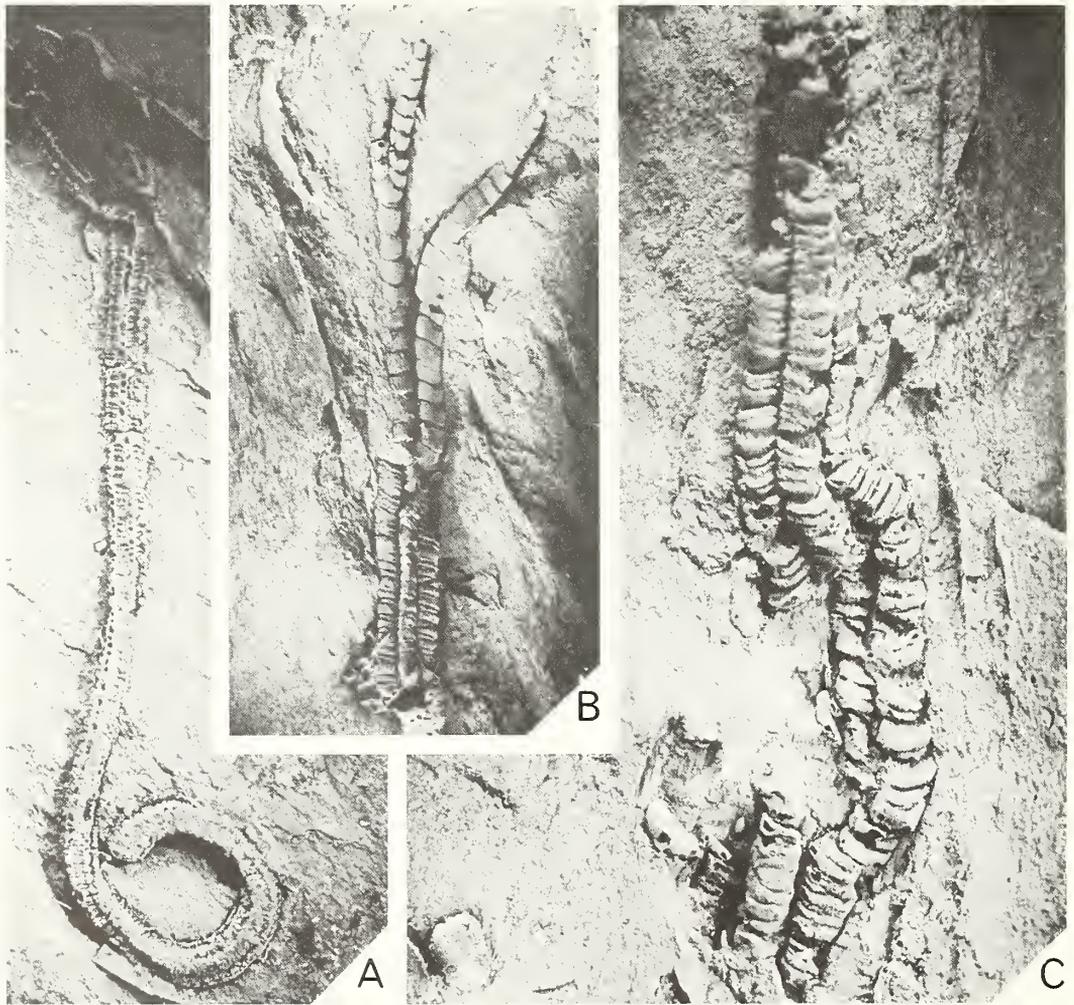
Material. Ramsbottom (1961, p. 5) recognized Sedgwick Museum (SM) A16739 as a syntype (Hicks's fig. 17; also a gutta-percha impression in the Geological Survey Museum collection, IGS GSM 82819) and noted IGS GSM 59428 as a gutta-percha impression of the specimen in Hicks's fig. 20. His description is based mainly on British Museum (Natural History) specimen BM(NH) E3. Bates (1968, p. 407) discovered the counterpart mould of one of Hicks's syntypes (now numbered SM A16739a, b) but based his description on National Museum of Wales (NMW) 29.308.G296 and G318 (counterpart moulds). This description is based on these specimens and also NMW 29.308.G220 and G470(a) (not counterparts), and University College of Wales, Aberystwyth, specimen UCW 21467.

Horizon and Localities. Porth Gain Beds, Ogof Hên Formation (Lower Arenig), Ramsey Island, Dyfed, NGR SM 708 252 (Pringle 1930). Specimens are also known from a quarry on Lleithyr Farm, Dyfed, near to the ruins and by the side of the road to Carnedd, NGR SM 748 248 (Jenkins 1979).

Description. Stem (text-figs. 2, 3A, C) wide proximally, tetrameric, quadrilobate, lobes almost parallel-sided beneath cup, becoming less pronounced distally. Columnals tend to be irregular in height, particularly near the top of the stem (text-fig. 2C–E); diameter of columnals also varies slightly but no more than three orders of columnals are ever present, i.e. two orders of internodal. Articulation synostiosial. Lumen tetragonal with inwardly curved sides, angles corresponding to meric sutures (text-fig. 2A). Meres lozenge-like (text-fig. 2B). Distal stem square in section and holomeric; heteromorphic N212 (Webster 1974) but the sequence of internodals is sometimes incomplete. Articulation apparently synostiosial (text-fig. 2G). The stem terminates in a planar, coiled holdfast (text-fig. 3A). Basals hidden or absent (text-figs. 1C, D, 3B). Four radials, those in the A- and E-rays fused to form a single large plate (the line of fusion apparent as a groove on NMW 29.308.G318, whereas boundaries between separate plates are clearly evident). Four fixed brachials, two supported by the large radial and one by each of the small radials. Anal X lower than the radials and supported by the two small radials. Anal series of at least four plates of similar morphology. Tegmen not seen. Four arms (text-fig. 3B) supported directly by the four radials. Arms branch isotomously at least four times. At least ten primibrachs, elliptical in section, wider than high, with a narrow, shallow, ventral food groove. Maximum of thirteen secundibrachs, although there may be as few as four (Bates 1968, p. 407); the most proximal three are low, becoming about as wide as high more distally. Tertibrachs higher than wide, ten at most, quadribrachs tall, thin, about twelve, pentibrachs narrow, tall, at least ?five.

Discussion. Only four crinoid genera are known which have a tetrameric column: *Ramseyocrinus*, *Colpodecrinus* (Sprinkle and Kolata 1982; Donovan 1983), *Tetragonocrinus* (Yeltysheva 1964), and *Entrochus* Barrande (previously only known from dissociated columnals but to be fully described from more complete material by Dr. R. J. Prokop). *R. cambriensis* is also the oldest crinoid so far discovered in Britain. The proximal stem is well known from several well-preserved specimens (text-figs. 2A–F, 3B, C). These are all tetralobate and tetrameric, with a random intercalation of internodals often apparent (text-fig. 2C–F).

The columnal morphology has been deduced from NMW 29.308.G220 (text-figs. 2B, 3C). Details of the articular facet are not shown by specimens of 'whole' animals (none is preserved complete with the distal stem) but this specimen is partly disarticulated, enabling the morphology of individual meres to be determined. From this a reconstruction of the facet has been made (text-fig. 2A). The latera of the meres are sub-parallel and it is deduced that the stem fragment is from some distance beneath the cup. The minimal contact between meres of the same columnal did not favour preservation of whole columnals but instead the stem first disarticulated along its meric sutures, producing an effect analogous to peeling the skin from a banana. The separate stem lobes then disarticulated into individual meres.



TEXT-FIG. 3. *Ramseyocrinus cambriensis* (Hicks). A, NMW 29.308.G470(a), dististele with planar, coiled holdfast, $\times 4$. B, NMW 29.308.G318, cup with proximal column and arms, $\times 3.1$. C, NMW 29.308.G220, partially disarticulated stem with a dissociated mere in the bottom left corner, $\times 3.5$. All latex casts whitened with ammonium chloride.

The description of the distal stem is based on NMW 29.308.G470(a) (text-fig. 3A) from Ramsey Island. It cannot be proved that this is *R. cambriensis* but the assumption is based on the absence of evidence for other pelmatozoans at the type locality of the Ogif Hên Formation and the tetragonal symmetry of the specimen. If the assumption is correct, there must have been a change from tetramerism to holomerism distally. The planar coil of the pluricolumnal is suggestive of an attachment structure and is unlike the primitive holdfasts of certain other early crinoids such as *Echmatocrinus* (Sprinkle 1973) and *Aethocrinus* (Ubaghs 1969). A suggested reconstruction of the articular facet of a columnal of the dististele is shown in text-fig. 2G.

Bates (1968, p. 408) considers *R. cambriensis* to be the most primitive eustenocrinid, possibly closely related to the ancestral stock of the disparids. This may be so but it is unlikely that *Ramseyocrinus* is a direct ancestor of later monocyclic inadunates. It has many unique features not found in later disparids (apart from *Entrochus*), particularly the tetragonal symmetry of the stem and the presence of four arms and radials. Crinoid columnals with fourfold symmetry are not common in the British Ordovician until the Ashgill, when they are more likely to be derived from camerates such as *Xenocrinus* or *Colpodecrinus*.

A final reason for doubting the close relationship of *Ramseyocrinus* to eustenocrinids is stratigraphic. *R. cambriensis* is limited to the Lower Arenig of South Wales, whereas the earliest *Ristnacrinus* columnals are Upper Llandeilo (see below) and both *Eustenocrinus* and *Peniculoocrinus* are of Trenton age (mid Caradoc).

Family EUSTENOCRINIDAE Ulrich, 1925

Diagnosis. Monocyclic crinoids with compound radials in all five rays. Basals may or may not be seen. Anal X supported by the B-, C-, and D-ray superradials (*Eustenocrinus*), by the D- and C-ray superradials (*Ristnacrinus*), or by the D-ray superradial and a brachianal in the C-ray (*Peniculoocrinus*). Cup conical. Arms isotomously branched. Column round to sub-pentagonal in section.

Genus RISTNACRINUS Öpik, 1934

Type species. *Ristnacrinus marinus* Öpik, 1934, by original designation.

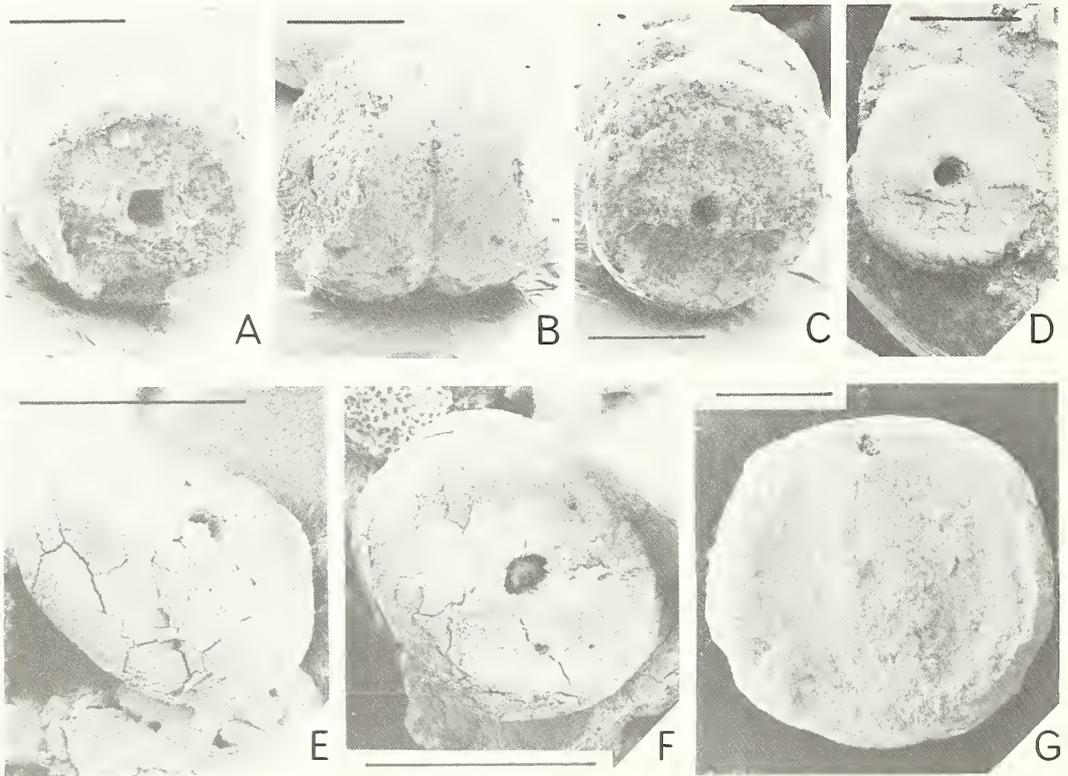
Diagnosis of stem. Stem circular in section; latera convex; proxistele heteromorphic, N1, with symplexially articulated columnals. Articular facet of a distal columnal has a central, synarthrial ridge flanked by two depressed ligament areas which are surrounded by a marginal rim; latera convex.

Discussion. *Ristnacrinus*, *Caleidocrinus multiramus*, and an undescribed columnal species from the Boda Limestone of Osmundsberget, Sweden, are the only Ordovician crinoids known to have columnals with synarthrial articulation. The latter is elliptical and low (possibly myelodactylid) and the columnals of *C. multiramus* have less convex latera and are proportionally taller than those of *Ristnacrinus*.

The type species of *Ristnacrinus*, *R. marinus*, is founded on a particularly complete specimen, three cups and fragmentary columnals and pluricolumnals from the Caradocian D₁ (Jõhvi) Stage of Estonia (Öpik 1934), which is approximately equivalent to the late Harnagian to early Soudleyan of Britain (Williams *et al.* 1972). The near-complete specimen lacks a distal termination to the column but retains about 35 cm of the stem. This is divided into a short proxistele and a much longer dististele. The proxistele of fifteen columnals is heteromorphic, N1 (Webster 1974), with alternating nodals and internodals with convex and concave latera, respectively. These have a radial symplexial articulation (Öpik 1934, p. 4). The dististele is highly flexible, homeomorphic, and composed of columnals with a synarthrial articulating ridge on each articular facet. Dissociated columnals of this type are easily recognized as belonging to *Ristnacrinus*. Öpik (1934, p. 1) notes that similar columnals are also found below (Kukruse Limestone and Oil Shale, Stages C₂ and C₃, Upper Llandeilo to early Harnagian) and above (Keila Limestone, D₂ Stage, late Soudleyan) the Jõhvi Stage.

D. K. Wright (1983) has noted columnals from the Longvillian and Woolstonian of Snowdonia, North Wales, which are almost certainly *Ristnacrinus* (his *Cyclocyclopa* D). The species *R. cirrifer* Le Menn is based upon dissociated, cirriferous columnals from the Upper Ordovician (Ashgill) of Coat-Carrec, Argol, south-east of Brest, Brittany, France (Chauvel and Le Menn 1972). *Ristnacrinus* cf. *cirrifer* is also known from the Ashgill of Aragon, Spain (Chauvel *et al.* 1975; Chauvel and Le Menn 1979). Briskeby (1981) described columnals of *R. ?marinus* from the Upper Ordovician of Hadeland, north of Oslo, Norway. Finally, columnals of *Ristnacrinus* sp. have been found below the Swedish Kullberg Limestone (Upper Llandeilo) at Kullberg, Dalarna, and in the Ashgill Boda Limestone (C. R. C. Paul, pers. comm.).

Synarthrial articulation has evolved three, or perhaps four, times in crinoid columnals, in inadunates (ristnacrinids, including *C. multiramus*, and myelodactylids), camerates (platycrinids), and articulates (bourgueticrinids). The British Ashgill *Ristnacrinus* columnals are similar to those illustrated by Öpik (1934, pl. 1 (labelled pl. 2), fig. 2). One of Öpik's columnals appears to bear some sort of process, possibly a cirrus. If so, this would seem to invalidate *R. cirrifer* Le Menn. Indeed, columnals of this genus show such limited morphological variation, despite their distinctive appearance, that it is here considered expedient to regard them all as *Ristnacrinus* sp.



TEXT-FIG. 4. Scanning electron micrographs of *Ristnacrinus* sp. from the Ashgill of Britain. A-C, BM(NH) E69201. A, C, articular facets at each end of the pluricolossal; B, lateral view. D, BM(NH) E69202, articular facet. E, F, BM(NH) E69207. E, lateral view; F, articular facet. G, BM(NH) E69199, articular facet. Scale bars represent 1 mm.

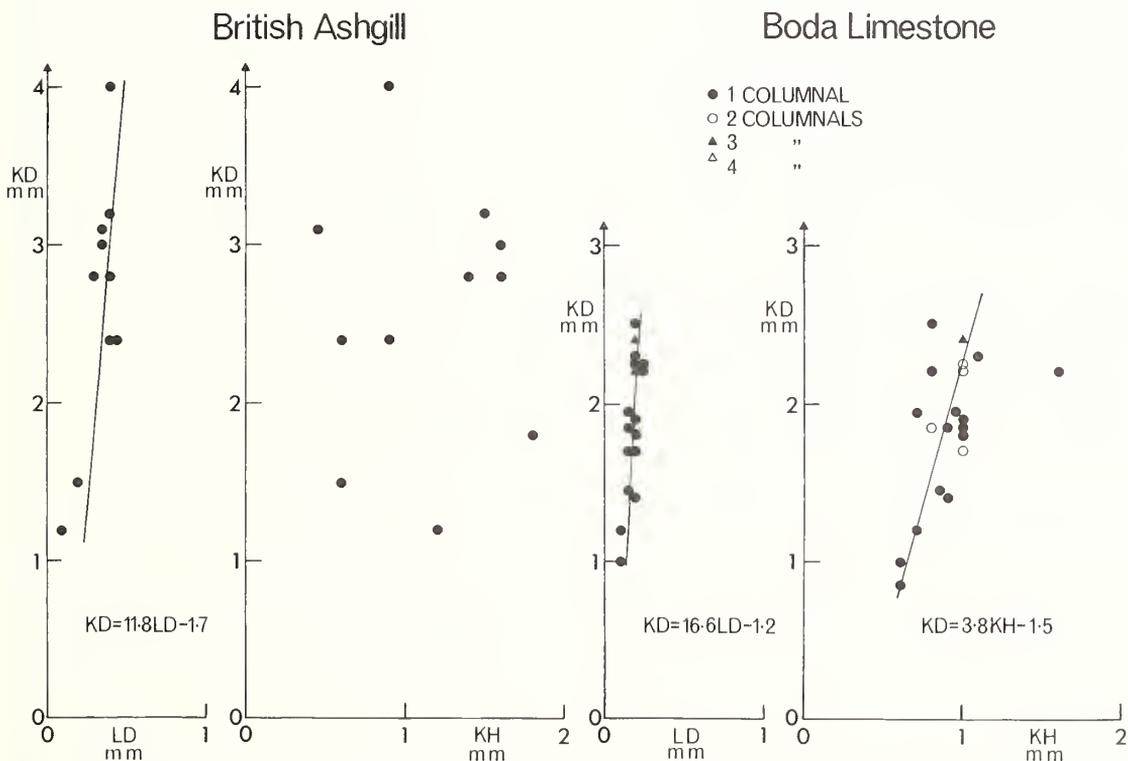
Ristnacrinus sp.

Text-figs. 4, 5

Material. Eleven British Museum (Natural History) specimens: BM(NH) E69197 to E69207.

Horizons and Localities. These columnals come from four localities.

- (a) BM(NH) E69205. At the top of the quarry in the wood, behind the school, Corwen, Clwyd. NGR SJ 071 433. Rawtheyan siltstones. Collected by Mr. B. Cullen.
- (b) BM(NH) E69206. Loose at the +39.70 to +41.00 m level, west side of Sholeshook railway cutting (Paul 1973, fig. 5, loc. 1/2W), near Haverfordwest, Dyfed. NGR SM 968 171. Sholeshook Limestone. Cautleyan (Price 1973, 1980).
- (c) BM(NH) E69207. Old factory wall at Ffrydan, near Bala, Gwynedd. NGR SH 922 367. Rhiwlas Limestone. Rawtheyan Zone 5.
- (d) BM(NH) E69197 to E69204. Keisley Limestone (Upper Ashgill), Keisley, near Appleby, Westmorland. E69202 came from Keisley Bank, above the west quarry, NGR NY 7140 2390 (these are the lowest exposed beds of the Keisley Limestone). E69204 is from the interbedded mudstones and nodular limestones in the north face of Keisley west quarry, NGR NY 7130 2385 (lowest horizons in the quarry). E69198 was *in situ* in the younger limestone horizons of the east face of this quarry. E69197 and E69199 to E69201 come from the east face of the west quarry, where they were washed out from a muddy horizon about 10 m from the top of the section. Finally, E69203 was part of the infill of a trench in the path to the quarry, NGR NY 7135 2380 (A. D. Wright 1982).



TEXT-FIG. 5. KD/LD and KD/KH plots for *Ristnacrinus* sp. from the British Ashgill (left) and the Boda Limestone (right), where KD = columnal diameter, LD = lumen diameter, and KH = columnal height. Lines of best fit determined by Bartlett's method (Fryer 1966).

Description. Columnal circular to slightly elliptical in outline (cp. text-fig. 4D and 4G with 4F). Lumen circular, central. Axial canal planar-sided. Articular facet traversed by a central, synarthrial articulating ridge which sometimes has a shallow longitudinal groove. In elliptical specimens the articulating ridge lies close to, but not on, the shortest radius (text-fig. 4F). Synarthrial ridge flanked by two large, depressed, semicircular ligament areas. Circumference of the articular facet bordered by a raised rim. Columnals low or barrel-shaped with a convex latus (text-fig. 4B, F). None of the British Ashgill specimens shows an appreciable divergence of the articulating ridges. Columns homeomorphic, although some columnals are apparently wedge-shaped (text-fig. 4B) possibly due to adjacent columnals not resting parallel to each other on their fulcral ridges.

Discussion. Crinoid columnals may be examined by bivariate analysis of suitable parameters (Jeffords and Miller 1968; Roux 1977, 1978; Le Menn 1981). *Ristnacrinus* sp., from the British Ashgill and the Swedish Boda Limestone (Ashgill), have been examined using KD/LD and KD/KH plots (text-fig. 5), where KD = columnals diameter, LD = lumen diameter, and KH = columnal height. The Swedish specimens came from a single horizon and give a very close correlation to lines of 'best fit'. It is probable that only a single species of *Ristnacrinus* is present at this horizon. These columnals seem to differ from the British specimens by showing fulcral ridge divergences of up to about 90°. The British columnals, however, despite having a good KD/LD relationship, generate an apparently random distribution of points on the KD/KH graph. This may be because the columnal height of a single species is highly variable, or it is possibly due to more than one species being represented. As specimens come from four localities, which span the interval Cautleyan to Rawtheyan (Hirnantian?), the latter is most probable. However, it is unlikely that these species could be readily separated without analysing large collections from each of the four localities. These are not readily available, the entire known *Ristnacrinus* fauna from the British Ashgill having been used to produce text-fig. 5.

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RECONSTRUCTION OF THE JAWS AND BRAINCASE IN THE DEVONIAN PLACODERM FISH *BOTHRIOLEPIS*

by G. C. YOUNG

ABSTRACT. New material of the antiarch *Bothriolepis*, from the Gogo Formation (early Upper Devonian, Canning Basin, Western Australia), provides morphological details of the visceral jaw elements, which were not previously known in antiarchs. The palatoquadrate lacks a high orbital process, and was attached to the ventral part only of the suborbital (mental) plate. This shows that the ethmoidal region of the braincase must have been considerably deeper than previously thought. Detailed descriptions are given of the dermal elements in the jaws (suborbital and infragnathal) and cheek (submarginal, prelateral, infraprelateral). On the evidence of the palatoquadrate the mental plate of antiarchs is homologized with the suborbital in other placoderms. The absence of supragnathals may be secondary, and the differentiation of the infragnathal into biting and non-biting divisions probably evolved independently in antiarchs and euarthrodires. Reassembly shows that the submarginal and infraprelateral plates in *Bothriolepis* fitted closely against the anterior ventrolateral to close the operculum. A new restoration of the endocranium is presented, based on the identification of a posterior postorbital process and cucullaris fossa in *Asterolepis*. It is suggested that in *Bothriolepis* the palatoquadrate had an amphistylic connection to subocular and subnasal shelves, that the lateral pit was bounded posteriorly by the anterior postorbital process to form a mandibular muscle fossa, and that the preorbital recess housed the rhinocapsular bone. Comparison with *Yunnanolepis* indicates that the preorbital depression in this form contained a discrete rostral capsule with lateral nasal openings, and that the 'orbital fenestra' in those antiarchs with a preorbital depression is equivalent to the suborbital fenestra of *Bothriolepis*. Certain characters defining the relationships of antiarchs to other placoderm groups are summarized in cladogram form; prelaterals, infraprelaterals, a long obstatic margin, and prominent posterolateral corners on the skull are proposed as synapomorphies of antiarchs and euarthrodires. Fusion of the quadrate to the postsuborbital is a possible additional synapomorphy of actinolepids and phlyctaenioids.

THE remarkable preservation of fishes from the Frasnian (early Upper Devonian) Gogo Formation in the Canning Basin of north-western Australia is now well known through the publications of Miles (1971, 1977), Gardiner and Bartram (1977), Miles and Young (1977), Miles and Dennis (1979), and Dennis and Miles (1979*a, b*; 1980–1983). A preliminary faunal list and brief comments on the occurrence of this diverse fish fauna was presented by Gardiner and Miles (1975). The new information on the structure of the placoderm *Bothriolepis* presented here is based on material from a large collection of Gogo fish specimens made in 1972 by the Bureau of Mineral Resources and the Geological Survey of Western Australia. *Bothriolepis* is a well-known member of the highly specialized placoderm order Antiarcha, which had a cosmopolitan distribution during the Late Devonian, typically in non-marine sediments. Over fifty named species have been referred to the genus (e.g. Denison 1978). However, the occurrence of *Bothriolepis* in strictly marine calcareous sediments, as is the case with the Gogo fish fauna, is very uncommon. The mode of preservation in the Gogo material (whole fish in calcareous nodules) has permitted preparation using acetic acid techniques as developed by Toombs (1948) and Toombs and Rixon (1959), to reveal in intricate detail the skeletal morphology of this form. This new information largely confirms, but also supplements and enlarges upon, the comprehensive previous accounts of the morphology of *Bothriolepis* (see Stensiö 1931, 1948).

Many prepared specimens of *Bothriolepis* from the Gogo Formation are held in the British Museum (Natural History) and will be described in a forthcoming account as a new species by Dr.

R. S. Miles. The new information on jaw and braincase structure described here is based on a single specimen in which delicate and extremely fragile surface (perichondral) ossifications of various cartilaginous elements were recognized during preparation. These structures have not previously been identified in *Bothriolepis*, in which the braincase and gill arches were predominantly cartilaginous. The material described below is housed in the Commonwealth Palaeontological Collection (prefix CPC) in the Bureau of Mineral Resources, Geology and Geophysics, Canberra. The terms 'interperichondral space', 'closed margin', and 'open margin' are used in the description of perichondrally ossified elements as defined by Miles and Young (1977, p. 145). The following terms for dermal bones of the cheek region are substituted for those previously applied to antiarchs: submarginal for extralateral, and suborbital for mental plate. Evidence for establishing these homologies is presented below.

MATERIAL

The specimen (CPC 25205) on which this study is based includes the three major cheek bones (submarginals, infraprelaterals, and the left prelateral), upper and lower dermal jaw elements from both sides, a possible extramandibular plate, both palatoquadrates, and the left Meckel's cartilage, the latter elements attached to their respective dermal bones. The nuchal plate is missing from the skull-roof, but the complete anterior region of the skull together with the well-preserved and articulated ventral trunk armour has enabled the space containing the orobranchial cavity to be delineated by direct reassembly of the specimen.

DESCRIPTION

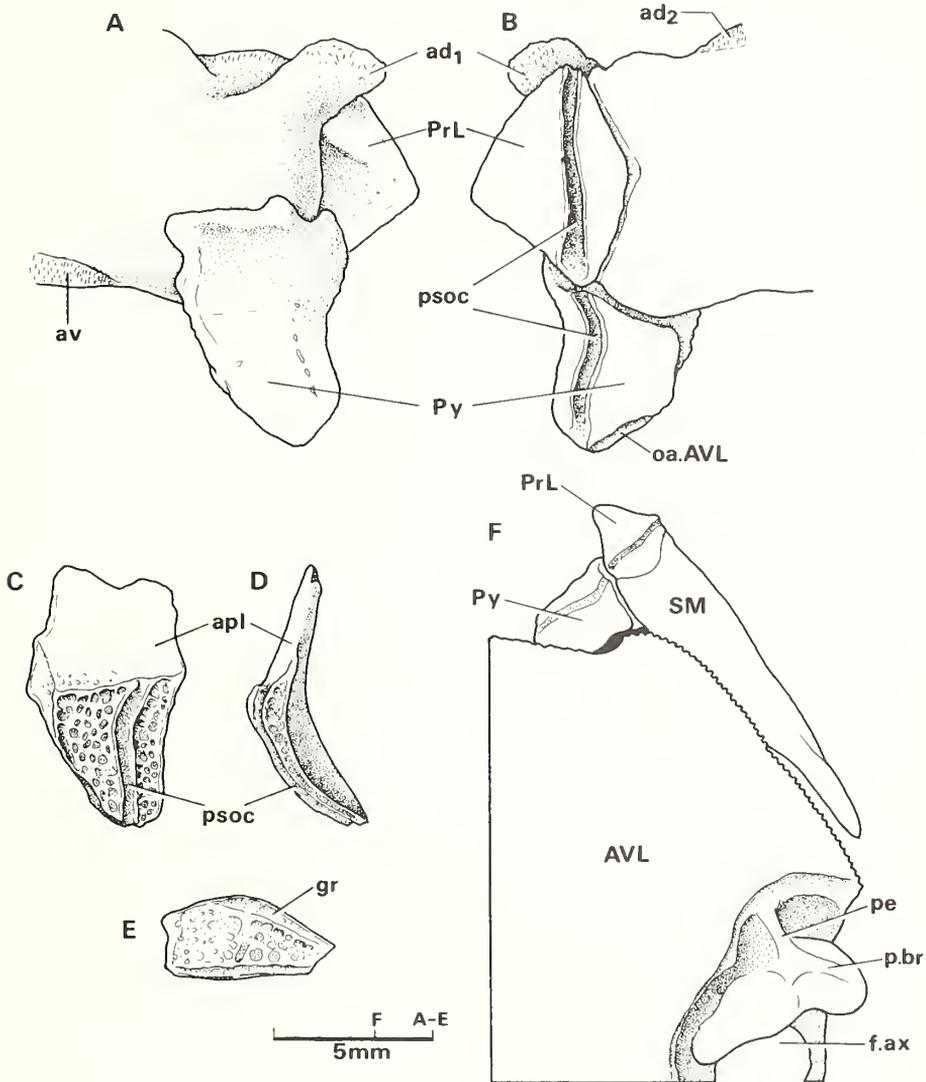
1. *Dermal elements of the jaws and cheek.* Because of their excellent preservation these bones provide several new morphological details not previously covered in Stensiö's comprehensive descriptions (1931, 1948).

The suborbital (mental) plate, which is the upper dermal jaw element, is shown in external view in Pl. 58, fig. 1. In shape it corresponds well with this bone in *B. canadensis*, but the lateral notch is more pronounced, with a longer posterior process (p.pr, text-fig. 2), and the posterodorsal corner is less marked, as in *B. cellulosa* or *Grossilepis* (Stensiö 1948, fig. 35). The external surface is ornamented in its dorsal part, with a broad strip of smooth bone along the denticulated ventral margin. Stensiö regarded these as distinct 'tooth' and 'sensory canal' components of a compound bone, but this seems unlikely. The shallow groove (gr.ul, text-figs. 2, 3) separating these two regions probably housed soft tissue forming an upper lip. The infraorbital sensory groove (ifc) crosses the bone in a similar fashion to that of other antiarchs.

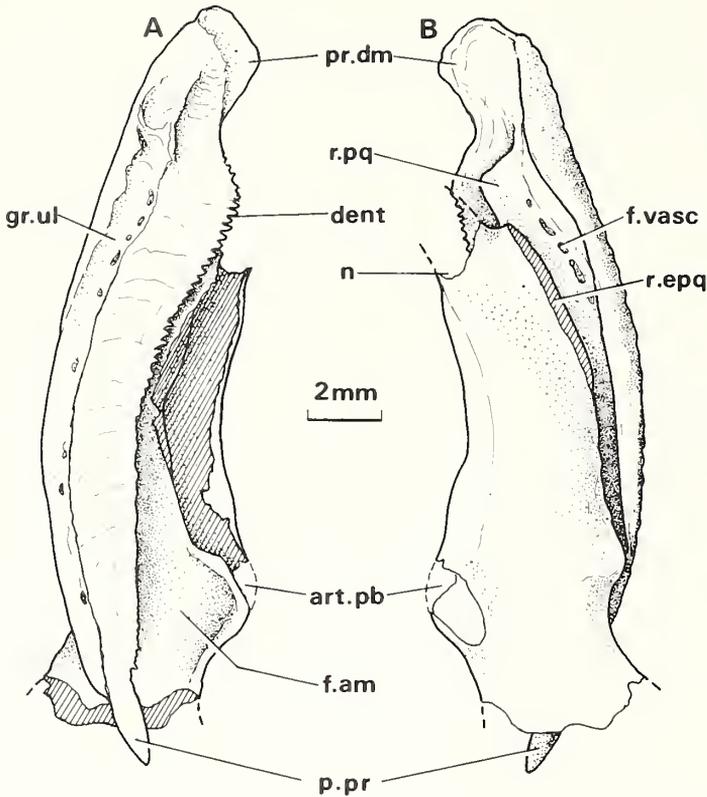
On the inner surface of the plate is a distinct ridge (r.pq), as previously noted in *B. canadensis* (Stensiö 1931, 1948). Posteriorly it forms an inconspicuous thickening, but anteriorly it is well developed to support the palatoquadrate (text-fig. 3D, E), with its concave upper surface forming a shallow groove pierced by several foramina (f.vasc, text-fig. 2B). In both specimens the anterior end of this ridge is clearly seen in front of the broken perichondral lining of the palatoquadrate (Pl. 59). The groove-like upper surface of the ridge may correspond to the 'neurovascular groove' in *Holonema* (Miles 1971, p. 135), although at least some of its contained foramina appear to open externally into the groove (gr.ul) delineating the biting portion of the bone on the outer surface. In its relationship to the palatoquadrate this ridge might be thought to correspond to the suborbital crista on the suborbital plate in brachythoracid euarthrodires (e.g. Miles and Westoll 1968, fig. 13), but the possibility that the adductor mandibulae musculature may have passed above it (see below) argues against this comparison.

A final structure of note is the rounded inner projection just beneath the anterodorsal corner of the plate (pr.dm, text-figs. 2, 3, 5). This forms a narrow flattened area on the anterior (mesial) margin, facing towards the symphyseal plane with the suborbital in position against the skull. It may have been an attachment site for an anterior ligamentous connection between the suborbital plates of each side.

The infragnathal (Pl. 58, figs. 2, 3) is, as previously noted (Stensiö 1931, 1948), made up of a posterior non-biting and an anterior biting division, as in some euarthrodires. Some new details can be added to previous descriptions of this bone. The presence of a denticulate biting margin on the anterior division (Stensiö 1931, p. 64) is confirmed. The posterior division is broader than the anterior, with fairly straight lateral and posteromesial margins, and a convex anteromesial margin.



TEXT-FIG. 1. (See list of Abbreviations used in Text-figures, p. 661.) *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. A, left prelatral and infraprelateral plates reassembled against the anterior end of the left submarginal plate, visceral view. B, the same, in lateral view. C, D, right infraprelateral in lateral and anterior views respectively. E, possible right extramandibular plate, external view. F, reassembly of the left submarginal, prelatral, and infraprelateral plates against the anterior ventrolateral plate of the trunk-shield, ventral view.



TEXT-FIG. 2. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Right sub-orbital plate with palatoquadrate attached, in ventral (A) and dorsal views (B).

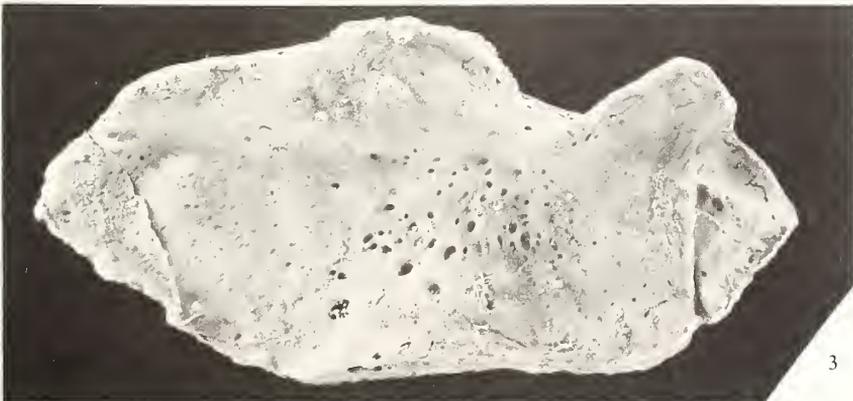
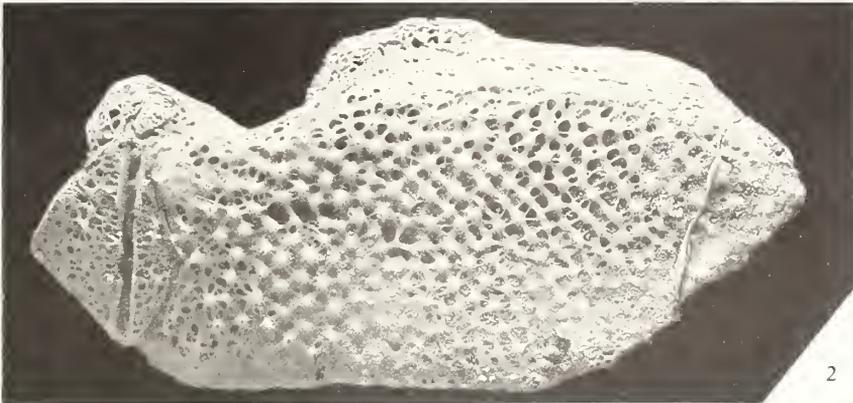
There is a prominent posterolateral corner (plc, text-fig. 5D). The dorsal surface is partly divided into mesial and lateral parts (mf,df) by a posterior continuation of the biting margin of the anterior division (dent). In these respects the bone closely resembles the infragnathal of *Grossilepis* (Stensiö 1948, fig. 36C-E). The ventral surface of the bone (Pl. 58, fig. 3) is concave over its whole length, where it was affixed to Meckel's cartilage (see below). Anteriorly this concavity forms a deep groove, giving way on the posterior non-biting division to a shallow depression flanked by low crests along the lateral and anteromesial margins. The posteromesial margin (pmm, text-fig. 5D) has a bevelled edge with a somewhat cancellous texture, and lacks a crest. Just inside this margin in both examples is a conspicuous groove (Pl. 58, fig. 3) for a nerve or vessel positioned between the cartilage and the dermal bone. This may correspond to the groove on the posterior division of the infragnathal in coccosteids (e.g. Dennis and Miles 1979a, fig. 14), where, however, it runs on the mesial surface of the bone.

EXPLANATION OF PLATE 57

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

Fig. 1. Incomplete skull-roof in visceral view, with right submarginal plate attached, $\times 2$.

Figs. 2, 3. Left submarginal and prelaterals plates in lateral and mesial views respectively, $\times 4$.



YOUNG, *Bothriolepis* from Gogo

Stensiö (1948, p. 96) suggested that the anterior and posterior divisions of the infragnathal in *Bothriolepis* lay respectively lateral and mesial to Meckel's cartilage, this being the same arrangement as in brachythoracid euarthrodires. It is clear from this new material that the infragnathal was positioned mainly dorsal to the cartilage element, but Stensiö's interpretation would still seem to be correct. On the anterior biting division the outer ventral crest delimiting the groove for the cartilage is much more pronounced (Pl. 58, fig. 3), and the reverse applies on the posterior division. In addition, the anterior and posterior divisions are twisted with respect to each other about the long axis of the bone, to accentuate this special morphological relation between dermal and cartilage elements.

Of the dermal cheek plates the prelateral is known only from the left side. In life it was closely attached to the submarginal (extralateral) plate (Pl. 57, figs. 2, 3). It is essentially a triangular bone, as in *B. cellulosa* (e.g. Stensiö 1948, fig. 31), and lacks the short dorsal margin seen in *B. canadensis*. However, it is proportionately higher and shorter in CPC 25205 than in the prelateral of *B. cellulosa*, although plate proportions are known to be somewhat variable in *B. canadensis*. Externally the bone is crossed by a sensory groove between its dorsal and ventral corners (psoc, text-fig. 1), presumably equivalent to the postsuborbital sensory canal of euarthrodires. The crest on the visceral surface beneath the sensory groove, previously known in *B. cellulosa*, is shown in this specimen to represent the anterior margin of the area in contact with the submarginal plate. The submarginal plate of the right side is shown in position against the skull-roof in Pl. 57, fig. 1. It makes two moveable attachments with the skull, the anterior connection in the form of a distinct anterodorsal process (ad₁, text-fig. 1), as in other species (e.g. Stensiö 1948, fig. 105). On both sides the ventral margin of the submarginal is thickened about half-way along its length and displays a flattened articular surface of spongy bone (av, text-figs. 1A, 9B) in a corresponding position to the ventral longitudinal crista in *B. canadensis* (Stensiö 1948, fig. 105C). Reassembly of the specimen shows that this surface abutted against a dorsally facing bevelled edge along the lateral margin of the subcephalic division of the anterior ventrolateral plate, immediately lateral to its anterolateral corner (text-fig. 1F). This would have effected a seal to the branchial chamber when the operculum was closed.

The infraprelateral plates, which are poorly known in other species, are excellently preserved in CPC 25205. As figured by Stensiö in *B. canadensis* (e.g. 1948, fig. 34), the ornamented part comprising the ventral division of this bone lies against the ventral border of both the submarginal and prelateral plates, and carries a continuation of the sensory groove from the latter plate. The unornamented lateral part of the plate (apl, text-fig. 1C, D) fitted inside the prelateral and submarginal plates in a loose attachment. The three plates from the left side are shown reassembled in text-fig. 1A, B. Also of interest is the way the infraprelateral fitted along the anterior margin of the anterior ventrolateral plate, immediately inside its anterolateral corner. Here a slight notch is developed, and a narrow overlap area on the posteromesial edge of the infraprelateral fitted loosely inside the anterior ventrolateral. Direct reassembly of the specimen suggests a small gap around the anterolateral corner of the anterior ventrolateral (text-fig. 1F), and it seems probable that the infraprelateral was carried in a flexible region of skin forming the floor of the branchial chamber. An associated thin dermal plate (text-fig. 1E) may be a right extramandibular, since it resembles this element as figured in *B. canadensis* by Stensiö (1948, fig. 110), and carries a groove along its presumed anterior margin which may have been a sensory canal or pit-line.

EXPLANATION OF PLATE 58

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

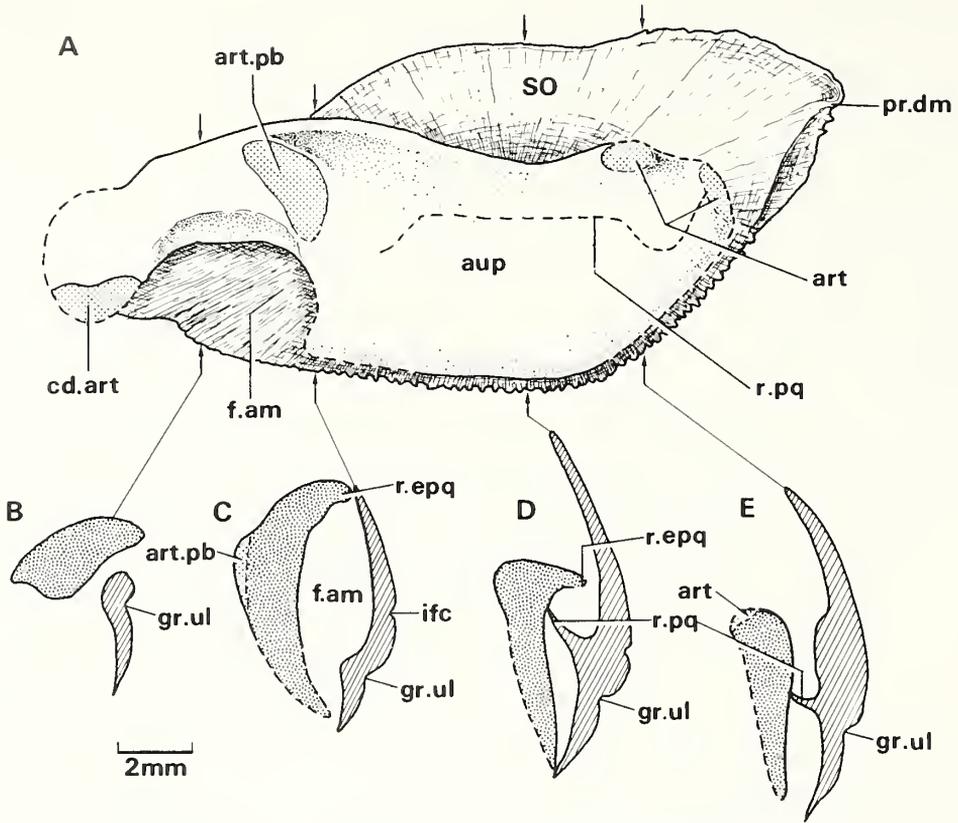
Fig. 1. External view of right suborbital plate with palatoquadrate attached, × 6.

Fig. 2. Right infragnathal in dorsal view, × 6.

Fig. 3. Left infragnathal in ventral view, × 6.



YOUNG, *Bothriolepis* from Gogo



TEXT-FIG. 3. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Restoration of the left suborbital plate and palatoquadrate. A, internal view (cf. Pl. 59, figs. 1, 2). B-E, sections at the levels indicated (dermal bone cross-hatched, cartilage stippled, articular surfaces with regular stipple).

2. *Palatoquadrate*. This element is similarly preserved on the inner side of each suborbital (mental) plate (Pl. 59, figs. 1, 2). Contrary to the reconstruction of Stensiö (1969, fig. 135), the palatoquadrate is long and low, and attaches mainly to the more ventral parts of the plate. Its closed dorsal margin lies just above the inner ridge (r.pq, text-fig. 3) in the central part of the plate. Posteriorly it curves slightly upward and over the lateral notch in the plate (Pl. 58, fig. 1). The autopalatine part of the palatoquadrate was relatively deep, its lateral (labial) perichondral surface extending and attached to the biting margin of the plate (text-fig. 3D). Exactly the same situation is seen in both plates, so any displacements between visceral and dermal elements can be discounted. The mesial (lingual) perichondral lining of this region is incomplete, but shows the autopalatine to have decreased in thickness ventrally. It is unlikely that the palatoquadrate would have projected past the biting margin of the suborbital, and it is assumed that it terminated here as a thin ventral border (text-figs. 3A, 5B). A similar situation is met with in *Holonema* and *Romundina* (Miles 1971, fig. 34; Ørvig 1975, pl. 2, fig. 5). The anteromesial extent of the palatoquadrate is not shown, but it is assumed that it formed an anterolateral connection with the braincase, as in other forms. The broken anterior edge of the outer perichondral lining curves away from the visceral surface of the suborbital at this level, and suggests an inward flexure of the palatoquadrate to form the orbital connection with the braincase. On both

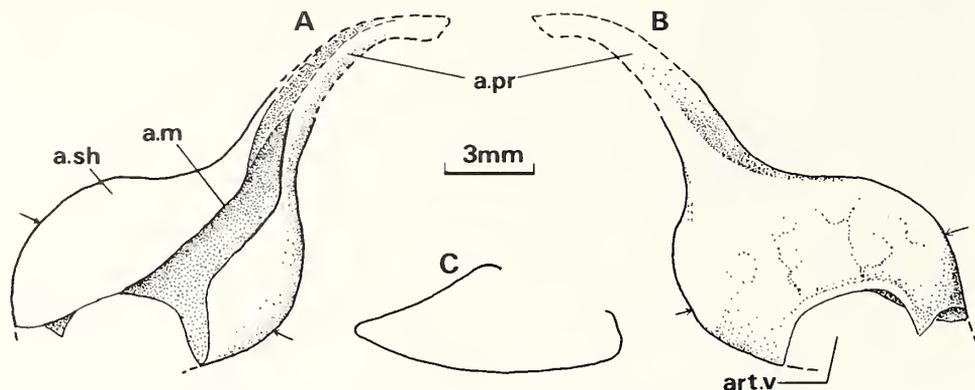
sides the anterodorsal edge of the perichondral lining is similarly preserved as a distinct notch (Pl. 59, figs. 1, 2; n, text-fig. 2B), which may have been the posterior border of an articular area (art, text-fig. 3A). However, this needs confirmation on better material, as it is not certain that this perichondral edge is a natural margin. Just behind the notch the dorsal margin of the palatoquadrate forms a laterally directed shelf (r.epq, text-fig. 3D), which extends posteriorly until it touches the suborbital plate at its dorsal margin (text-fig. 3C). At least on the right palatoquadrate this shelf has an open lateral margin (text-fig. 2B). This shelf delimits dorsally the space described below as an extension of the adductor fossa. As such it corresponds in position to the extra-palatoquadrate ridge in acanthodians or elasmobranchs (e.g. Miles 1973; Young 1982).

The metapterygoid region of the palatoquadrate is less deep but wider than the autopalatine, with a conspicuous dorsal flexure forming a ventral embayment, clearly the fossa for the adductor mandibulae musculature (f.am, text-fig. 3). Just in front of this fossa the palatoquadrate is separated from the suborbital ventrally, but is in contact dorsally. The inner ridge of the suborbital plate is reduced here to a low thickening, above which the concave inner surface of the suborbital and the concave outer (labial) surface of the palatoquadrate enclose a space in open communication ventrally with, and probably forming a dorsal extension of, the adductor fossa (f.am, text-fig. 3C). The dorsal-most opening through the perichondral lining, high on the lingual face above the adductor fossa, has slightly thickened rims showing it to be a natural opening representing another articular surface in contact with the endocranium (art.pb, text-fig. 3). The homologization of these various connections with the braincase amongst different placoderms is still uncertain. In *Romundina*, *Ctenurella*, and *Buchanosteus* there are three or more connections between the anterior portion of the palatoquadrate and the subocular shelf. The posterior two in *Buchanosteus*, by their close association with the groove for the efferent pseudobranchial artery, may be assumed to correspond, topographically at least, to the palatobasal connection in other fishes (Young 1979, p. 336). It is not clear how these correspond to the articular areas in *Romundina*, but in relation to the groove for the efferent pseudobranchial artery on the endocranium the posterior area labelled by Ørvig (1975, pl. 2, fig. 5) may correspond to the anterior part of the palatobasal connection in *Buchanosteus*, and another articular area may have been developed in the non-preserved part of the palatoquadrate immediately behind. This latter connection would have had an anterodorsal position relative to the adductor fossa, as with this posterior articular area in *Bothriolepis* (art.pb). However, in *Holonema* an articular area in much the same position was interpreted by Miles (1971) as for the orbital connection. In *Bothriolepis* a more anterior double orbital articulation has been restored after *Romundina* (art, text-fig. 3A), but it should be noted that in at least one euarthrodire (*Dicksonosteus*; see Goujet 1975) this was reduced to a single connection. In *Holonema* there were apparently no articular areas on the autopalatine corresponding to those of *Romundina* (Miles 1971, fig. 57).

At its lateral end the palatoquadrate of *Bothriolepis* is constricted, broader than high, and protrudes through the lateral notch in the suborbital plate (text-fig. 2), so that it lies above the posterior process (text-fig. 3B). The most posterior part of the ventral perichondral surface in both examples is inflected downwards, and this is interpreted as the edge of the condyle for the mandibular joint (cd.art). The more completely preserved palatoquadrate from the right side indicates that the condyle partly straddled and was in contact with the end of the posterior process of the sub-orbital plate.

In previous reconstructions of the palatoquadrate in *Bothriolepis* (Stensiö 1948, fig. 7; 1969, figs. 41, 42, 135; Miles 1971, fig. 112; Denison 1978, fig. 3) it has been depicted as a high short element somewhat similar to that of ptyctodontids, with a prominent orbital process extending dorsally to articulate with the endocranium beneath the orbital cavity. The closed dorsal margin of the perichondral lining in this new material shows this reconstruction to be incorrect. The palatoquadrate was low and long, without an orbital process, and occupied a position inside the ventral part only of the suborbital plate.

3. *Meckel's cartilage*. The posterior portion of this element was identified attached to the non-biting posterior division of the left infragnathal, from which it was subsequently detached (Pl. 59, figs. 3, 4). It is a fairly flat broad element which was fixed to the ventral surface of the posterior



TEXT-FIG. 4. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Posterior part of left Meckel's cartilage (cf. Pl. 59, figs. 3, 4). A, dorsal view, showing flat surface affixed to posterior non-biting division of the infragnathal. B, ventral view. C, section through level indicated by arrows.

division of the infragnathal as oriented in text-fig. 4A. A dorsal view of the detached element (Pl. 59, fig. 3) shows clearly the area in contact with the dermal bone as a largely unossified region bounded anteriorly by a thickened perichondral margin (a.m, text-fig. 4A). As preserved, the area of contact corresponds closely in shape to the flat central region bounded by ridges on the ventral surface of the posterior non-biting division of the infragnathal (Pl. 58, fig. 3). There can be little doubt that a long narrow process of the cartilage (lost during preparation) extended to the extremity of the biting division of the infragnathal, in its ventral groove. The expanded posterior part of the cartilage projected anteriorly from beneath the infragnathal (a.sh, text-figs. 4A, 5D). This, together with the dorsolateral face of the non-biting division, probably formed the ventral area of attachment for the adductor mandibulae musculature.

The ventral surface of the preserved portion of the cartilage is completely ossified (text-fig. 4B, C), except for a deep embayment in its posterior margin (art.v), which has a slightly everted rim and was probably a cartilaginous articular surface. The function of such an articulation is uncertain, however, as it would have faced ventrally beneath the mandibular joint. It might correspond to the facet on the articular bone of ptyctodontids which may have received an element of the hyoid arch (Stensiö 1969, fig. 152; Miles and Young 1977, fig. 24). A similar facet is present also in brachythoracids, and was referred to by Stensiö (1963) as the 'supraglenoid area' (see Miles and Dennis 1979, p. 52). The mandibular articulation is not preserved in CPC 25205, but its likely position can be inferred from a consideration of the relationship between the upper and lower jaw elements (see below).

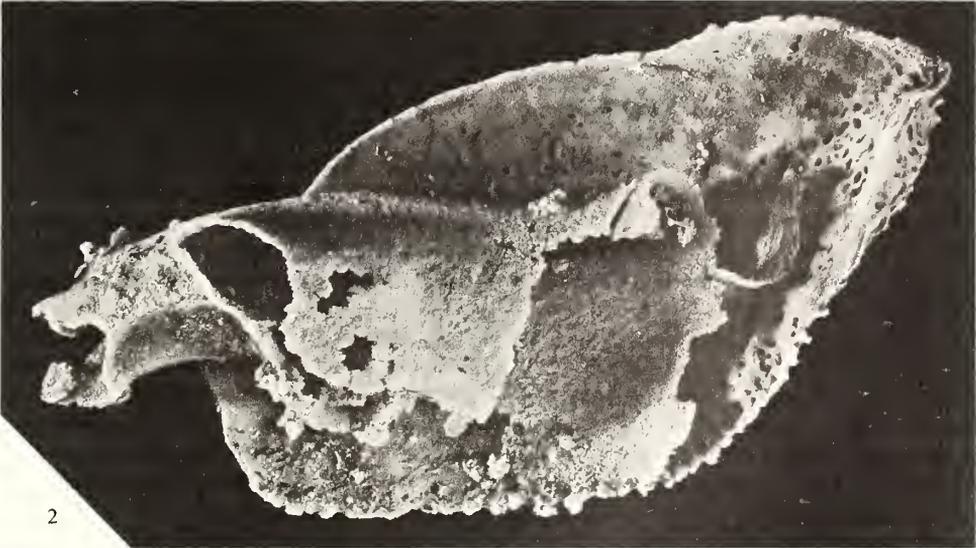
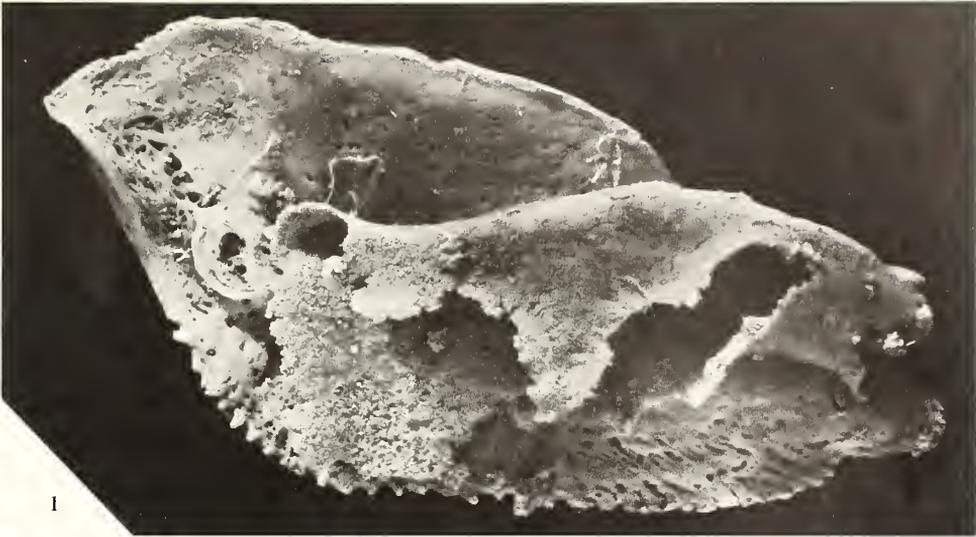
Again this element is much shorter and broader than restored by Stensiö (1948, 1969), and there is evidence that the mandibular joint was located adjacent to the posterior end of the infragnathal, and not some distance from it.

EXPLANATION OF PLATE 59

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

Figs. 1, 2. Internal views of right and left suborbital plates with palatoquadrates attached, $\times 6$.

Figs. 3, 4. Posterior part of left Meckel's cartilage in dorsal and ventral views respectively, $\times 6$.



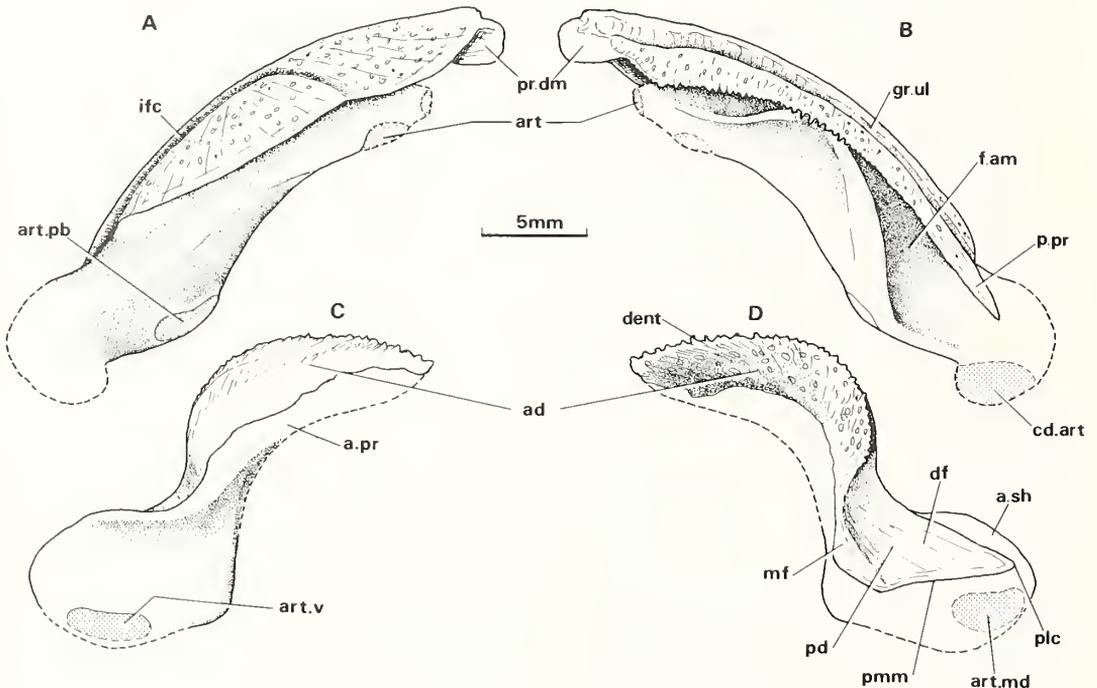
YOUNG, *Bothriolepis* from Gogo

RESTORATION

1. *Jaws*. A restoration of upper and lower dermal and visceral jaw elements in biting position is presented in text-fig. 5. The following constraints were applied in this restoration.

(a) Reassembly shows that the flat mesial edges of the suborbital plates do not fit against each other, indicating an intervening ligamentous or cartilaginous connection, as previously suggested for *Bothriolepis* (e.g. Stensiö 1948, 1969). As preserved (text-fig. 6) these plates lay symmetrically about the midline, but by fitting together the skull-roof and trunk armour and laying in the upper elements in the available space (see below) it became evident that they had been subject to post-mortem rotation. The configuration of the dorsal (anterior) margins of the suborbital plates in relation to the rostral margin of the skull-roof indicates a slight separation between left and right elements, as Stensiö concluded from a study of *B. canadensis* (1948, fig. 34).

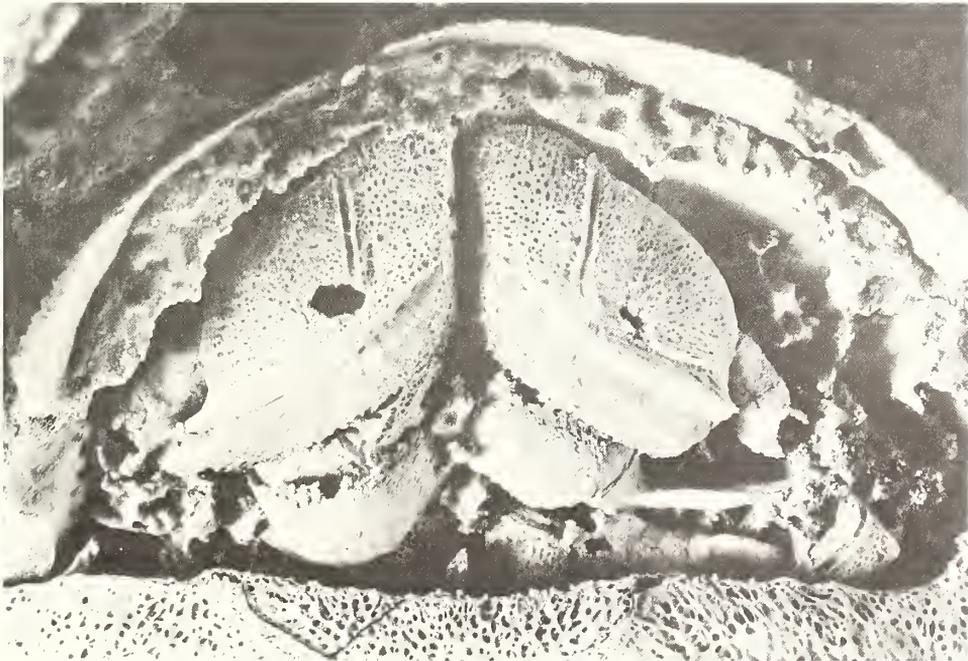
(b) By direct experimentation with upper and lower dermal elements their biting margins were oriented in presumed biting position, with the denticle rows subparallel. The biting margin of the infragnathal has much stronger curvature, and it is clear that it could not have closed outside the upper biting margin. It also seems unlikely that it bit inside this margin, because of obstruction by the palatoquadrate. It is possible, however, to place the jaw elements with good alignment between upper and lower denticle rows such that they occluded against each other. There is little freedom to adjust the two elements with respect to each other without the biting edges losing their alignment, so this is assumed to be a reasonable approximation of the correct biting position. Camera lucida drawings were prepared of each element in biting view.



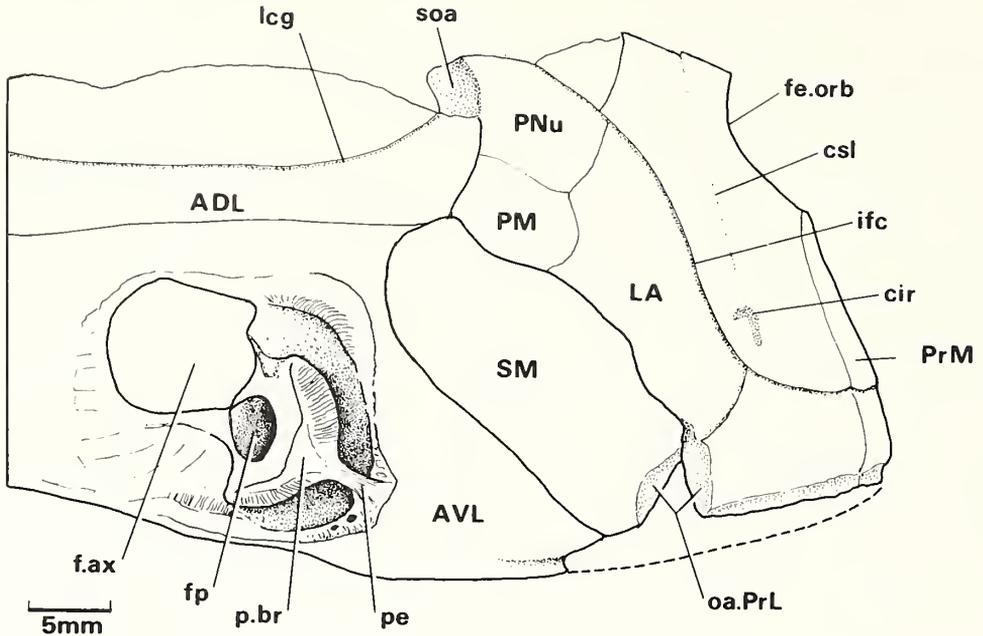
TEXT-FIG. 5. Restoration of jaw cartilages in *Bothriolepis*, after CPC 25205. A, dorsal view of a left suborbital and palatoquadrate, oriented as in B. B, ventral (occlusal) view of left suborbital and palatoquadrate. C, ventral view of right infragnathal and Meckel's cartilage, oriented as in D. D, dorsal (occlusal) view of right infragnathal and Meckel's cartilage.

(c) The likely position of the mandibular joint provides a third constraint on jaw position. As noted above, the posterior end of the palatoquadrate protrudes laterally to the posterior process of the suborbital plate. From the shape of the broken perichondral margins it is probable that the articular facet on the quadrate was immediately adjacent to the end of this dermal process, and the corresponding surface on the articular was immediately adjacent to the posteromesial margin of the posterior division of the infragnathal. To bring these surfaces together in the reconstruction the posterior division of the infragnathal needed a position as far lateral as possible, and it was necessary to assume some mesial flexure of the quadrate inside the posterior process of the suborbital plate. The restored position of the mandibular joint was determined both by superimposing outline drawings of the two elements, and by direct reassembly of the specimens. It should be noted that in this new restoration (text-fig. 5) the palatoquadrates are separated anteriorly, and do not form a symphysis (cf. Stensiö 1948, 1969). This is a primitive condition for placoderms at least (e.g. euarthrodiros, palaeacanthaspids, gemuendinids, petalichthyids), and probably also for gnathostomes (acanthodians, osteichthyans). The lower jaws of each side are also widely separated, but were possibly connected anteriorly by a median basimandibular, as restored by Stensiö (1969, fig. 135A). However, there is no preserved evidence in this material for the existence of this element.

The above procedure permits the reconstruction of upper and lower jaw elements with respect to each other, but gives no indication of their relationship to the skull-roof and endocranium. However, by reassembling the skull-roof against the trunk-shield the space available for the orobranchial cavity could be delimited. The submarginal and prelateral plates close in the gill chamber laterally, the former plate fitting closely against the anterior ventrolateral to effect an adequate seal with the operculum closed, as in other placoderms (e.g. Young 1980, fig. 18). As previously determined (Stensiö 1931, 1948) the mouth must have opened through that semicircular space delimited by the fairly straight leading ventral edge of the trunk-shield and the strongly curved rostral margin of the



TEXT-FIG. 6. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Specimen in ventral view, partly prepared, to show preserved position of jaw elements, $\times 3$.



TEXT-FIG. 7. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Right lateral view showing skull-roof reassembled against the trunk-shield. The dashed line from the leading ventral edge of the trunk-shield to the rostral margin of the skull-roof includes the assumed mouth position.

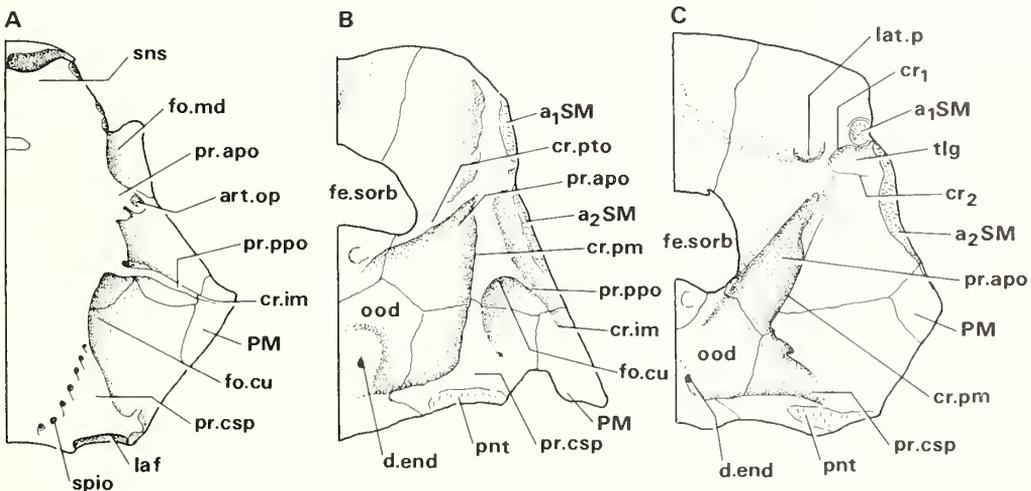
skull-roof. A lateral view of the reassembled Gogo specimen (text-fig. 7) confirms that this rostral margin and its lateral extremities lie in a slightly curved plane forming the anterior continuation of the flat ventral surface of the trunk-shield. The lack of angularities or projections in the overall conformation of the skull and trunk armours suggests that protruding jaws would have been most unlikely. As in previous restorations therefore (e.g. Stensiö 1948, 1969), it is assumed that the mouth was a transverse opening situated behind and slightly below the rostral margin of the skull-roof.

By suitably elevating the posterior part of the trunk-shield in CPC 25205 with the skull attached, it was possible to lay in the upper and lower jaw elements in their approximate positions on the flat surface supporting the specimen. At this angle the curved dorsal margins of the suborbital plates conform fairly well with the concave rostral margin of the skull-roof. The limited space available anterior to the anterior ventrolaterals shows that the upper jaws must have been carried adjacent to the rostral margin in a flap of skin. In this position it is clear that the mandibular joint must have been located approximately inside the prelateral plate, with the preserved dorsal articular surface (art.pb, text-fig. 3A) facing toward the lateral pit, but some distance below it. The palatoquadrate lies anteromesial to the articular process of the submarginal plate, the slope of its upper surface in the quadrate region conforming fairly well to the slope of the articular process. It is reasonable to suggest therefore that the epiphyal fitted between these two structures. If the epiphyal articulated against the anterior postorbital process of the endocranium, as it does in some other placoderms, then this process must have terminated approximately adjacent to the prelateral crista, and slightly above the anterior articular area for the submarginal. This assumes, of course, that the epiphyal was neither attached to nor incorporated in the submarginal plate and its articular process.

2. *Endocranium*. The form of the palatoquadrate, as described above, demonstrates that the endocranium of *Bothriolepis* must have been much deeper than previously supposed, at least in its anterior parts, in order to effect an articulation with the palatoquadrate. The previous restoration of the endocranium by Stensiö (1948, figs. 6, 7; 1969, figs. 41, 42), largely followed by other workers (Miles 1971, fig. 112F; Denison 1978, fig. 3A), was based on the well-developed impressions for the dorsal surface of the endocranium on the visceral skull-roof surface in the region behind and lateral to the orbital fenestra (the 'otico-occipital depression' of Stensiö). Anteriorly little information is provided by the skull-roof, and here Stensiö relied on the assumption that the palatoquadrate was a short, deep element, with a prominent dorsal process which formed an orbital connection with the endocranium in a similar position, relative to the orbits, to this connection in other forms. To develop a new restoration of the braincase, based on the morphology of the palatoquadrate as described above, it is first necessary to consider the various endocranial processes in placoderms and their relations to visceral arch elements and associated muscles.

I have previously suggested (Young 1979, 1980) that there are grounds for homologizing most of the endocranial processes and associated fossae amongst the various major groups of placoderms, on the assumption that these structures were developed in different ways according to differences in the arrangement of the main muscles controlling movement of the cheek and jaws against the skull-roof and endocranium. By using these previously proposed homologies (text-fig. 8), and assuming constancy of morphological relations and function of corresponding endocranial structures in *Bothriolepis*, a new restoration of the endocranium has been prepared (text-fig. 9). The major changes in proportion resulting from dorsal migration of the orbits and nares, and the development of a prominent rostrum, appear to have had less effect on the posterior parts of the endocranium, where homologies to corresponding structures in other forms are fairly clear. These may be considered first, to establish a framework for interpreting the ethmoid and orbital regions.

The craniospinal process (pr.csp, text-fig. 8) in *Bothriolepis* supports the dermal neck-joint, and can be assumed homologous to this process in other placoderms as identified by Young (1980, fig. 24). The same process in Stensiö's restoration (1969, figs. 41, 42) was termed the 'supravagal process'. The supravagal process as redefined by Young (1980, p. 56) was apparently either extensively reduced or absent in *Bothriolepis*, as was the posterior postorbital process. However, there is evidence that in

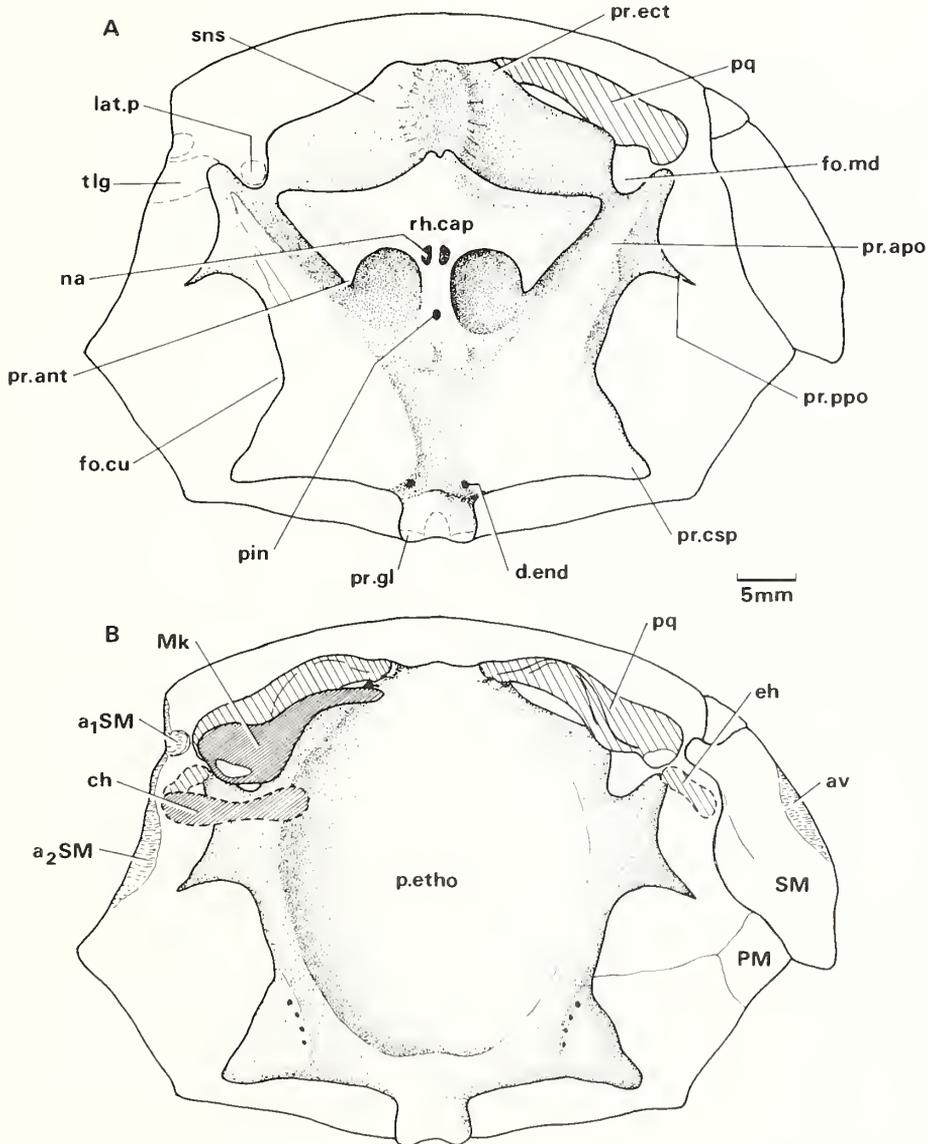


TEXT-FIG. 8. Endocranial processes in placoderms. A, ventral view of skull-roof and endocranium in *Buchanosteus* (after Young 1979, fig. 2). B, *Asterolepis*, skull-roof in ventral view (after Stensiö 1969, fig. 138C). C, *Bothriolepis*, skull-roof in ventral view (after CPC 25205). Not to scale.

some antiarchs the latter process was retained. A deep pit lying lateral to the paramarginal crista and opening posteriorly is known in *Asterolepis* (e.g. Stensiö 1948, fig. 17). This pit is bounded laterally by a crest of bone passing on to the postmarginal plate, which can be readily homologized with the inframarginal crista in euarthrodires such as *Cocosteus* (e.g. Miles and Westoll 1968). This homology is supported by the presence of a postmarginal sensory groove on the postmarginal plate in some primitive antiarchs (e.g. Zhang Miman 1980, pl. 1). In *Buchanosteus* the inframarginal crista (cr.im, text-fig. 8A) forms an extension to the posterior postorbital process, and marks the anterior boundary of the cucullaris fossa. Comparison with the visceral skull-roof surface in *Asterolepis* (e.g. Stensiö 1969, fig. 138c) indicates that this lateral pit, which faces posterolaterally toward the obstantic margin, also represents the cucullaris fossa (fo.cu, text-fig. 8B). Although there is no evidence that the posterior postorbital process was retained in *Bothriolepis*, a small process corresponding in position to that of *Asterolepis* is shown in the restoration (pr.ppo, text-fig. 9), to facilitate homologization of surrounding structures. However, there is good evidence of the shape of the dorsal aspect of the anterior postorbital process, which in *Bothriolepis* and other antiarchs must have occupied an anterolateral extension of the otico-occipital depression (pr.apo, text-fig. 8B, C). In most other placoderms this process carried one or two subterminal articular surfaces for visceral arch elements (palatoquadrate, epiphyal, opercular cartilage). In *Asterolepis* the depression for this process lies adjacent to a dermal thickening which supported the connection and articulation of the submarginal plate against the skull-roof (a_1SM , a_2SM , text-fig. 8). In *Bothriolepis* there is a similar arrangement, although a more complex (apparently dermal) moveable articulation is developed between the articular process of the submarginal plate and the skull-roof. Whether the thickening supporting these articulations is entirely dermal in origin, or in fact represents the ossified terminal part of the anterior postorbital process, depends on the likely position of the epiphyal element and its relationship to the submarginal plate. This is further considered below. In the restorations the anterior postorbital process is shown extending as far forward as the transverse lateral groove (tlg, text-fig. 9).

In *Buchanosteus* the subocular shelf formed a floor to the orbital cavity, and was continuous anteriorly with the subnasal shelf (sns, text-fig. 8A) which extended beneath the separately ossified rostral capsule (Young 1979). A similar arrangement is seen in *Romundina*, where the rostral capsule and nasal openings are dorsally placed (Ørving 1975), and also in *Brindabellaspis*, where the two elements of the braincase show incipient fusion (Young 1980). The distribution of this character indicates that the separation of the endocranium into rhinocapsular and postethmo-occipital components was probably a primitive placoderm feature. Again, in both *Buchanosteus* and *Romundina* the palatoquadrate articulated against the lateral edge of the subocular shelf, or was closely held to it by ligaments, and this is also likely to be a primitive placoderm feature. In *Bothriolepis*, Stensiö (1969, figs. 41, 42) restored a high orbital process on the palatoquadrate, which articulated against the braincase in a dorsal position beneath the orbital fenestra, with the autopalatines of each side forming an anterior symphysis. However, as shown above, the palatoquadrate was low and broad, and it is clear that there must have been considerable anteroventral extension of the braincase to receive the palatoquadrate articulation. By comparison with *Buchanosteus*, and especially *Romundina* (in which the nares are dorsally placed), it can reasonably be assumed that the palatoquadrate retained its normal connection with subocular and subnasal shelves, even though the orbits and nasal openings had migrated dorsally to a mid-line position. In the restorations, therefore, three articulations between the palatoquadrate and subocular and subnasal shelves are shown: an anterior double articulation with an ectethmoid process, corresponding to the orbital connection known in *Kujdanowiaspis*, *Dicksonosteus*, *Ctenurella*, *Buchanosteus*, and probably *Romundina* (Stensiö 1963; Goujet 1975; Ørving 1975; Miles and Young 1977; Young 1979); and a posterior single articulation, corresponding topographically to the palatobasal articulation, which is also known in *Buchanosteus* and probably *Romundina* (Young 1979, fig. 12; cf Ørving 1975, pl. 1). To what extent the subocular and subnasal shelves of *Bothriolepis* were in contact with the visceral surface of the skull-roof is uncertain, but the poriferous area and associated ridges beneath the premedian plate (e.g. Stensiö 1948, fig. 15) suggest attachment in this region (the endocranial 'rostral

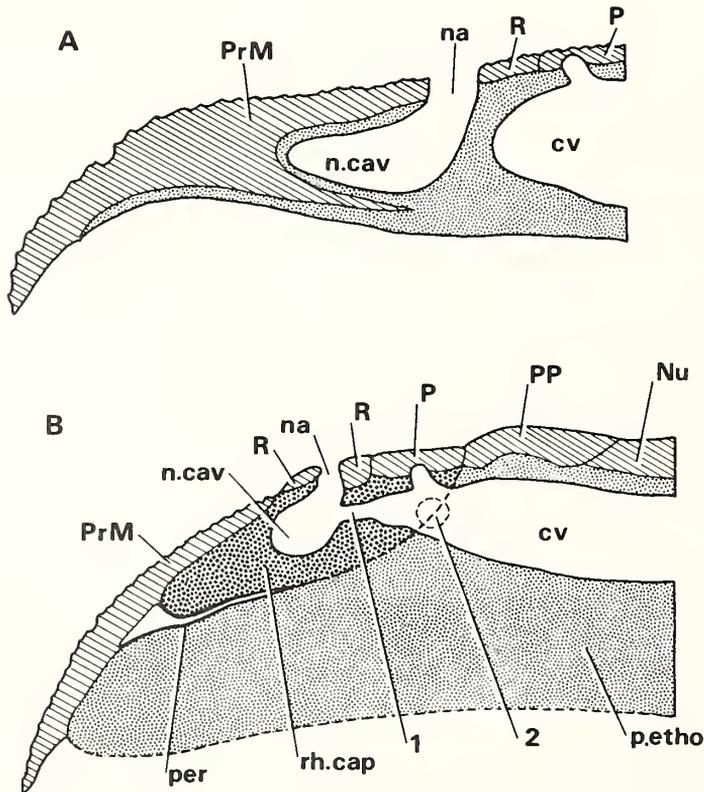
process' of Stensiö's restoration). The anterolateral corners of this rostral process in *B. canadensis* approximate in position to the ectethmoid processes restored here (pr.ect, text-fig. 9A). As such they are appropriately placed to have received the anterolateral ends of each palatoquadrate, with the jaws in their correct position.



TEXT-FIG. 9. Restoration of endocranium, mandibular and hyoid arch elements in *Bothriolepis*, Dermal skull-roof, and cheek plates of one side, shown in outline. A, dorsal view, with right palatoquadrate in approximate position (modified in part after Stensiö 1969, fig. 41). B, ventral view, with epihyal (unknown) and palatoquadrate in approximate positions. Position of right ceratohyal (unknown) and right Meckel's cartilage based on assumed position of palatoquadrate and epihyal.

Clearly there must have been muscles of mandibular derivation controlling movement of the palatoquadrate against the braincase, and in other forms (Young 1979, 1980) an embayment in the lateral endocranial wall, bounded posteriorly by the anterior postorbital process, has been proposed as the likely site of insertion of the *m. levator palatoquadrati* (fo.md, text-fig. 8A). In *Bothriolepis* the thickening on the lateral plate determined above as adjacent to or part of the anterior postorbital process, forms the posterior boundary of the lateral pit, which in this Gogo specimen (Pl. 57, fig. 1) is a distinct irregular depression readily interpreted as a site for muscle insertion. An embayment in the endocranial wall in this position, corresponding to the mandibular muscle fossa identified in *Buchanosteus* (Young 1979, fig. 2), is shown on the restorations (fo.md, text-fig. 9). It is possible, however, that this fossa was partly closed in ventrally by the subocular shelf.

The presence of extensive subocular and subnasal shelves in *Bothriolepis*, as is required to effect a connection with the palatoquadrate, leads to a new interpretation of the preorbital recess in this form. This structure, a backwardly opening cavity beneath the posterior part of the premedian plate, has been interpreted by Stensiö (1948, 1969) as a cartilage-lined space completely occupied by the nasal sacs (text-fig. 10A). The recess is floored by a lamina of bone projecting posteroventrally from the visceral surface of the premedian plate, and enclosed in cartilage under Stensiö's restoration. The shape of the recess amongst different species of *Bothriolepis* is well known (e.g. Stensiö 1948, figs. 13–15; Miles 1968, figs. 7, 43, 58), and there can be no doubt that the recess was either filled or



TEXT-FIG. 10. Paramedian sections through the preorbital region of the head in *Bothriolepis*. A, after Stensiö (1969, fig. 135B). B, new interpretation showing suggested position of rhinocapsular bone.

lined with cartilage. In view of the position of the preorbital recess in relation to the remainder of the braincase as restored here, I suggest that this structure was in fact the rhinocapsular bone of the endocranium (rh.cap, text-figs. 9A, 10B). Disregarding changes in proportion, it can be noted that this structure occupies the same position in relation to the subocular and subnasal shelves of *Kujdanowiaspis*, *Buchanosteus*, or *Romundina*, as does the rhinocapsular bone in these forms (Stensiö 1963; Ørvig 1975; Young 1979). The bony lamina forming the floor of the recess, and enclosed in cartilage under Stensiö's restoration (an anomalous relation if this lamina is of dermal origin), may be reinterpreted by comparison with *Brindabellaspis* (Young 1980, fig. 4). I suggest that it is a thickened remnant of a double perichondral layer representing contiguous surface ossifications of the two separate cartilages comprising the primitive braincase in placoderms. In *Brindabellaspis* this lamina is completely enclosed within the cartilage of the fused endocranium, and can be shown to have the correct morphological relations to surrounding nerves and vessels for it to represent the interface between rhinocapsular and postethmo-occipital portions of the endocranium. A similar interpretation for *Bothriolepis* presents no difficulty in relation to the optic nerve, which in other placoderms actually emanates between these two cartilages. Furthermore, the rhinocapsular bone thus delimited in *Bothriolepis* is attached to the rostral and pineal plates as in the other primitive placoderms mentioned above. The restoration shows posterolateral extensions of the rhinocapsular bone partly enclosing the orbits laterally, as do the antorbital processes in *Brindabellaspis* (Young 1980, fig. 8).

DISCUSSION

1. *Dermal bones of the jaws and cheek.* It is now evident that the so-called mental plate of antiarchs, a paired canal-bearing dermal bone forming the upper biting margin of the mouth, is homologous with the suborbital plate of other placoderms. This is confirmed by the fact that the palatoquadrate is attached to its inner margin. In view of the form of the palatoquadrate as demonstrated by this new material, any suggestion that the lateral plate incorporates homologues of the suborbital plate in whole or in part (e.g. Stensiö 1948, p. 200) may be discounted. On the other hand, the lower dermal jaw-bone in *Bothriolepis* includes differentiated blade and biting portions, as does the infragnathal in euarthrodires, and might therefore be considered the homologue of this bone. If so, it could be suggested that the absence of any supragnathal elements in *Bothriolepis* (and other antiarchs) is a secondary condition. This is consistent with assumed phylogenetic relationships of the antiarchs. However, there is other evidence indicating that the differentiated lower jaw-bone in antiarchs may have arisen within the group, in which case this argument would not apply. This is more fully considered below. Whether the antiarchs may have lost two pairs of supragnathals is an interesting question, since Miles and Young (1977) proposed this as a synapomorphy of euarthrodires. Further information on jaw structure in yunnanolepids may illuminate this point.

In advanced euarthrodires the quadrate part of the palatoquadrate is fused inside the postsuborbital plate, although in primitive euarthrodires and some other placoderms this plate is not readily recognized. In *Bothriolepis* both the prelateral and infraprelateral plates are canal-bearing bones lying adjacent to the mandibular joint, and one or both may represent a postsuborbital element which has either lost its close connection to the quadrate, or never had such a connection (see below).

Behind the suborbital-postsuborbital unit the operculum in placoderms is covered by a large dermal bone, the submarginal plate. In several groups this plate articulates with the endocranium through a cartilage fused to its inner surface. Again there is little doubt that the bone in antiarchs previously termed the extralateral plate is homologous to the submarginal (e.g. Miles 1971; Young 1980). In some asterolepidoids (e.g. Nilsson 1941) the plate carries a groove on its inner surface similar to the groove for the epihyal in phlyctaenioids (e.g. Goujet 1972, 1975), and in yunnanolepids the submarginal lies adjacent to a notch in the lateral skull-roof margin resembling the notch in a corresponding position in euarthrodires (Zhang Miman 1980; Young 1980, p. 53). However, the development of a dermal articulation between the submarginal and the lateral plate in *Bothriolepis* is unique amongst placoderms, although an analogous articulation is seen between the suborbital and

postorbital plates in *Buchanosteus* (Young 1979). It is worth noting that this articulation in *Bothriolepis* is supported by a thickened ridge of bone beneath the lateral plate, interpreted above as being adjacent to, or part of, the anterior postorbital process. In euarthrodires the submarginal has an equivalent position, being connected to the endocranium through an articulation between the epiphyal and the end of the anterior postorbital process.

2. *The preorbital recess and preorbital depression in antiarchs.* It has been suggested above that the preorbital recess of *Bothriolepis* housed the rhinocapsular bone of the endocranium, which was incompletely fused to the postethmo-occipital bone. In placoderms generally, the occurrence of a discrete rostral capsule in several distantly related groups indicates that this is a primitive placoderm feature (Young 1979, p. 341; 1980). It is of interest therefore that in the primitive yunnanolepid antiarchs from south China, and some other forms, the preorbital recess is not developed (Zhang Guorui 1978; Zhang Miman 1980). Instead, there is a broad dorsal depression in front of the orbital fenestra, recently interpreted by Janvier and Pan (1982) as the primitive condition for antiarchs, which was modified to form the recess of *Bothriolepis* and other more advanced forms by posterodorsal growth of the anterior border of the depression. This being so, one could suggest that the rostral capsule occupied the preorbital depression in yunnanolepids, and because it retained its primitive relation to the main portion of the endocranium as a discretely ossified unit, it is commonly lost and has largely gone unrecognized in these forms. In fact, remains of the rostral plate are known only in one specimen of *Yunnanolepis parvus*, as described by Zhang Miman (1980), who has, however, restored the nasal openings in a posterior position behind the preorbital depression and within the orbital fenestra. Consistent with this interpretation is the suggestion by Janvier and Pan (1982) that the preorbital depression in Yunnanolepiformes is homologous to the depression described by Ørvig (1975) on the 'median prerostral plate' of *Romundina*.

There are thus two alternative interpretations of the preorbital depression in primitive antiarchs. Under my interpretation of the preorbital recess in *Bothriolepis*, the preorbital depression is no more than a cavity which contained a discretely ossified rostral capsule in a position somewhat similar to that proposed by Zhang Guorui (1978). Under this interpretation the nasal capsules have a wholly dorsal position relative to the premedian plate. The alternative interpretation of Janvier and Pan (1982) proposes that the preorbital depression lies largely in front of and above the nasal capsules, and may be homologous to the depression in the dermal bone surface described by Ørvig (1975) as lying in front of the rostral capsule in *Romundina*. Under this interpretation the nasal capsules are ventrally situated relative to the premedian plate, perhaps extending forward on either side of the subpremedian ridge, as proposed by Zhang Miman (1980, p. 186).

In support of the second interpretation might be cited the fact that in *Y. parvus* the floor of the preorbital depression is ornamented, as is the depression on the prerostral plate in *Romundina*. But this raises a difficulty with Janvier and Pan's explanation of the fate of the depression in more advanced antiarchs, which requires that the ornamented (dermal) floor of the depression must have sunk into the endocranium to become enclosed in cartilage as the floor of the preorbital recess in bothriolepids. Similarly, the dermal ornament on the floor of the preorbital depression would appear to contradict my suggestion that the depression contained the rostral capsule, since under this interpretation the floor of the depression (like the floor of the preorbital recess in *Bothriolepis*) must be of perichondral derivation.

Since the preorbital depression in *Sinolepis* and *Microbrachius* is entirely lacking in ornament (Liu and Pan 1958; Hemmings 1978), the nature of the dermal tubercles in the preorbital depression of yunnanolepids is of particular interest. My observations on specimens in the Institute of Vertebrate Palaeontology and Paleoanthropology, Beijing, confirmed that in *Y. chii* the preorbital depression is smooth in the region of the premedian plate, but tuberculate in more lateral parts of the depression. The situation is less clear in *Y. parvus* because of its small size, but tubercles are again present in the lateral parts of the depression, and may extend towards the mid-line. The observation that these tubercles are much finer in the depression than on the surrounding bone surface indicates an explanation of their occurrence consistent with the interpretation of the preorbital recess in *Bothriolepis* presented above. I suggest that these fine tubercles surrounded the nasal openings, just as

very similar fine ornament is observed in the notch of the nasal opening in *Romundina* (Ørvig 1975), and *Buchanosteus* (e.g. Miles 1971, fig. 105). In *Yunnanolepis* the preorbital depression has groove-like lateral extensions, and I suggest that the nares opened laterally into these grooves. Any contact between the floor of the depression and the rhinocapsular bone of the endocranium would thus have been restricted to a narrow region of the mid-line. Under such circumstances dermal bone may grade imperceptibly into unornamented bone of perichondral derivation, as is the case in the rostral capsule of *Buchanosteus* (Miles 1971, p. 186). It should be noted that this interpretation is at variance with the conclusion of Zhang Guorui (1978, p. 154) that the nares in *Yunnanolepis* may have opened anteriorly, as in *Remigolepis*, and not laterally as in *Bothriolepis*, but there is also a phylogenetic argument supporting my view (see below).

A final point relates to the position of the nasal capsules in yunnanolepids and whether they may have been partly or wholly contained beneath the premedian plate on either side of the subpremedian ridge as proposed by Zhang Miman (1980). In *Y. chii* the so-called 'orbital fenestra' is a constricted oval-shaped opening facing anteriorly and somewhat dorsally into the preorbital depression. By comparison with the morphology of the orbital cavity as now known in some detail in other placoderms (e.g. Ørvig 1975; Young 1979, 1980) it can be suggested that the following nerves and vessels (all paired) must have gained access to the orbital cavity through this opening: optic (II), oculomotor (III), trochlearis (IV), profundus (V), and abducens (VI) nerves, the ophthalmica magna artery and possibly a branch of the orbital artery, and presumably an orbital or orbitonasal vein. In view of the small size of the 'orbital fenestra' in *Yunnanolepis* it seems inconceivable that the nasal capsules themselves could have been situated beneath it—this would require a similar position for the telencephalon of the brain, and a tortuous dorsal path for the optic nerves to reach the orbits, and of extensive nasal tubes to reach the nares. Considerations of space make it equally unlikely that the nasal capsules were positioned above the fenestra, through which the olfactory nerves passed in addition to those nerves and vessels just mentioned. In my opinion the only interpretation of the known structure of yunnanolepids and other antiarchs which is consistent with detailed endocranial morphology as known in other placoderms, is as follows: that the 'orbital fenestra' in various antiarchs with a preorbital depression is misnamed, being strictly homologous to the suborbital fenestra of *Bothriolepis*; and that the suborbital fenestra of antiarchs generally corresponds, at least in its dorsal parts, to the anterior fenestra of the endocranial cavity in forms like *Buchanosteus* (Young 1979, fig. 8), or *Romundina* (Ørvig 1975, pl. 2, fig. 2). As such, the equivalents of the crista supraethmoidalis in these forms, in antiarchs would have attached to the anterior edge of the postpineal plate, thereby marking the anterior limit of attachment of the postethmo-occipital bone of the endocranium to the dermal skull-roof. It is possible that the eye-stalk as known in other placoderms was secondarily lost in antiarchs. Vessels such as the orbital artery, which in other forms passed up through the suborbital shelf to reach the eyeball (e.g. Young 1980, fig. 10), must have entered the orbit through the ventral part of the suborbital fenestra.

3. *Phylogenetic implications.* The adoption of cladistic techniques in analysing phylogenetic relationships within the placoderms (e.g. Miles and Young 1977; Dennis and Miles 1979–1983; Miles and Dennis 1979; Young 1979, 1980, 1981b; Janvier and Pan 1982; Lelievre *et al.* 1982; Long 1983) has during the last few years generated a number of new ideas regarding placoderm evolution. These are testable in the sense that they make predictions about the morphology of various groups which can be checked as new information becomes available. An important aspect in this procedure is that any new morphological observation or interpretation of any taxon within the group under study is relevant to all other observations and interpretations of other taxa within the group. This results from the unifying character imparted to phylogenetic hypotheses by the use of cladistic techniques. With regard to antiarch phylogeny, an outline cladogram was presented by Young (1981a), and a more detailed proposal along similar lines was put forward by Janvier and Pan (1982). Interrelationships of antiarchs have been most recently discussed by Long (1983) and Young (in press), and relationships of antiarchs by Goujet (in press). In the context of these proposals, and more general schemes of placoderm interrelationships (e.g. Denison 1975, 1978; Miles and Young 1977; Young 1980), several ideas and observations developed above regarding the morphology of the head in *Bothriolepis* have

wider phylogenetic implications. These are the number of supragathal elements in the upper jaw, the differentiation of the infragathal into distinct blade and biting portions, the dermal articulation between the submarginal plate and the skull-roof, the relation between the quadrate and the postsuborbital plate, and the position of the nares in antiarchs. The phylogenetic arguments on each are briefly presented in points *a-e* below, and summarized in the cladogram of text-fig. 12.

(*a*) *Supragathals*. The suggestion by Miles and Young (1977) that two pairs of supragathals may be a synapomorphy of euarthrodires predicts that other placoderm groups will have one or none of these elements. There are no supragathals in *Bothriolepis*, but a single pair has recently been reported in phyllolepid (Long, in press), which would mean that this was also the primitive condition in antiarchs, under the scheme of placoderm interrelationships proposed by Miles and Young (1977). Alternatively, the absence of supragathals in *Bothriolepis* can be seen as consistent with Goujet's (in press) view of antiarch relationships.

(*b*) *Infragathal*. Similarity between the infragathal of *Bothriolepis* and that of some euarthrodires has been mentioned above. In a series of papers on brachythoracid euarthrodires from Gogo (Dennis and Miles 1979*a, b*, 1980–1983; Miles and Dennis 1979), the differentiation of the infragathal into distinct posterior blade and anterior biting regions has been used as a synapomorphy of various brachythoracids (see also Young 1981*b*, fig. 17). This was based on the evidence that in *Holonema* the infragathal is not differentiated into two portions (Miles 1971), that in *Phlyctaenius* the few known infragathal remains (assumed by Heintz 1933 to be incompletely preserved) show only a biting region, and that various isolated denticulate bones from the early Devonian of Utah, also lacking a blade portion (Denison 1958, fig. 101), have been attributed to actinolepid euarthrodires. In view of the specialized nature of the dentition in *Holonema* it is possible that the blade on the infragathal has been secondarily lost, and the evidence relating to *Phlyctaenius* is equivocal (e.g. Heintz 1933; Miles 1969). However, it seems reasonable on available evidence to attribute the isolated infragathals of Denison (1958) to the associated actinolepids, and it is noteworthy that the corresponding element in phyllolepid resembles these examples in general form (Long, in press).

Taking account of the differentiated infragathal in *Bothriolepis*, therefore, there are three alternative interpretations of the history of this element worthy of consideration, under an assumption that antiarchs and euarthrodires are sister groups:

- (i) The differentiated infragathal was present in the common ancestor of antiarchs and euarthrodires, and was secondarily lost in more primitive members (actinolepids, some phlyctaenioids) of the latter group.

This alternative seems unlikely, in view of the form of the phyllolepid element mentioned above, and is unparsimonious in requiring two reversals in evolution.

- (ii) Euarthrodires are paraphyletic, the absence of the blade on the infragathal in some phlyctaenioids (e.g. *Holonema*, ?*Phlyctaenius*) is secondary, and the differentiated infragathal was inherited from the common ancestor of antiarchs and phlyctaenioids, which are sister groups.

Evidence against this proposal is evidence supporting euarthrodiran monophyly. Of three characters proposed as euarthrodiran synapomorphies by Miles and Young (1977, p. 134), only one can now be sustained (see Young 1979, p. 347; 1981*b*, p. 261; Young and Gorter 1981). This is the possession of two pairs of supragathals, but even this is not firmly established for actinolepids. An anterior supragathal is preserved *in situ* in *Kujdanowiaspis* (Stensiö 1963, pl. 62), and disarticulated elements which may be actinolepid posterior supragathals have been described by Denison (1958, 1960; see also Miles 1969, p. 145). However, better evidence is required to confirm that there is a posterior supragathal on the autopalatine in actinolepids. (Also of relevance in this connection are the position of the supragathals in phyllolepid—on the palatoquadrate or the braincase—and the number of supragathals in *Wuttagoonaspis*.) Another possible euarthrodiran synapomorphy is proposed below (point *d*).

- (iii) Actinolepids and some phlyctaenioids are primitive in possessing an infragathal which lacks

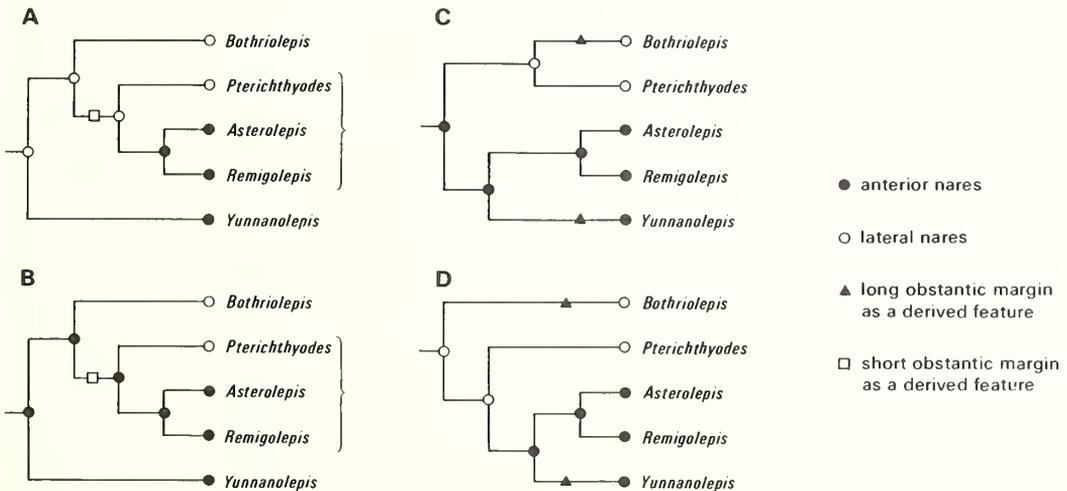
differentiated blade and biting portions. Resemblances between these and the infragnathal of phyllolepidids are symplesiomorphies. The differentiated infragnathal of brachythoracids and antiarchs arose independently in these two groups.

Assuming that the Euarthrodira is a monophyletic taxon, this hypothesis is to be preferred on the grounds of parsimony. If, however, actinolepidids are shown not to possess two pairs of supragnathals, then alternative (ii) would emerge as the preferred hypothesis. It also follows that the structure of the infragnathal cannot be used as evidence against Goujet's (in press) alternative hypothesis of antiarch relationships.

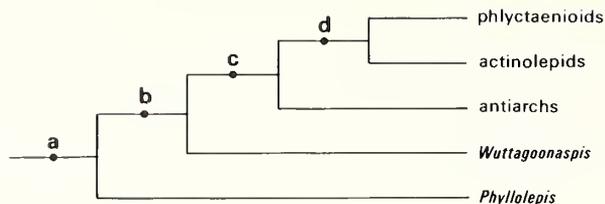
(c) *Submarginal articulation*. As noted above, the development of a dermal articulation between the submarginal plate and the skull-roof is a condition so far known only in *Bothriolepis*, and it thus has the status of an autapomorphy. However, further information on the presence or absence of this structure in other antiarchs thought to be closely related to *Bothriolepis* (e.g. *Dianolepis*, *Wudinolepis*, *Microbrachius*, *Hyrcanaspis*) should clarify relationships within the Bothriolepidoidei.

(d) *Quadrate and postsuborbital plate*. It is well known from the works of Stensiö (e.g. 1963, 1969) that the palatoquadrate in many advanced brachythoracids is represented only by autopalatine and quadrate ossifications. However, the notion that the intervening region may have been reduced to a ligamentous connection (e.g. Miles 1969, p. 144; 1971, p. 194; Ørvig 1975, p. 65) is no longer held (Miles and Dennis 1979, p. 49). On the evidence of *Holonema* (Miles 1971), *Dicksonosteus* (Goujet 1975), and *Buchanosteus* (Young 1979) it is clear nevertheless that there was a phyletic reduction and loss of perichondral ossification of the metapterygoid region within the Phlyctaenioidae.

In phlyctaenioids, and presumably in euarthrodirids generally, the quadrate is closely connected to the postsuborbital plate of the cheek. However, in the palatoquadrate of the palaeacanthaspid *Romundina*, Ørvig (1975, p. 65) has noted that the metapterygoid is perichondrally ossified on all sides at its posterior end, and neither the quadrate nor the postsuborbital plate is known. In view of the condition of the palatoquadrate in other gnathostomes, I am not convinced by Ørvig's suggestion that in *Romundina* the quadrate was a separate unit connected only by ligaments to the metapterygoid. Perhaps the mandibular joint had a high position on the non-preserved mesial surface of the palatoquadrate (see Ørvig 1975, pl. 2, fig. 5). Whatever the correct interpretation for *Romundina*, the apparently anomalous condition of the quadrate in relation to its dermal bone cover,



TEXT-FIG. 11. Alternative cladograms for some antiarchs, under an assumption that *Yunnanolepis* had anterior nares. In A and B the Asterolepidoidei (bracketed) are assumed monophyletic on the evidence of the short obstantic margin as a derived feature (synapomorphy). This feature is assumed primitive in C and D, making the asterolepidoids a paraphyletic group.



TEXT-FIG. 12. Interrelationships of some placoderms. Proposed synapomorphies, as discussed here, are: *a*, sliding dermal neck joint, posterior median ventral plate (if absent in petalichthyids), one pair of supragnathals. *b*, posterior lateral plate and pectoral fenestra in trunk-shield. *c*, long obstantic margin with prominent posterolateral corners on skull-roof, elongate rather than subovate submarginal plate, dermal prelateral and infraprelateral plates (or their homologues) in the cheek unit. *d*, second pair of supragnathals, quadrate fused to postsuborbital plate.

together with the fact that there was also no close association between the quadrate and an overlying dermal bone in *Bothriolepis*, points to the possibility that the postsuborbital/quadrate connection may be another synapomorphy defining euarthrodires. In addition, if the prelaterals and infraprelaterals of antiarchs are homologous with the postsuborbitals and infrapostsuborbitals of euarthrodires (Miles 1971; Denison 1978), then the possession of these bones may be proposed as another synapomorphy uniting these two groups.

(*e*) *Position of the nares in antiarchs.* To account for the presence of fine ornament in the preorbital depression I suggested above that the nares in *Yunnanolepis* opened laterally. This was also the opinion of Zhang Miman (1980), although in other respects (position of nasal capsules, etc.) our interpretations of the nasal region differ considerably. Conversely Zhang Guorui (1978) proposed that in *Yunnanolepis* the nares opened anteriorly as in *Remigolepis* (e.g. Stensiö 1948, fig. 16) and *Asterolepis* (e.g. Lyarskaya 1981, fig. 67). It is of significance, however, that in *Pterichthyodes* and probably *Gerdalepis* (Gross 1941; Stensiö 1948; Hemmings 1978) the rostral plate is developed like that of *Bothriolepis*, with lateral notches for the nares bounded anteriorly by a prenasal division of the plate. In a phylogenetic context this character distribution can be interpreted in several ways, depending on whether the asterolepidoid antiarchs are regarded as monophyletic or paraphyletic.

Young and Gorter (1981) suggested that the short obstantic margin facing posteriorly with posterolaterally extended postmarginal plates was an asterolepidoid synapomorphy, and that the group was monophyletic. If the nares opened anteriorly in *Yunnanolepis*, this would require either that the condition developed independently of that seen in *Asterolepis* and *Remigolepis* (text-fig. 11A), or that it was the primitive antiarch condition, which was separately lost in *Bothriolepis* and *Pterichthyodes* (text-fig. 11B). Both alternatives are less parsimonious than the assumption that in *Yunnanolepis* the nares were laterally placed, this being the primitive condition for antiarchs generally.

On the other hand, if the asterolepidoid antiarchs were assumed to be paraphyletic, the interpretation of *Yunnanolepis* as having anteriorly opening nares could be explained either as the primitive condition for antiarchs, which was lost in the common ancestor of *Pterichthyodes* and *Bothriolepis* (text-fig. 11C), or as a unique specialization of *Asterolepis*, *Remigolepis*, and *Yunnanolepis* (text-fig. 11D). However, under neither interpretation can the similarities in the obstantic margin and configuration of the postmarginal plate in *Bothriolepis* and *Yunnanolepis* be adequately explained. This must be the derived condition under this interpretation (since the other state of this character, as developed in *Asterolepis* and *Remigolepis*, is assumed to be symplesiomorphic) and in both schemes is independently acquired (text-fig. 11C, D). On the grounds of parsimony therefore it

can be concluded that laterally opening nares, as in *Bothriolepis*, was the primitive antiarch condition, and that the anterior position of the nasal openings in *Asterolepis* and *Remigolepis* is a synapomorphy of these genera. This is consistent with the observation that in other placoderms with ventral nares these are also directed more or less laterally (e.g. Stensiö 1963, figs. 10, 17). It can be predicted therefore that better material of *Yunnanolepis* will demonstrate that this form also had the primitive arrangement of lateral nares.

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ABBREVIATIONS USED IN TEXT-FIGURES

1	olfactory nerve	ifc	infraorbital sensory groove
2	approximate position of optic nerve	LA	lateral plate
ADL	anterior dorsolateral plate	laf	articular structure for dermal neck-joint
AVL	anterior ventrolateral plate	lat.p	lateral pit
a ₁ SM	anterior articular area for submarginal plate	leg	main lateral line sensory groove
a ₂ SM	posterior articular area for submarginal plate	Mk	Meckel's cartilage
ad	anterior biting division of infragnathal	mf	dorsomesial face of non-biting division of infragnathal
ad ₁	anterodorsal process of submarginal plate	Nu	nuchal plate
ad ₂	posterior articular area for connection with skull	n	notch, possibly representing part of an articular area
a.m	thickened perichondral margin of area in contact with dermal bone	na	nasal opening
apl	unornamented lateral division of infra-prelateral plate	n.cav	nasal cavity
a.pr	anterior process of Meckel's cartilage	oa.AVL	overlap area for anterior ventrolateral
art	articular areas for orbital connection with braincase	oa.PrL	overlap areas for prelateral
art.md	articular surface for mandibular joint	ood	otico-occipital depression
art.op	articular area for opercular cartilage or epihyal	P	pineal plate
art.pb	articular area for palatobasal connection with braincase	PP	postpineal plate
art.v	ventral articular area, possibly for hyoid arch element	PM	postmarginal plate
a.sh	anterior shelf of Meckel's cartilage	PNu	paranuchal plate
aup	autopalatine part of palatoquadrate	PrL	prelateral plate
av	ventral articular area of submarginal plate	PrM	premedian plate
cd.art	articular condyle for mandibular joint	Py	infraprelateral plate
ch	ceratohyal	p.br	brachial process
cir	semicircular pit-line groove	pd	posterior non-biting division of infragnathal
cr ₁	prelateral crista	pe	pars pedalis of brachial process
cr ₂	postlateral crista	per	perichondral bone
cr.im	inframarginal crista	p.etho	postethmo-occipital section of endocranium
cr.pm	paramarginal crista	pin	pineal foramen
cr.pto	postorbital crista	plc	posterolateral corner of infragnathal
csl	central sensory line	pmm	posteromesial margin of posterior division of infragnathal
cv	cranial cavity	pnt	articular structure for dermal neck-joint
d.end	endolymphatic duct	p.pr	posterior process of suborbital plate
dent	denticulate biting margin	pq	palatoquadrate
df	dorsolateral face of non-biting division of infragnathal	pr.ant	antorbital process
eh	epihyal	pr.apo	anterior postorbital process
f.am	adductor fossa	pr.csp	craniospinal process
f.ax	axillary foramen	pr.dm	dorsomesial process of suborbital plate
fe.orb	orbital fenestra	pr.ect	ectethmoid process
fe.sorb	suborbital fenestra	pr.gl	glenoid process
fo.cu	cucullaris fossa	pr.ppo	posterior postorbital process
fo.md	mandibular muscle fossa	psoc	postsuborbital sensory groove
fp	funnel pit	R	rostral plate
f.vasc	foramina, probably vascular	r.epq	extrapalatoquadrate ridge
gr	groove, possibly for sensory pit-line	rh.cap	rhinocapsular section of endocranium
gr.ul	groove for upper lip	r.pq	dermal ridge supporting palatoquadrate
		SM	submarginal plate
		SO	suborbital plate
		sns	subnasal shelf
		soa	subobstantic area
		spio	foramina for spino-occipital nerves
		tlg	transverse lateral groove

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Cover: The Coralline Crag (Pliocene) bryozoan *Cribulina* sp. showing a group of ten feeding zooids each with an ovicell and paired adventitious avicularia on either side of the orifice. This specimen was figured as *Lepralia punctata* Hassall in G. Busk's Palaeontographical Society monograph of *Crag Polyzoa* (1859, pl. 4, fig. 1). It is reillustrated here by means of a new technique, scanning electron microscopy of the uncoated specimen using back-scattered electrons. ×75.

REVIEW OF THE DISTRIBUTION OF THE COMMONER ANIMALS IN LOWER SILURIAN MARINE BENTHIC COMMUNITIES

by L. R. M. COCKS and W. S. MCKERROW

ABSTRACT. The distribution of the commoner species, most of which are brachiopods, in thirty large collections from the late Llandovery of the Welsh Borderland gives extra data on the previously published *Lingula*, *Eocoelia*, *Pentamerus*, *Stricklandia*, and *Clorinda* communities. The constituents of the communities were not usually interdependent, but lived together in comparable habitats with similar external parameters. The depths at which the communities lived are reviewed and it is concluded that the total depth range of the community spectrum was probably less than 200 m.

STUDIES of brachiopod-dominated associations of lower Silurian age from the Welsh Borderland began over twenty years ago, and these associations were subsequently grouped into animal communities (Ziegler 1965; Cocks 1967; Ziegler *et al.* 1968*a*) which were distributed stratigraphically into organized patterns subparallel to the inferred shoreline (Ziegler *et al.* 1968*b*). It is now opportune to review some aspects of these studies, which came before most scientific work on Palaeozoic communities of other ages; to present more data on the variation within the described communities; and to discuss some aspects of the ecology of the individual constituents.

Exceptional preservation, such as that in the Cambrian Burgess Shale or the Carboniferous Mazon Creek beds, sometimes enables a palaeontologist to glimpse the whole range of flora and fauna to be found on the sea floor, and to compare it with that living today. However, it has long been realized that the average preserved fossil collection from the vast majority of ordinary localities represents only a small proportion of the original biota, both in biomass and diversity, even assuming that the fossils have not been carried dead into the area of deposition. Thus some palaeontologists have questioned the use of the word 'community' when describing repetitive associations of fossils such as those from the Welsh Borderland Llandovery rocks. However, we are unrepentant since, as can be seen by comparison with modern-day situations, such associations assuredly reflect the original communities of which they formed part, and we feel that the shorthand terminology of referring to these preserved associations as 'communities' is justified. We continue to define our communities in a relatively broad way (Cocks and McKerrow *in* McKerrow 1978), unlike the narrower community groupings of Boucot (1975).

Upper Llandovery communities

The Llandovery is an exceptionally good period to study clastic level-bottom animal communities for several reasons: first, there is an excellent framework for accurate correlation (Cocks 1971) using both graptolites and shelly fossils, in particular by using the evolution of selected brachiopods such as *Stricklandia* (Williams 1951 and later authors) and *Eocoelia* (Ziegler 1966); secondly, because there was a very widespread distribution of a single faunal province due to the relative nearness of several land masses at that time (Cocks and Fortey 1982, fig. 5): the same communities are very widely distributed across North America, Europe, and parts of Asia; and thirdly, because of the substantial erosion during the glacioeustatic regression at the Ordovician-Silurian boundary, the edges of the Llandovery shelves were relatively well marked (like the continental shelves of the present day following the Pleistocene glaciation), and can be recognized using sedimentological criteria as well as by the distribution of benthic communities.

To construct text-fig. 2, only genera that occur as 10% or more in more than one collection were selected for inclusion. The total distributions of these genera in all thirty collections are shown, so that the relative abundance and community ranges may be seen at a glance. Superimposed on the community structure are some distributions caused by local clumping. To eliminate these random effects we do not show forms that occur as over 10% in only one collection, and these are the brachiopods *Dolerorthis* (10% in Collection 11), *Isorthis* (11% in Collection 9), *Salopina* (10% in Collection 9), *Brachyprion arenacea* (16% in Collection 12), and '*Meristina*' *furcata* (12% in Collection 13), and the bryozoan *Hallopora* (16% in Collection 16).

From text-fig. 2 it can be seen that the community range of each taxon varied widely both in selectivity and abundance, from *Pentamerus*, which is rare outside its named community but very abundant within it, through *Atrypa*, which occurs in the *Eocoelia* to *Clorinda* communities but with a weak indication of an abundance maximum in the *Pentamerus* and *Stricklandia* communities, to streptelasmatic corals, which (apart from their absence in the *Lingula* and part of the *Eocoelia* communities) are widespread throughout the rest of the community spectrum with little indication of an abundance maximum. Although the brachiopod diversity increased steadily up to the *Clorinda* community, the largest brachiopods are to be found in the *Pentamerus* and *Stricklandia* communities; not just the eponymous pentamerides but the bigger strophomenides such as *Leptostrophia* and the larger species of *Leptaena* and also the larger specimens of atrypids. We have no quantitative data on the biomass involved, but from our collecting we would estimate that these mid-shelf communities appear to have been the areas representing the optimal conditions for the growth of large brachiopods, in contrast to the higher-energy shallower environments on the one hand and the relatively plankton-starved deeper water on the other. Further aspects of the size and feeding efficiency of some Silurian brachiopods were considered by Fürsich and Hurst (1974).

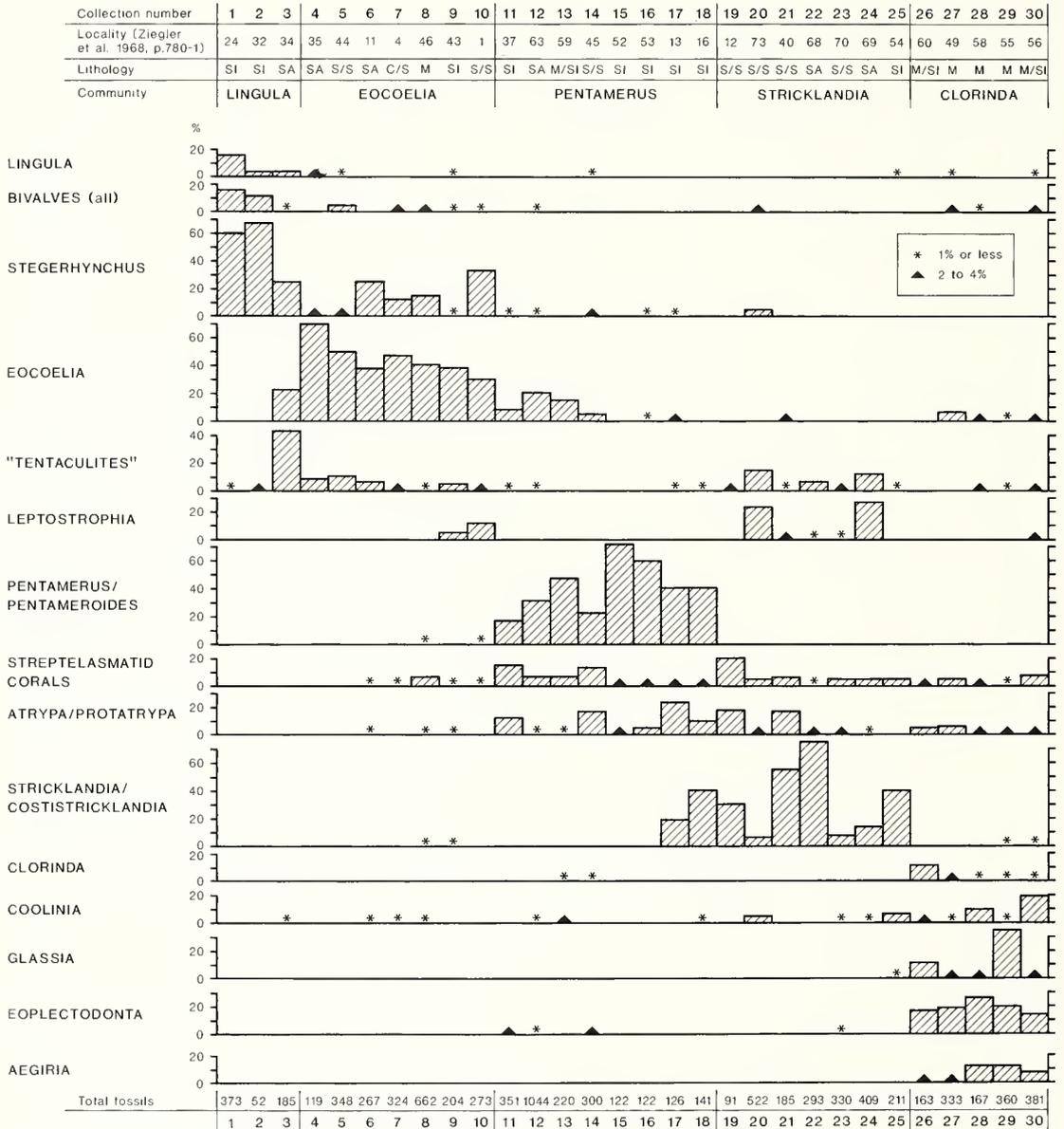
The Llandovery communities are made up of an agglomeration of animals, each of which had a distinct but specific tolerance to a range of marine bottom conditions, but which do not appear to have had any marked degree of mutual interdependence. Of course there are exceptions, for example, some of the bryozoans and cornulitids needed larger shells for their attachment, but most of the individual brachiopods, trilobites, molluscs, corals, and other larger benthos would have been unaware of, and independent from, their neighbours. The normal relationships between interdependent members of the same community today are either as successive members of a food chain or as providing shelter or anchorage. In the Llandovery most food chains were not long; the vast majority of the fauna were suspension feeders or deposit feeders. The numbers of predators and scavengers was probably small, and confined to echinoderms, cephalopods, a small minority of arthropods such as eurypterids (not phyllocarids, *contra* Watkins 1979, p. 249), and, perhaps, some soft-bodied worms. The gastropods present were all archaeogastropods which were almost certainly algal grazers or to a lesser extent deposit feeders; there are no confirmed predatory gastropods of Silurian age. Thus the distribution of the sedentary benthos must have been controlled partly by the availability of food and partly by physical factors (Fürsich and Hurst 1974). When two or more species persistently occur together, particularly in substantial numbers, then this indicates that the external parameters would have been suitable for them all, but this does not mean that they need have been biologically interdependent.

Relationships with depth and sediment type

Since the work of Ziegler (1965) there has been dispute as to the extent to which the distribution of Llandovery communities is (a) depth related and (b) dependent on sediment type. Let us examine these in turn. Critics such as Watkins (1979, p. 250) have pointed to the discrepancy between the interpretation of Ziegler *et al.* (1968*b*, fig. 13), which shows a smooth gradient across the late Llandovery shelf and communities, and the subsequent sedimentological work of Bridges (1975, fig. 11*A*), which shows a more varied gradient, and in particular an emergent Longmynd spur in Shropshire at that time. In fact a situation such as the latter was explicitly envisaged by Ziegler *et al.* (1968*b*, caption to fig. 12). Their fig. 13 was inevitably generalized, but an analysis of the sediments

and faunas round the Longmynd shows that they do yield progressively more off-shore ecogroups in each section as the transgression proceeded.

The best proof that the Llandovery communities were depth-related comes from the studies of eustatic changes in Silurian sea levels (McKerrow 1979; Johnson 1980; Johnson *et al.* 1981; Colville and Johnson 1982). The mere fact that these studies show that the communities shifted seawards or shorewards synchronously on the various different palaeocontinents indicates conclusively that the water depth and the communities are directly linked, and that the sequence of ecogroups is



TEXT-FIG. 2. Commoner taxa in thirty collections from the late Llandovery of the Welsh Borderland (only taxa occurring as more than 10% in two or more collections are included). The collections are attributed to the various animal communities described in Ziegler *et al.* (1968a).

everywhere the same during late Llandovery time. Of course depth is not directly linked to distance from shore—the width of the community bands seen in the central and eastern United States can be over 200 km per community, a tenfold increase over many of the band widths seen in the Welsh Borderland.

The actual depths involved have been debated. Ziegler (1965) calculated from the displacement of communities by lava flows in Pembrokeshire and Gloucestershire that the depth ranges were in 'tens of feet rather than hundreds of feet', but more rigorous field work in the same areas left these conclusions doubtful. Hancock *et al.* (1974) postulated depths of up to 1500 m for later Silurian communities, although this view was subsequently modified by Hurst (1976) after Shabica and Boucot (1976) had pointed out that the cephalopods were not imploded in the deepest assemblages, indicating that the maximum depth range was probably less than 600 m.

We incline to a shallower figure. The distinctive porous coenosteoid structure of heliolitid corals is also found in Recent scleractinian corals (B. R. Rosen pers. comm.), but amongst which it is confined almost exclusively to zooxanthellates, i.e. those corals that are symbiotic with dinoflagellate algae (Rosen 1981). Zooxanthellate corals do not live in depths greater than 240 m and the vast majority of genera live in water shallower than 100 m (Rosen 1977). In the Silurian, heliolitids are most common in carbonate bioherm environments, but they are a subsidiary element of the tabulate coral fauna (text-fig. 1c) in clastic environments, being recorded from the *Eocoelia*, *Pentamerus*, and *Stricklandia* communities up to Collection 23 of text-fig. 1, 2. This suggests that the *Stricklandia* Community inhabited depths of less than about 200 m, and probably even less than 100 m, leaving only the *Clorinda* Community as a candidate for deeper water in Llandovery times. Offshore of the *Clorinda* community the diversity and abundance of shelly benthos drops rapidly (the Marginal *Clorinda* Community of Cocks and Rickards 1969). Although it is dangerous to compare the relative widths of community band distribution, such a comparison in the Welsh Borderland indicates that the *Clorinda* community is unlikely to have occupied substantially more space and width on the sea-floor than the *Stricklandia* community, and thus a total depth range of not more than 250 m and perhaps less than 150 m seems the most likely. If it was greater then the community shifts caused by eustatic changes in sea-level would indicate that the real figures for the rising or lowering of the water would have been improbably high; for example, if the *Clorinda* community had really occupied a depth band of from 200 m to 600 m, then a 400 m rise in sea-level (which could have been caused by a combination of eustasy and local tectonics) would have been needed to change from the *Stricklandia* to the Marginal *Clorinda* communities, a shift seen in many other places as well as the Welsh Borderland. It would seem that this is less probable than the more modest changes needed if it were postulated that the total *Lingula* to *Clorinda* community depth range was less than 200 m.

Brenchley and Cocks (1982, p. 807) also concluded that the depth spectrum of the latest Ordovician communities found in the Oslo region, Norway, was unlikely to have been much more than 100 m; this figure was based both on an analysis of the sedimentological structures present and also on estimates of the depth differences likely to have been involved in the contemporary glacio-eustatic fall in sea-level.

In normal non-glacial littoral and sublittoral environments today the clastic sediments found can be of any grain size from cobbles to mud, but towards the deeper parts of the shelf (in areas not subject to major tectonic activity) the coarser fractions are progressively eliminated such that only silt and mud are common at the outer shelf margin. On text-fig. 2 we have indicated the sediment type for each of the Llandovery collections and these range from conglomeratic sandstone (C/S) through sandstone (SA), silty sandstone (S/S), siltstone (SI), muddy siltstone (M/SI) to mudstone (M). It can be seen that, although there is a higher proportion of mudstones in the *Clorinda* community collections, nevertheless there is a very poor correlation between sediment type and individual communities, an obvious example being the *Eocoelia* community which has been found in the widest variety of sediments from conglomeratic sandstones to mudstones. The same applies to individual species and genera, e.g. *Stegerhynchus* (text-fig. 2). Of course this does not mean that all benthic animal communities are or were substrate independent, but merely that the dominant shelly benthos of Llandovery age, such as brachiopods, corals, and tentaculitids, were mostly epifaunal, and,

assuming that a suitable spat attachment surface had been found, the individuals were tolerant of a wide range of substrates. Infaunal forms and burrowers would have been more likely to have been sediment specific, but these were not common in Llandovery time, and even lingulids have been found in a wide range of sediment types and grain size. Trilobites, on the other hand, appear to have been more directly linked to particular substrates in some cases, but no trilobite is recorded at more than 5% in the thirty collections (*Warburgella* in Collection 30 and *Phacops s.l.* in Collection 23), and only *Encrinurus* and *Dalmanites* are known from many of the shallower-water localities. Some trace fossils are also considered to have been related to bathymetry (Seilacher 1967).

It is difficult to assess the effect of varied turbulence on the animals present. The greater the water turbulence the greater the food supply, but the greater the strength needed for pedicle attachments, holdfasts, etc., which was probably a direct factor in the distribution of some of the more common taxa. Most strophomenides, for example, thrived best in lower energy environments, and the large pentamerides were clearly less vulnerable to wave damage in the middle part of the shelf, particularly since their pedicles were no longer functional as adults. The effects of turbidity are better known. Most brachiopods can clean any excess sediment from their lophophores, unlike most bivalves, whose gills become clogged fairly rapidly (Steele-Petrović 1975). Corals can also survive after fairly turbid episodes, although they will be killed if the sediment covers the polyps completely.

Comparison with communities of other ages

It is instructive to compare the Silurian palaeoecological regime with those both earlier and later. In the Cambrian, although most communities are dominated by trilobites and are thus related to sediment type, brachiopods appear to have chiefly occupied a single, relatively shallow-water community niche, with the middle to deeper shelf inhabited mostly by other phyla. During the Ordovician there was a gradual spatial expansion of brachiopods, crinoids, and corals. Lockley's review (1983) suggests in the text that Ordovician communities were very sediment specific; however, the actual data that he presents (1983, text-fig. 6) only loosely bears out his assertion in that just 5 out of 24 communities are found in a single sediment type, and the remaining 19 occur in two or more sediment types, and, moreover, Lockley's sediment categories are very broad. It seems more probable that, at least in post-Arenig times, the distributions of Ordovician brachiopods were also depth-related in a general way. Certainly by late Ashgill times, the associations were distributed in a regular order across the shelf, as can be demonstrated in the well-preserved regressive sequence seen around Oslo, Norway (Brenchley and Cocks 1982); and because the shelf sediments there are so similar throughout (mostly varieties of lime-mud), some other factor more directly related to water depth must be invoked to account for the community distribution.

After the Llandovery there were changes in the community structure, partly due to extinctions of some of the dominant forms, which resulted in changes in the relative abundances of certain families and genera; Calef and Hancock (1974), Hurst (1975), and Watkins (1979) have described these later Silurian communities. During the Devonian, bivalve autecology underwent a dramatic change to exploit many more infaunal as well as semi-faunal and epifaunal habitats. From that time onwards molluscan-dominated benthic communities became much more common than hitherto, and the infauna much more dominant than the epifauna. Some Silurian ecogroups, such as the shallow-water lingulid-rhynchonellid associations, persisted into Carboniferous or even later times, but the complete spectrum of brachiopod-dominated communities across the entire shelf is seldom fully developed after Devonian times. However, the autecology of individual brachiopod genera and species continued to evolve so that they could live in every-increasing absolute water depths, culminating in the abyssal forms known living today; although even now most brachiopods live in water shallower than 200 m.

The time from the later Ordovician to the Devonian was that in which the brachiopods were the dominant forms of shelly benthos across the widest variety of habitats, and thus this was the period when brachiopods can be used as indices for the whole spectrum of level bottom clastic communities. It is these communities that were more directly depth related, in contrast to some others in earlier and later times.

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GROWTH ANALYSIS OF SILURIAN ORTHOCONIC NAUTILOIDS

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ABSTRACT. Evidence from orthocone septal strength implies approximate depth limits of 200 m for the near-shore dwelling actinocerids, 500 m for large orthocerids, and no more than 1500 m for the small pelagic orthocerids found in 'graptolitic shales'. These estimates refer to the initial depositional depth of fully septate conchs; not the habitat depth of pelagic species, nor the occurrence of fragmented and reworked specimens. The further interpretation of the autecology of the large orthocerids must be based either on the distantly related, coiled genus *Nautilus*, or their large coleoid descendants. Studies of the growth rate of large orthocerids test their ecological similarity to large predatory coleoids. Cycles of lirae spacing in *Geisonocerina*, annulation amplitude in *Dawsonoceras*, and septal spacing in a variety of Silurian orthocones, show annual periodicities implying growth rates of about 100 mm per year. Large conchs with a length of 1.0 to 1.5 m had a protracted growth phase for over fifteen years, followed by at least one year as a slowly growing mature stage. The adolescent increase in body weight and mantle cavity volume is even less than that of *Nautilus*, suggesting little ecological similarity to coleoids.

ALTHOUGH the depth limits (Table 1) and swimming position of orthoconic nautiloids can be estimated from their shell morphology (Westermann 1973, 1977), it is difficult to interpret other aspects of their autecology. Perhaps the main dilemma results from their greater phylogenetic affinity with descendant lower Devonian to Recent coleoids (Bandel *et al.* 1983), than the primitive *Nautilus*. Although *Nautilus* resembles the coleoids in being a voracious predator (Saunders *et al.* 1978), it is not well equipped for rapid swimming by jet propulsion, diurnal or other rapid changes in depth, and visual capture of prey (Packard 1972, p. 292; Chamberlain 1981; Ward *et al.* 1981). Hewitt and Watkins (1980) pointed out that the small body size and mantle cavity volume of most pelagic orthocerids are inconsistent with interpretations involving intelligent and highly mobile, squid-like predators (McKerrow 1978; Gould 1983, p. 249). But the 0.5 to 3.0 m long orthocones found in relatively inshore Silurian facies are consistent with this autecological reconstruction.

This latter hypothesis was tested and rejected by an esoteric approach based on the view of Packard (1972) and Chamberlain (1981), that the volumetric increase in the mantle cavity during ontogeny was of paramount importance to cephalopods which capture prey, or avoid the cannibalistic attentions of their larger relatives, through efficient jet propulsion. Although *Nautilus* moves by jet propulsion, it has not developed the rapid escape reactions of coleoids and presumably obtains protection from an external shell and retiring habits. These and other ecological differences between Recent cephalopods are evident from their growth rates. One *Sepia* species probably grows a 0.5 m long shell and 10 kg body within two years (Packard 1972); but the tiny mesopelagic *Spirula* has a similar growth period. It grows about twenty chambers per year (deduced from Clarke 1970) compared to up to one per day in *Sepia* (Choe 1963). Cochran *et al.* (1981) and Ward *et al.* (1981) imply that *Nautilus* grows five to sixteen chambers per year, over a period of two to six years required to attain a body weight of about 0.5 kg. The growth rate and population turnover of the larger squids is sometimes even faster than that of *Sepia*, but there appears to be little reduction in growth rate due to shell formation (Packard 1972). Small cephalopod species, with inferior or redundant jet-propulsion adaptations, have a slow growth rate. If it can be shown that the large Silurian orthocerids had a growth rate which is equal to, or less than, that of *Nautilus*, it may be reasonably assumed that the ecological diversity of coleoids only developed after they lost the external shell of their ancestors.

TABLE I. Strength indices of Carboniferous phragmocones calibrated by the penultimate chamber of *Nautilus* to estimate implosion depths. Terminology after Westermann (1977, 1982). The isotropic phosphate connecting rings in *Goniatites choctawensis* Shumard came from the same shale as brown sparry calcite connecting rings of *Bactrites quadrilineatus* Girty (Mapes 1979, sample M1). *Rayonoceras* (M21-2 and M26) has a perispatium cemented with pyrite and isotropic phosphate, surrounded by inner sparry calcite and brown prismatic layers. These actinocerid rings were calculated as spherical membranes. The 'horny tubes' of Buckhorn Asphalt orthocerids are composed of bituminous aragonitic laminae. Despite these differences from the *Nautilus* 'horny tube', there is a correlation between connecting ring and septal strength indices. The proportion of nacre in the shell thickness δ_w is nac. %. The δ_w and septal spacing Δ of coiled shells refers to the venter, and their r_1 is half internal whorl height.

Genus * = from	Connecting ring				Septa					Shell wall		
	h μm	r μm	$100h/r$	Depth m	Depth m	δ_s μm	R mm	$1000\delta/R$	Δ mm	δ_w μm	nac. %	r_1 mm
Westermann (1982)												
<i>Rayonoceras</i>	155	7300	2.1	260	200	133	22.7	5.9	17.5	1067	67?	20
<i>Rayonoceras</i>	78	2700	2.9	360	264	68	8.7	7.8	4.7	530	64?	9
<i>Nautilus</i>	*74	*480	15.4	955	559	210	12.7	16.5	7.3	440	60	14
<i>Nautilus</i>	*150	*1160	12.9	800	800	778	33.0	23.6	26.0	910	75	48
<i>Bactrites</i>	78	456	17.1	1060	610	178	9.9	18.0	5.4	325	70?	7.65
' <i>Pseudorthoceras</i> '	27	157	17.1	1060	712	29	1.4	21.0	1.3	67	41	1.28
<i>Goniatites</i>	16	89	18.2	1129	—	7	—	—	0.8	34	—	0.38
<i>Mitrothoceras</i>	85	355	23.9	1482	1469	117	2.7	43.4	4.6	440	57	2.26
<i>Goniatites</i>	21	64	30.6	1900	—	6	—	—	—	54	—	0.22

The *Nautilus* chambers measured by Denton and Gilpin-Brown (1966) increased in volume at four times the exponential rate of the larger chambers of the 1.5 m long Ludfordian orthocerid measured by Hewitt and Hurst (1983). Since the latter taxon ('*Orthoceras*' *ludense* J. de C. Sowerby, resembling '*O.*' *alienum* Hall) increased the shell volume to balance the weight of both the body and posterior aragonite deposits, it is evident that either the body grew slower than in *Nautilus* or that over twenty to sixty-four chambers were added per year. But the evidence for a cycle of ten orthocerid chambers per year (Hewitt and Hurst 1983), supported here by additional studies, indicates that they were added at a similar rate to *Nautilus*. This conclusion that large Silurian orthocones had a slower increase in body weight than *Nautilus*, is related to the controversy over the use of ornamentation in growth-rate studies (Pannella 1972, 1975; Kahn and Pompea 1978; Pompea *et al.* 1979; Saunders and Ward 1979; Hewitt and Watkins 1980; Hughes 1981; Doguzhaeva 1982).

Orthocone morphology cannot be analysed purely as adaptative autecology, physiology, environmental cycles, or life history. It is, however, difficult to explain the major growth cycles of large orthocerids, except by seasonal growth-rate changes.

Since the annual growth cycles of *Sepia* are not sinuous it is preferable to analyse septal spacing and external lirae spacing by autocorrelation analysis. The method is discussed by Davis (1973, pp. 225-226) and the problems of analysis of nautiloid growth increments are reviewed by Hewitt and Hurst (1983). Briefly, the increment lag with the most significant parameter Z_L (which should be greater than 1.96) indicates the likely wavelength or repeat distance of a cycle. The parameter Z_L is only valid when the lag is less than one-quarter of the analysed series of growth increments and when there is no trend in the data. The latter can be standardized to remove ontogenetic trends, or larger growth cycles. Specimens are in Bristol Museum (BRSMG), Birmingham University (BU), Greene Memorial Museum (GMM), Milwaukee Public Museum (MPM), Field Museum (PE), Redpath Museum (RM), and McMaster University (S). Shell diameter was calculated from circumference.

CYCLIC VARIATIONS OF LIRAE SPACING

Kahn and Pompea (1978) admitted only three exceptions to their speculative thesis that orthocones grew eight to sixteen diurnal external transverse lirae (ridges) per synodic monthly chamber. Two were small aragonitic longicones from the Carboniferous Buckhorn Asphalt, i.e. *Mitorthoceras* (= '*Orthoceras unicamera* Smith') with forty-five lirae overlying each chamber and '*Pseudorthoceras knoxense* (McChesney)' with thirty lirae overlying each chamber. They proposed (p. 608) that these were unusual in being restricted to a 'shallow shelf and inland sea habitat (50–100 m depth)'. The criteria of Westermann (1973), cited by Kahn and Pompea (1978), shows that *Mitorthoceras* may have had the deepest-known nautiloid habitat (Table 1) and imply that only imploded or reworked nautiloids occur in strata deposited at depths much in excess of 1500 m.

A series of 315, 103 μm wide lirae, were studied in a 5 mm diameter *Mitorthoceras*. They averaged 44.8 per chamber in thin section. Asymmetric lirae of alternating amplitude grade into zones of narrow rounded lirae defined by striae. They originated as spherulitic prisms, radiating outwards from the nacreous layer of the shell wall. These 'cameral cycles' have thirty-four to seventy-nine increments (mean 55.4). Mural deposits formed over an interval of five to six cameral cycles (Crick 1982), and consist of 219 layers flanked by an outer translucent zone (180 μm) of seventeen layers, implying about one layer per lira. The siphuncle 'horny tube' has about twenty laminae per chamber. A retreat of the apertural mantle formed a high-amplitude lira passing into a translucent band within the outer prismatic layer. Five minor 'breaks' in growth were identified from the occurrence of these bands. They are associated with the narrow rounded lirae; but the retreat structure initiated the growth of asymmetric lirae. The number of lirae between breaks is: 87+, 4, 25, 8, 71, 4, and 115+.

The deep-water orthocerid displays gradational cycles of lirae spacing related to the internal layers of the conch, interrupted by mantle retreat events which may result from migration events. The latter should not be confused with unconformities defined by the pattern of the lirae, resulting from wounds or other local damage to the apertural mantle (Saunders *et al.* 1978, p. 138), and concentrated in mature growth stages.

Geisonoceria wortheui (Foerste) attained a diameter of 89 mm and a length of 1.48 m in the dolomites of the Telychian Brandon Bridge Member of Wisconsin (MPM 26360). A 558 mm series of 903 rounded lirae, defined by oblique external striae, was measured between diameters of 14 and 45 mm (MPM 25357 from Old Burlington Quarry, east side of White River). The lirae do not enlarge in proportion to the shell diameter, implying that fourteen were grown per chamber at the posterior end, compared to forty-five anteriorly. The anterior sutures and 180 mm long apex are missing. Unconformities occurring at an interval of 500 lirae increased lirae spacing. There are significant periodicities of eleven ($Z_L = 4.5$), nineteen ($Z_L = 4.3$), and ninety-four ($Z_L = 2.6$) lirae. The latter are related to eight major cycles of 110 ± 30 lirae defined by the variation in average lirae spacing within the shorter 'cameral cycles'.

An average of 6.32 festooned, 98 μm wide microlirae occur between the striae at the posterior end of this specimen, where there are bimodal cycles of twenty-one lirae ($Z_L = 2.5$) and a probable seasonal cycle of 128 lirae. If the poorly preserved microlirae are semi-diurnal they suggest that the periodicity of the lirae varied from 1.75 to 4.5 days.

Offshore Gorstian *G. recticinctum* (Blake) had a maximum diameter of 13 mm and a length of 150 mm. They show a similar ornamentation to *Mitorthoceras*. The external mould from Llangammarch Wells cited by Hewitt and Watkins (1980, p. 107) has cycles of lirae spacing with a lag of 18.0 ($Z_L = 3.87$ from 109 lirae). The 3 mm long cycles have a diameter of 2 to 4 mm. A series of eighty lirae (Watkins sample 214) show cycles of 31.17 lirae (lags 30 to 32 with $Z_L = 2.5$ to 2.6). The 7 mm long cycles have a diameter of 1.5–3.0 mm. They are too long to be 'cameral cycles' and give a plausible estimate of the number of solar days per synodic month.

CYCLES OF SEPTAL SPACING

Ludlow age longicones from Sardinia show minor cycles of septal spacing. *Sphaerorthoceras* (Serpagli and Gnoli 1977, pl. 4, figs. 2, 5, 6) contains six cycles between diameters of 0.7 and 4.0 mm. The mean wavelength/diameter ratio (4.7, range 3-9) differs from the mean periodicity of 9.27 chambers in showing no increase during ontogeny. *Arionoceras affine* (Meneghini) has a 30 mm long cycle of nine chambers at diameters of 5 to 10 mm (Serpagli and Gnoli 1977, pl. 6, fig. 4); but *A. submoniforme* (Meneghini) displays four cycles of four chambers (3-4 mm wavelength) between diameters of 1.3 and 3.4 mm (Serpagli and Gnoli 1977, pl. 7, fig. 2).

Typical cycles occur in the Waukesha and Racine Dolomites at Lannon, near Milwaukee. A 24 to 48 mm diameter *G. wauwatosense* (Whitfield) from the upper 0.04 m of the former horizon showed three cycles of eight chambers (mean length 91.2 mm and about ninety lirae). *Protokionoceras* from a 2 m 'Lannon Stone' section showed a 174 mm long cycle of nine chambers (diameter 21 to 25 mm); but more breviconic *Kionoceras* had six cycles of 4.1 chambers (32 to 51 mm diameter).

Kolebaba (1977, fig. 2) illustrated an asymmetric cycle of twenty-five chambers in a Gorstian *Vericeras ambigena* (Barrande) (diameter of 1.0 to 4.5 mm, length 21 mm). An '*O.*' *ludense* (Hewitt and Hurst 1983, fig. 4) has an asymmetric cycle of twenty-one, a major cycle of thirty-eight, and minor cycles of ten chambers. If the minor cycles are annual, they imply a growth period of ten to twelve years for 50 mm diameter longicones. This average growth rate is consistent with the growth period of ten years implied for 0.75 m long individuals of *G. wortheni* by lirae cycles. The 1.5 m long individuals of the two species were probably fully grown within twenty years and had a body weight of at least 1 kg.

SIGNIFICANCE OF ORNAMENTATION

Dawsonoceras has oblique annulations, ornamented with festooned transverse lirae forming 70 μm thick flanges. Lirae spacing is reduced over the thickened crests of the higher amplitude annulations. The annulation wavelength, which is also septal spacing, increased in proportion to the shell diameter until the diameter reached 30 mm, but then remained at 7-10 mm. Hughes (1981) found lirae composed of numerous lamellae. If the striae seen between lirae in annulation troughs define semi-diurnal increments, then these lirae formed in three solar or lunar days within a low-amplitude annulation with nine lirae, compared to 4.5 solar days in high-amplitude annulations with seven lirae. The implied monthly production of annulations was tested by assuming that the cycles of annulation amplitude had a seasonal origin.

The diameter of this 185 mm long increment increased from 38 to 50 mm. The twenty-one (BU Holcroft collection 56) annulations have an average of 7.1 lirae. The spacing of 158 lirae (up to fifteen measurements per lira at $\times 50$) and the distance between the base of each lira and a ruler attached to the annulation crests, were used to calculate their diameter and cross-sectional volume (excluding flanges). The diameter lags of six ($Z_L = 8.7$) and twelve ($Z_L = 6.6$) lirae, corresponded to lags of six ($Z_L = 6.9$), twelve ($Z_L = 2.8$), and thirteen ($Z_L = 3.3$) lirae obtained by volume. Their weighted first harmonic was 6.14. Longer periodicities with Z_L over 1.96 have a weighted mean of 84.52 lirae; but the most significant lag is ninety lirae (Z_L of 4.4 by volume and 3.0 by diameter). A smoothed moving average showed volume growth maxima separated by a 116 mm length of 97.5 lirae and 13.21 annulations.

This seasonal cycle has four low amplitude annulations (35 mm length) with a mean of 9.25 lirae, compared to 6.67 lirae in the remaining high amplitude annulations resulting from optimum growth. Similar cycles were seen in eight *Dawsonoceras* (Table 2). Racine Dolomite specimens show sixteen other cycles of annulation amplitude, with a mean of 9.50 annulations. Of these only the Dudley specimen (56) encrusted by *Halysites* and the Sussex specimen from a fissure in a bioherm without corals, grew one annulation per month. Adding together long specimens from these and other localities, we arrive at an estimate of 132 annulations between diameters of 3.8 and 57.3 mm. Conch

length increased at a single linear growth rate over the last ninety-three annulations, representing 780 mm out of a total length of 975 mm (another has forty-nine expanding annulations in 427 mm).

The existence of cyclic variations in ornamentation restricts the scope of functional interpretations of structural elements, camouflage patterns, and devices for reducing drag by increased surface roughness (Chamberlain 1981, p. 299). A depth limit of 500 m, implied by the septal strength index of Indiana *Dawsonoceras* (Laurel Member, Flower 1962; $\delta_s/R \cdot 1000 = 15$) appears excessive for life over epicontinental carbonate facies. *Dawsonoceras* from the argillaceous Rochester and middle Elton formations display unusually low annulations and narrow lirae. Thus if there was any advantage in the development of annulations, it was likely to be related to the greater value of camouflage over limestone facies than in dark, turbid environments.

The apertural end of a large specimen from argillaceous dolomite (RM 2644) shows a well-defined zone of 109 narrow lirae without annulations. This observation and the general tendency of mature nautiloids to show a greatly reduced septal spacing, suggests that the low amplitude phases of the growth cycles represent a less extreme reduction of growth rate than that associated with maturity. In contrast, the vast majority of coleoids grow rapidly, breed once, and then die (Packard 1972). The 1 m long *Dawsonoceras* grew at a slow and periodically variable rate for about fifteen years, grew even more slowly when mature, and may have lived longer without increasing body weight. The growth and breeding characteristics of coleoids are not a primitive trait.

It is not clear whether the cycles resulted from seasonal migrations between two different environments; or local changes in temperature, hydrography, and food supply through the year. The paucity of abrupt changes in growth and apertural unconformities supports the latter view. A sedentary life as benthonection would explain variation in growth cycles and ornamentation between localities (Table 2) and the problematical stratigraphic value of *Dawsonoceras* 'species' defined by gradational variations in these characters. Flower (1942, 1962) reviews some of these difficulties.

This interpretation is consistent with the evidence from lirae spacing and septal spacing in less-ornate orthocerids. Together they imply a mode of life combining the buoyancy of *Nautilus* and the

TABLE 2. *Dawsonoceras* show variation in their lirae/annulation ratio (L/a on left) which is not a function of mean diameter (dia.) or diameter/annulation wavelength (dia./ A). Cycles defined by L/a were one to four times longer than their diameter (Yr/dia.). Specimens are from: Homeric limestones of Dudley (BU Holcroft Collection 33, 56, 76; Ketley Collection 476); Sheinwoodian shales of Rochester Formation at Lockport (RM '1138'); Sheinwoodian Waukesha Dolomite of Lannon (PE 18943, 19017) and Sussex; Racine Dolomite of Milwaukee (including GMM 12965, 12445, and a 26th Street Quarry specimen); Homeric Lockport Dolomite, all members in Hamilton area (BRSMG Cc829; RM 2644, 2648; S699). n = number of annulations in sample.

Sample	Annulation sample						Seasonal cycles					
	n	dia. mm	range mm	dia./ A	L/a	range	Sample	dia. mm	Yr/dia.	Cycle		
										L	a	L/a
Dudley	57	40	22-57	4.8	8-17	5-18	BU 56	47.5	2.4	97	13	7.4
							BU 476	26.5	2.5	81	9	9.0
Rochester	24	31	26-36	6.2	8-83	5-12	RM 1138	28.0	1.9	84	10	8.5
							RM 1138	31.5	1.1	65	7	9.3
Waukesha	43	29	21-38	3.5	9-21	4-16	Sussex	26	3.8	84	13	6.5
							Sussex	34	2.2	103	11	9.4
Racine	22	34	12-51	3.6	11-84	7-10	12965	31.0	2.3		8	7.0
							12445	41.5	2.2		10	10.5
							26th st.	48.8	1.4		7	11.0
							RM 2648	40.6	2.2	112	9	12.4
Hamilton	48	39	19-45	4.4	13.00	9-23	RM 2644	44.6	1.5	74	5	14.8

swimming position of coleoids with the ponderous feeding behaviour of some carnivorous gastropods and arthropods. In addition, there were small orthocerid species, which probably drifted with the zooplankton rather than migrate like large squids.

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Note added in press. Although Landman (1984) has rightly questioned the assumptions of Doguzhaeva (1982), it would be unwise to base interpretations only on our present knowledge of *Nautilus*. A recent volte-face by Ward appears to have increased the chance that fossil nautiloids formed one or two growth increments per solar day, as a result of vertical migrations avoiding sunlight (Ward *et al.* 1984). The well documented migrations across the reef front in Palau and the lateral peregrination of one individual, recorded as 16 km in ten days, indicates that *Nautilus* is an active member of the benthonecton. Moreover, the life-span of seventeen to twenty years deduced by a questionable extension of growth rates seen in sub-mature *Nautilus* (Saunders 1984), is inconsistent with the evidence suggesting that a juvenile, barnacle encrusted *Nautilus* formed over sixteen chambers in 340 days (Landman 1983). But these debates do not seriously alter the above conclusions about Silurian nautiloids.

MODE OF LIFE AND AUTECOLOGY OF SILURIAN-DEVONIAN GRAMMYSIIDAE (BIVALVIA)

by L. F. MARSH

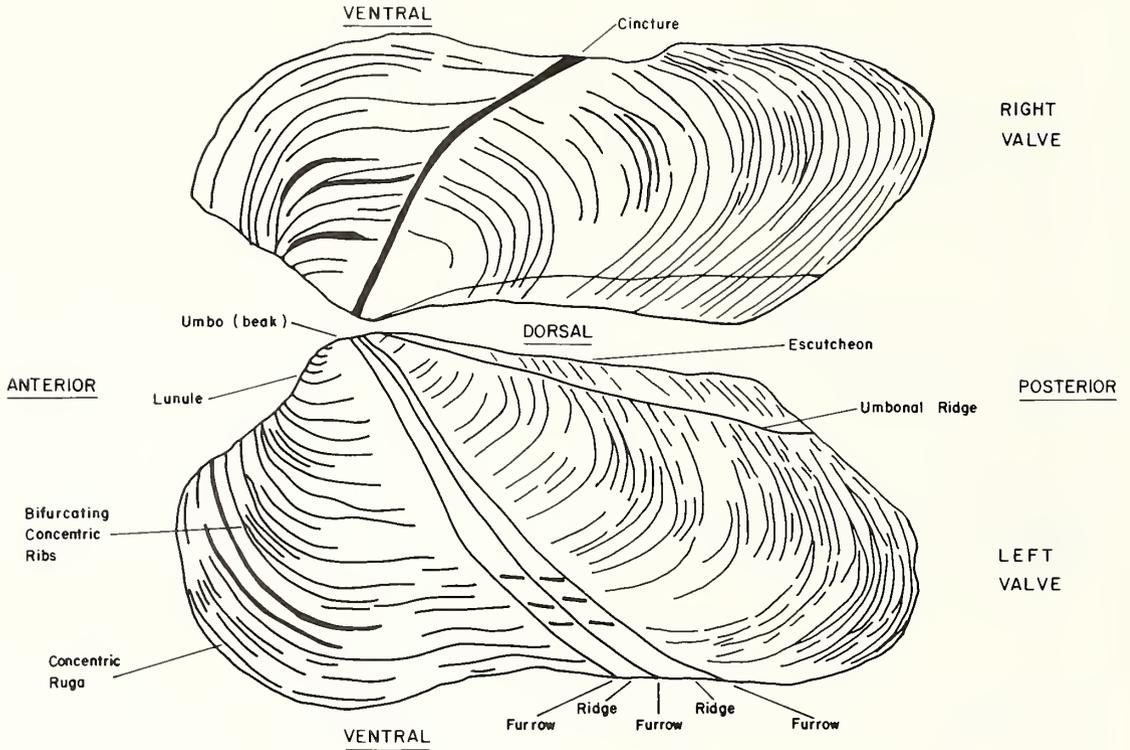
ABSTRACT. The Grammysiidae are a Palaeozoic family of mainly infaunal anomalodesmatan Bivalvia that lived in very shallow marine environments. Since they were edentulous, the problem of shearing of the valves during burrowing was overcome by the cincture (radial furrows and ribs), which folded the ventral margin. This folded venter provided an active saw during burrowing. Species that burrowed in very high-energy environments showed very marked ventral folding, strong concentric ribs on the anterior end, a fairly large anterior end, and usually a disc-shaped, not highly inequilateral, shell of low inflation. Byssally attached forms reduced the anterior end, expanded the posterior end, had a less folded venter, more elongate shell, lost the strong anterior concentric ribbing, and were more inflated. Shell form and ornamentation is related to the environment and mode of life.

BIVALVES of the Palaeozoic family Grammysiidae (largely Silurian and Devonian) belong to the subclass Anomalodesmata and, like most forms in this subclass, lack dentition. The main external morphological features of the family are shown in text-fig. 1. The most important characteristic is the radial cincture, composed of ribs and/or furrows which pass from the umbones to the ventral margin. The only inequality in the valves is in the form of the cincture. This differs in the two valves so that a rib on one valve alternates with a furrow on the other to cause the ventral margin to be folded (Pl. 60, fig. 3). The function of this is discussed further below. Most Grammysiidae also possess concentric, bifurcating ribs (text-fig. 1), a lunule, and an escutcheon. By comparison with modern bivalves (and particularly the work on modern bivalves by Stanley 1970), it is possible to ascertain the functional significance of the shell morphology in the Palaeozoic Grammysiidae.

MORPHOLOGY AND MODE OF LIFE

Since all species of the Grammysiidae show the greatest inflation in the dorsal to central part of the shell, they must all have been, at least partly, infaunal. The relationship between position of maximum inflation and mode of life in modern bivalves is shown by Stanley (1970, p. 27 and fig. 8). The Grammysiidae must also have lived close to the sediment surface, in permanent contact with the sediment-water interface, since none of them possessed a pallial sinus. Many species of Grammysiidae lived in the littoral zone and all species lived in very shallow water. Interpretation of the life environments are readily confirmed by sedimentary structures and lithologies as recorded, for example, by Potter and Price (1965) and Potter (1967, p. 280). Some species, however, lived in lower energy environments (Holland and Lawson 1963) and were not frequently exhumed. Consequently they appear to be more streamlined for permanent infaunal life. The morphology of some species indicates that they became infaunally or semi-infaunally byssally attached. All members of the Grammysiidae lack dentition. This would have presented problems to an active burrowing bivalve, since the valves would have sheared over each other during burrowing if some assistance to burrowing was not available. I consider that this lack of dentition, associated in most cases with active burrowing, led to the development of the radial and concentric ornament in most of the species. The radial cincture (ribs and furrows) combined with concentric ribbing would have provided an active sawing mechanism to aid rapid, repeated burrowing. Stanley (1970, p. 64) recognized the importance of the function of this type of ornament in modern bivalves. It is of note that the species

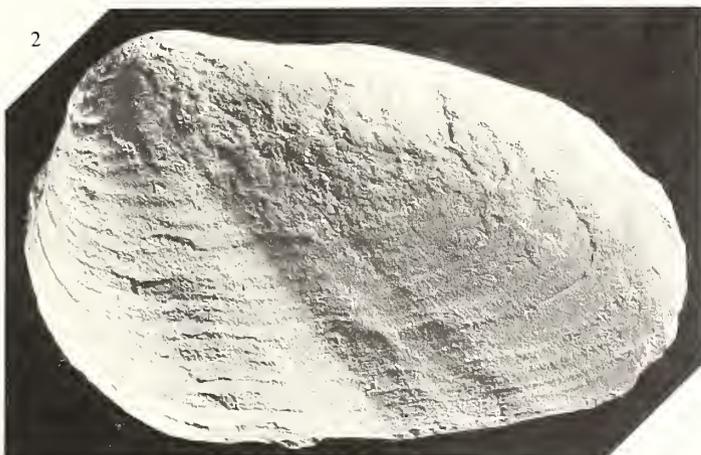
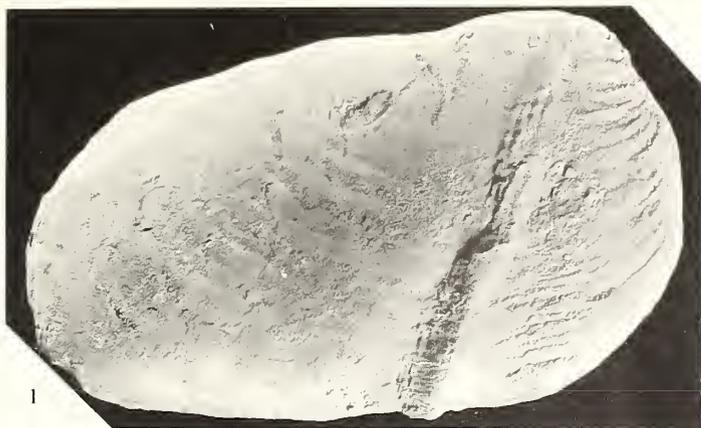
that lived in the higher energy conditions, and hence were more likely to be exhumed frequently, have better developed ornament, e.g. *Grammysia triangulata* (Salter) (Pl. 61, fig. 1; text-fig. 3k) and *G. grammysioides* (Salter) (Pl. 61, fig. 2; text-fig. 3p). The latter species also shows marked bifurcation of the concentric ribbing as an additional burrowing tool, as do *G. sp. nov. d.* (Marsh 1976, pp. 359-363, pl. 14, figs. 1-9; pls. 15-18; pl. 19, figs. 1-9) (herein Pl. 60, figs. 4, 5; text-fig. 3d) and *G. cingulata* (Hisinger) (Pl. 60, figs. 1-3; text-fig. 3c). The cincture alone folded the venter (Pl. 60, fig. 3) and would have provided a sawing mechanism. Most of the species of this family can be shown to have had a strong ligament to help prevent shearing of the valves, which would have occurred owing to the lack of dentition. Scars made by ligament attachment along the hinge line have been illustrated by Bambach (1971, p. 180, fig. 10).



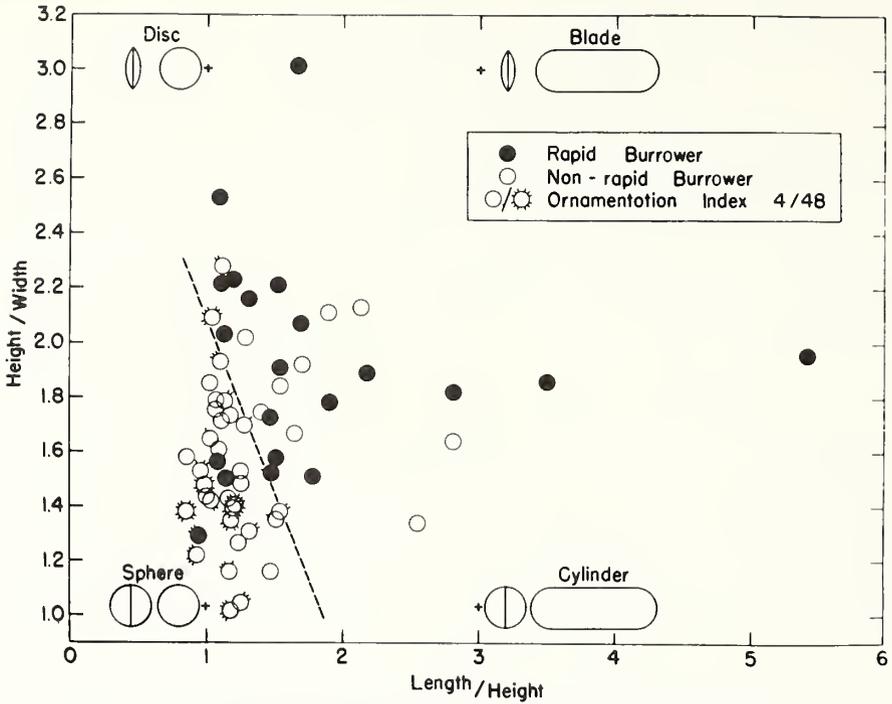
TEXT-FIG. 1. Main morphological features of Grammysiidae.

EXPLANATION OF PLATE 60

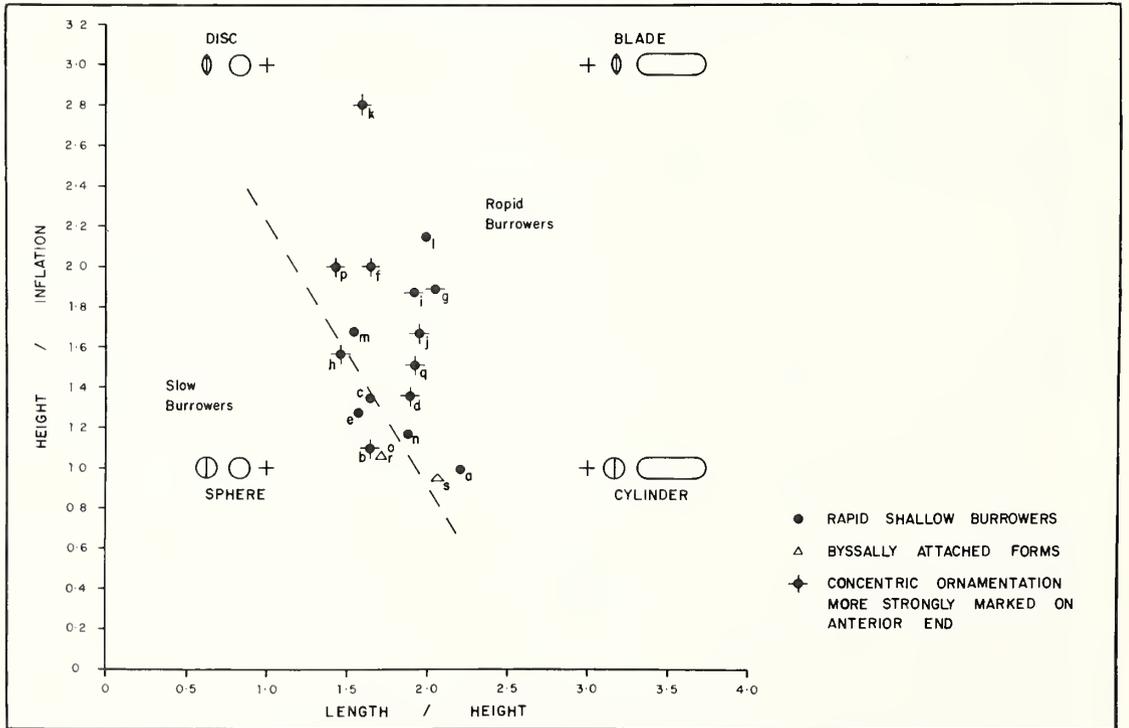
Figs. 1-5 = ancestral grammysiid species. Figs. 1-3, *Grammysia cingulata*, Much Wenlock Limestone, Formation, Dudley, BM L49130, right valve, left valve, and ventral view showing folding produced by the alternation of ribs and furrows of the cincture in each valve. Figs. 4, 5, *G. sp. nov. d.*, Much Wenlock Limestone Formation, Dudley, BU 276, 294, right and left valves. Figs. 6, 7, *G. sp. nov. o.*, Wenlock sandstone, Bryn Craig, Usk inlier, IGS 24217, right and left valves. All $\times 2$.



MARSH, Silurian *Grammysia*



TEXT-FIG. 2. Relation of burrowing rate to gross shell shape and shell ornamentation in recent bivalves (from Stanley 1970, fig. 25).



TEXT-FIG. 3. Relation of inferred burrowing rate to gross shell shape and shell ornamentation in Grammysiidae.

The shapes of the shells of Grammysiidae vary considerably. The shape of a particular species is a reflection of its mode of life and adaptation of the animal to its environment, as produced by natural selection. A change in the environment and, therefore, in the mode of life of a species resulted in a change in morphological features such as the shell form. Species evolved owing to selection pressure produced by environmental changes. In areas where environmental changes occurred speciation was much more rapid than in areas where environmental conditions were stable (Raup and Stanley 1971, p. 99). Bretsky (1973, p. 2090) recognized this in stating that '... the degree of morphological distinctiveness at any one time in the fossil record for a particular clearly defined ecological grouping probably reflects ... the degree of difference between local environmental settings'. A particular species of grammysiid thus survived in one area where the environment did not change and yet was replaced by different species in an area where the environment did change. Stratigraphical ranges of any one species thus vary considerably from place to place, being dependent on the environment. Grammysiid bivalves are therefore very good environmental indicators. It is common to find morphologically similar bivalves developed at different horizons owing to convergent evolution in unrelated species living in similar environments.

From the generalized, straight-hinged ancestors *G. cingulata* and *G. sp. nov. d.*, differently shaped species evolved as adaptations to different environmental conditions. Disc- and triangular-shaped forms, with concentric ribs much more strongly marked on the anterior end, evolved to cope with very high energy conditions and frequent exhumations. Other forms became byssally attached, lived in rather lower energy conditions and developed more elongated shells, and reduced the anterior end.

The relationship of shell form to mode of life in living bivalves was shown by Stanley (1970, p. 60, fig. 25) (herein text-fig. 2). Compare text-fig. 3 for the Palaeozoic Grammysiidae, which shows the positions of the type specimens of each of the grammysiid species. The more rapid burrowers have a high height/inflation ratio and high length/height ratio. They are therefore either disc- or blade-shaped shells. Concentric ornamentation more strongly marked on the anterior end also appears to assist burrowing speed. If, however, the shell shape itself allows extremely rapid burrowing, then the additional concentric ornament appears to be unnecessary, e.g. plot 1 of *G. extrasulcata* (Salter), an elongate shell with very low inflation.

From detailed biometric studies of Silurian-Devonian Grammysiidae, two groups which exhibit distinctive morphological features have been recognized. These are interpreted as follows:

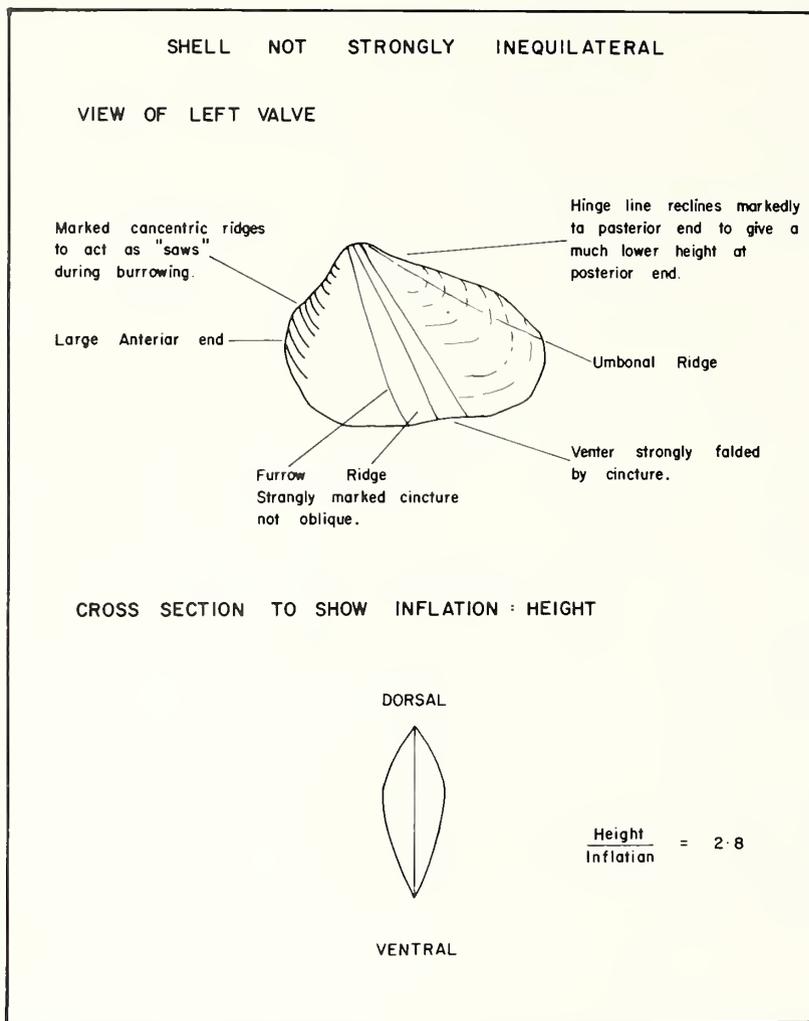
Group (i). Rapid, shallow burrowers (text-fig. 4).

Group (ii). Semi-infaunal, byssally attached species (text-fig. 5).

Group (i)

The shallow-burrowing Grammysiidae living in very high energy environments (where exhumation from the sediment during life is commonplace and, therefore, the ability to carry out rapid, repeated burrowing throughout life is a necessity) show a combination of the following morphological features (text-fig. 4):

- (a) A shell that is not highly inequilateral, to aid ease of rocking from side to side during burrowing.
- (b) A shell shape that is discoidal or triangular, or very elongate and of very low inflation.
- (c) A hinge line that is either strongly reclining towards the venter or parallel to the venter, not divergent (text-fig. 6, e.g. *G. triangulata*).
- (d) The greatest height of the shell at the umbones.
- (e) Low inflation.
- (f) High height/inflation ratio.
- (g) A large anterior end, to allow ease of penetration into the sediment as burrowing was initiated (text-fig. 7), e.g. *G. triangulata* to contrast with the byssally attached *G. obliqua*.
- (h) An anterior end furnished with strong concentric ridges (for sawing) that are either absent or are only very weakly marked on the rest of the shell.
- (i) A well-developed, strongly marked cincture that causes a very marked folding of the entire venter, to act as a sawing mechanism.
- (j) The valves usually found disarticulated and frequently broken.



TEXT-FIG. 4. Typical morphological features of the shell developed in rapid, shallow burrowing Grammysiidae, e.g. *Grammysia triangulata*.

EXPLANATION OF PLATE 61

Fig. 1, *Grammysia triangulata*, Whitcliffian, Kirkby Moor Flags, Benson Knot, Kendal, Cumbria, a rapid burrower in very high energy conditions, IGS 12487, left valve. Fig. 2, *G. grammysioides*, derived fossil in Triassic Budleigh Salterton Pebble Bed, SE Devon, specimen derived from Lower Siegenian, Devonian of Brittany, BM L15, 821, a right valve, another rapid burrower.

Figs. 3-6, *G. obliqua*, Ludlow, Usk inlier, a byssally attached species showing oblique cincture, very small anterior end, and greatest height of shell at posterior end. Fig. 3, IGS 12468, holotype, right valve. Fig. 4, NMW G482, left valve. Fig. 5, IGS G Sb 4225, dorsal view, showing dorso-posterior gape and scars of attachment of the strong external ligament along the escutcheon. Fig. 6, BM L 5438 (a) antero-ventral view, with anterior end uppermost, showing narrow antero-ventral byssal gape (bg) and folded venter (fv) near posterior end, produced by the alternation of the cincture in each valve. All $\times 2$.

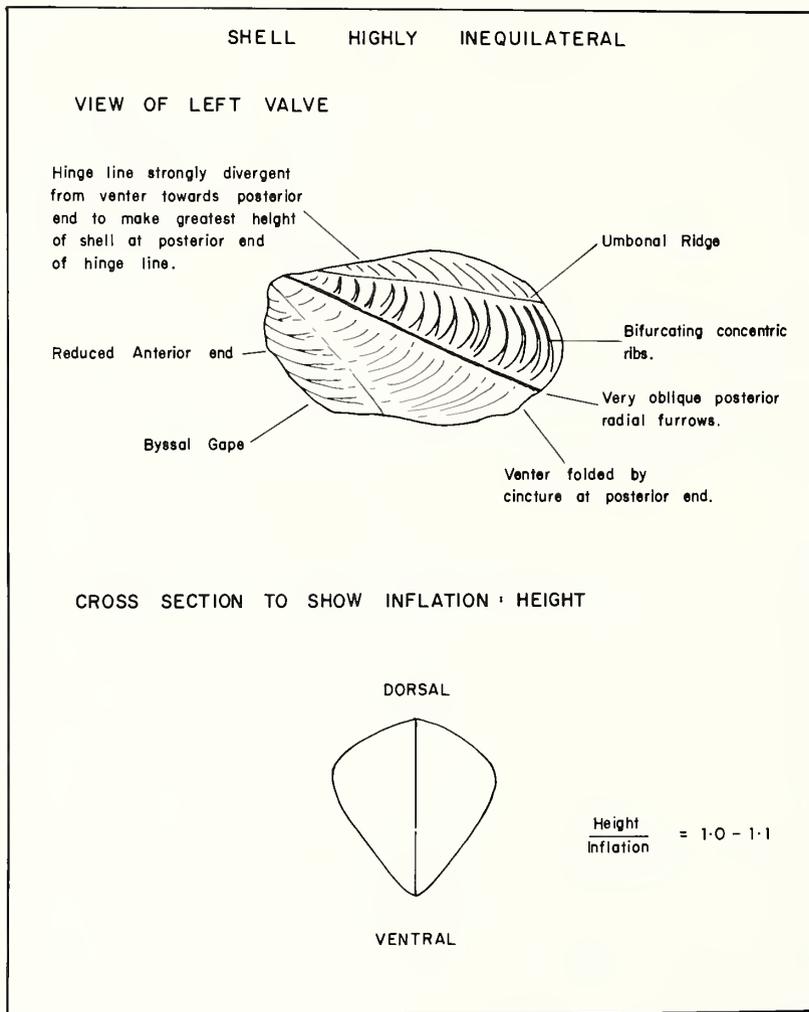


MARSH, Silurian *Grammysia*

Group (ii)

Byssally attached infaunal or semi-infaunal Grammysiidae show a combination of the following morphological features (text-fig. 5):

- (a) An elongate shell.
- (b) A highly inequilateral shell.
- (c) A hinge line that is strongly divergent from the venter towards the posterior end (text-fig. 6, e.g. *G. obliqua*).
- (d) The greatest height of the shell at the posterior end of the hinge line.
- (e) High inflation.
- (f) Low height/inflation ratio.



TEXT-FIG. 5. Typical morphological features of the shell developed in semi-infaunal byssally attached Grammysiidae, e.g. *Grammysia obliqua*.

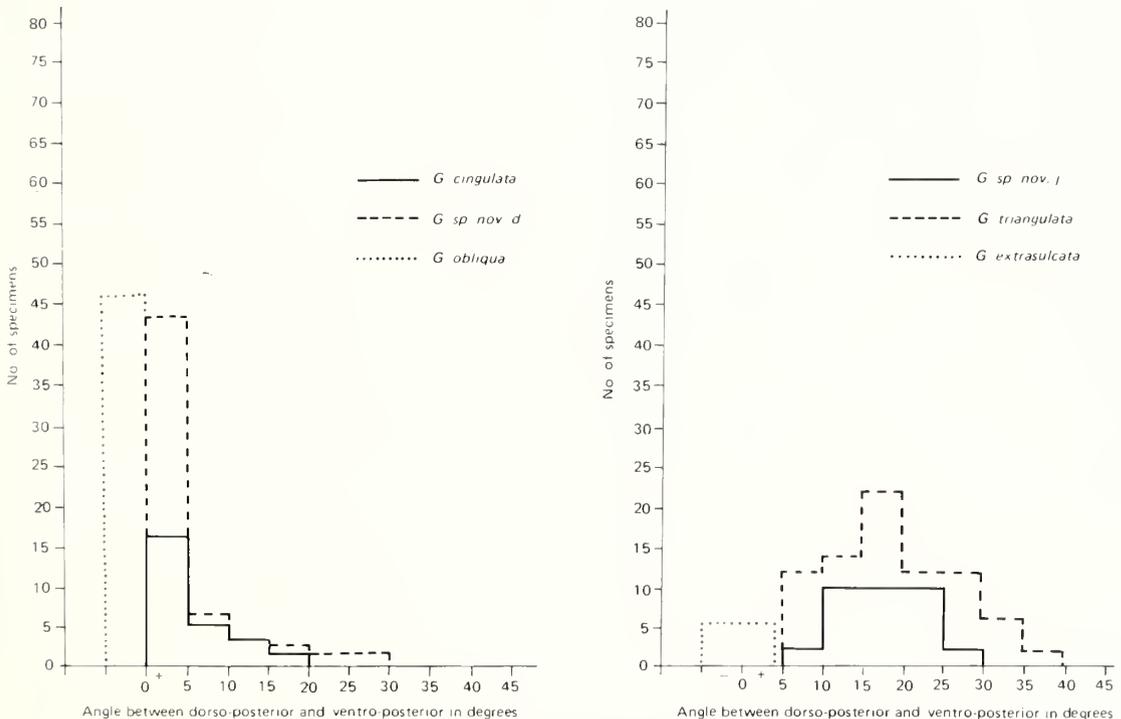
- (g) A greatly reduced anterior end (text-fig. 7, e.g. *G. obliqua*).
- (h) The small anterior end marked with fine concentric ridges that are not better marked on the anterior end than they are on the rest of the shell.
- (i) A reduced, very obliquely marked cincture composed only of furrows, which causes a folding only of the extreme posterior end of the venter.
- (j) An expanded posterior end.
- (k) An anterior-ventral byssal gape.
- (l) The valves usually found closed and articulated.

G. obliqua McCoy illustrates all the above features (Pl. 61, figs. 3-6).

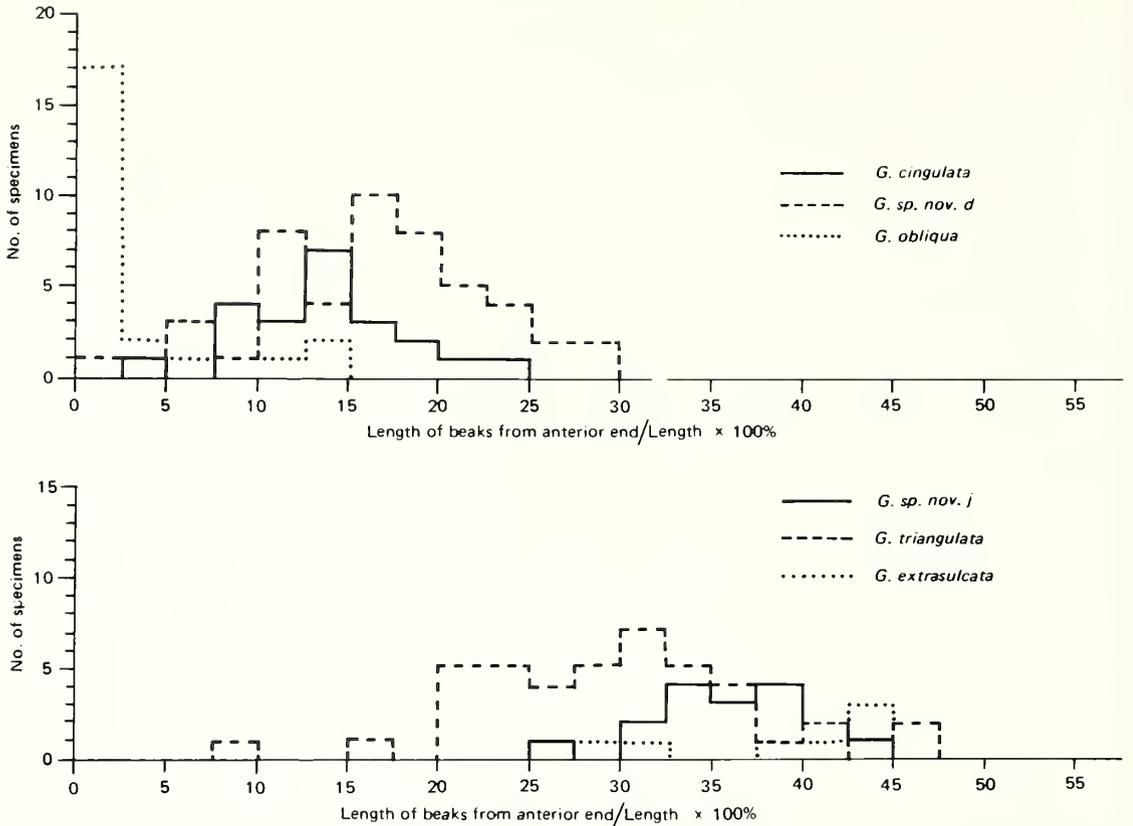
SPECIAL ADAPTATIONS

Some specialized adaptive morphology has been noticed in certain species. The byssally attached *G. obliqua* (text-fig. 3r) evolved from *G. cingulata* (text-fig. 3c), a moderately active shallow burrower, via a new species *G. sp. nov. o.* (text-fig. 3o) (Marsh 1976, pp. 405-411, pls. 34-36; herein Pl. 60, figs. 6, 7) which became byssally attached. From text-fig. 3 it can be seen that both the byssally attached species are much more inflated than active burrowing species like *G. triangulata* (k). Even *G. cingulata* (c), the ancestral species, would have had only a modest burrowing speed as indicated by its plot on the graph in text-fig. 3.

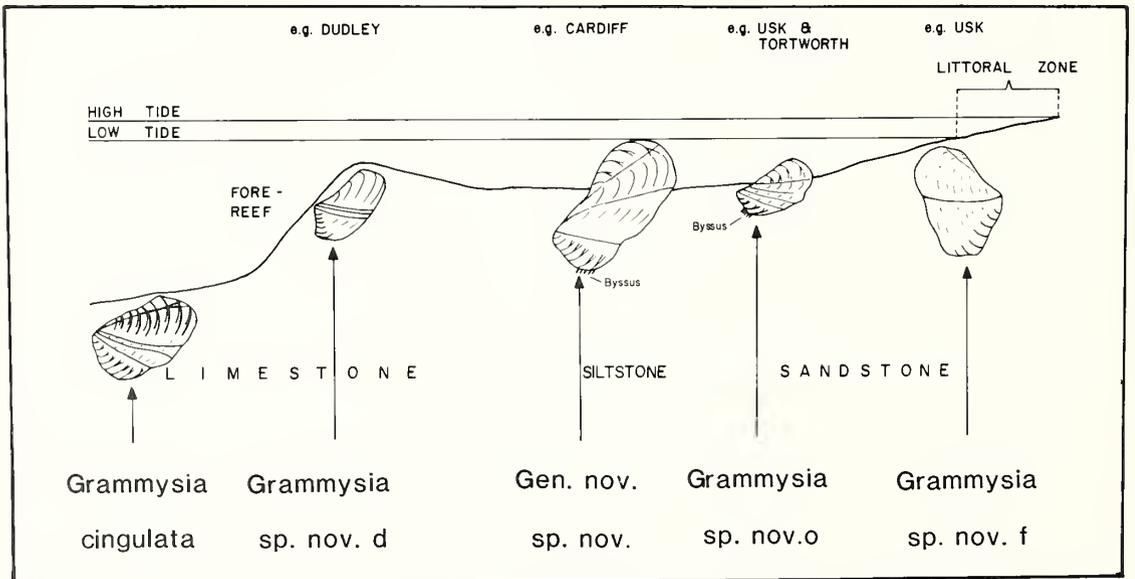
G. sp. nov. o. (text-fig. 8) shows certain changes in its morphology (compared with *G. cingulata*) concurrent with the acquisition of an adult byssus. The anterior end is reduced and the cincture is more oblique. Certain of the ancestral features, however, remain, e.g. the straight hinge line.



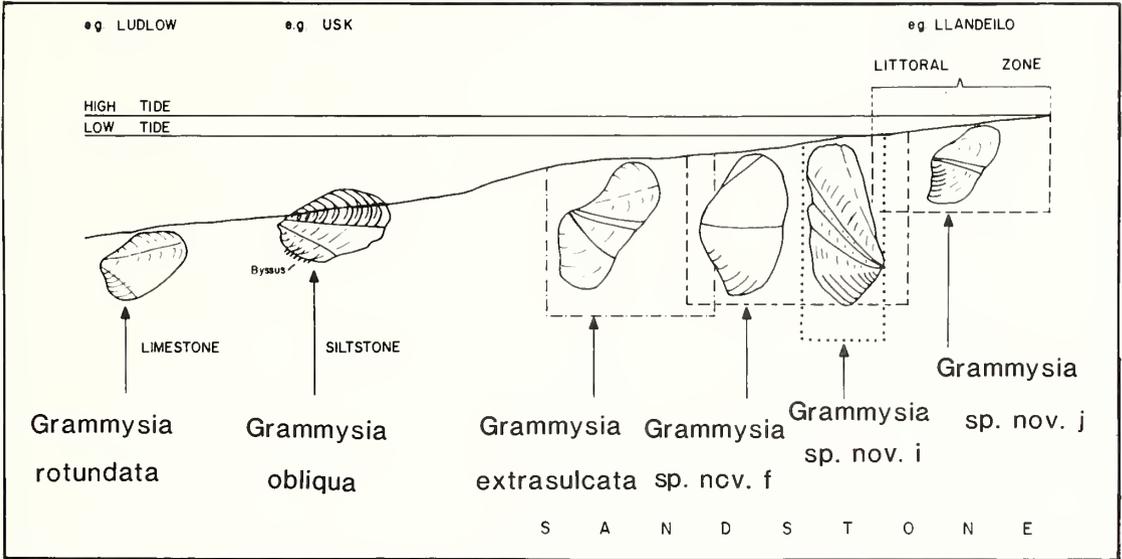
TEXT-FIG. 6. The angle in degrees between dorso-posterior and ventro-posterior in six grammysiid species.



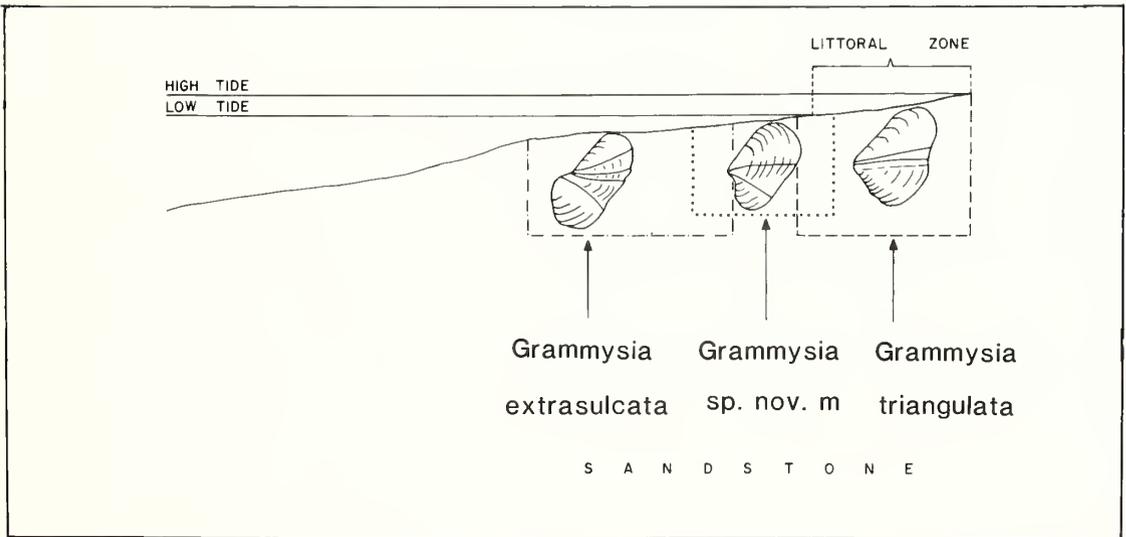
TEXT-FIG. 7. The length of the beaks from the anterior end as a percentage of the total length in six grammysiid species.



TEXT-FIG. 8. Grammysiid life position and environmental zonation in the upper Wenlock (Homerian).



TEXT-FIG. 9. Grammysiid life position and environmental zonation in the Ludlow (upper Bringewoodian).



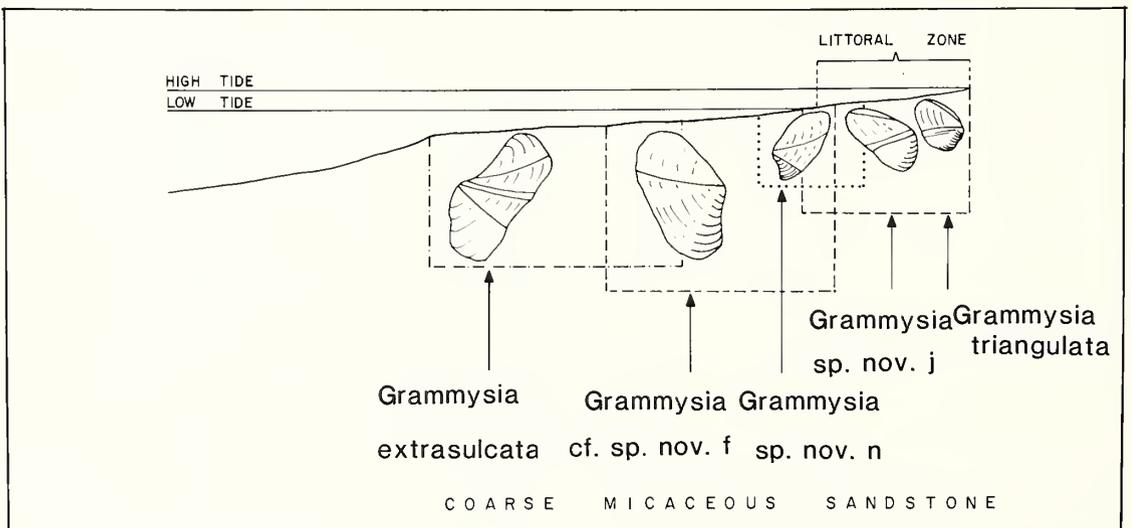
TEXT-FIG. 10. Grammysiid life position and environmental zonation in the Ludlow (Whitcliffian) of the Lake District, England

The umbonal ridge (text-fig. 8) running from the umbo to the postero-ventral angle marks off a much less-inflated dorso-posterior slope to the shell. I believe that the dorso-posterior slope would have been above the sediment in life position and that the umbonal ridge marked the sediment-water interface. I do not believe that the posterior furrow of the cincture marked the sediment-water interface, nor that the whole of the posterior end of the shell protruded from the sediment as Bambach (1971, p. 175, fig. 9) suggested for '*G. obliqua*' (although the species he discussed was the very similar, but more highly evolved species *G. acadica* Billings). The two posterior furrows of the cincture are not in the same position on the two valves and, therefore, if the posterior furrows did represent the sediment-water interface, then this interface would have been at different levels on the two sides of the specimen. The umbonal ridge therefore probably represents the sediment-water interface in life and only the extreme dorsal posterior end protruded from the sediment. It is, however, certainly possible that from time to time some of the sediment was removed from above the bivalve by current, tidal, and wave action, and indeed the nature of the sediments suggest this.

With the frequent inwashes of sediment that occurred, *G. sp. nov. o* must have been able to retain contact with the sediment surface. It seems likely that it did this by changing the angle at which it lived relative to the sediment-water interface. As suggested by Bambach (1971, p. 178) for '*G. obliqua*', *G. sp. nov. o* probably normally lived at an angle of about 40° to the sediment-water interface. If it was inundated with sediment, I believe that it could have increased this angle by action of the foot and use of the cincture and concentric ridges, to maintain contact between the siphons and the sediment-water interface (text-fig. 8). It could have done this without damage to the byssus (Marsh 1976, p. 410, fig. 67). Certainly in the high-energy environment in which it lived, *G. sp. nov. o* must have been able to cope with small influxes of sediment that would have occurred from time to time. At other times erosion took place and this species then returned to its more normal life position. The shell of *G. sp. nov. o* therefore shows special adaptation to a semi-infaunal byssally attached mode of life in an environment of moderately high energy.

The descendent species *G. obliqua* probably retained a cincture to pull itself down into the sediment from time to time to avoid exhumation (Marsh 1976, pp. 421, 422) and to avoid complete inundation when moderate rates of sedimentation occurred, in a similar way to *G. sp. nov. o*.

General life positions are illustrated in text-figs. 8-11.



TEXT-FIG. 11. Grammysiid life position and environmental zonation in the topmost lower Downton of South Central Wales.

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JANEIA SILURICA, A LINK BETWEEN NUCULOIDS AND SOLEMYOIDS (BIVALVIA)

by LOUIS LILJEDAHL

ABSTRACT. *Janeia silurica* Liljedahl, 1984 from the Silurian of Gotland has unusual characters in common with the deposit-feeding nuculoids and the systematically controversial solemyoids, generally considered to have a life habit intermediate between deposit- and suspension-feeding but which in fact lives in symbiosis with chemoautotrophic bacteria. The extensive silicified material available is occasionally extremely well-preserved, reflecting soft-part anatomy of the muscles of the foot as well as of the mantle. *J. silurica*, which has conspicuous traces of the pallial muscles of the mantle (fused margins?), probably had an efficient system of cleaning the mantle cavity, a typically solemyoid feature. However, it was probably a more active burrower than the extant *Solemya* since it presumably had a larger foot and smaller gills. The gills were thus used for respiration only, as in nuculoids, while the inferred character of the mantle indicates an evolutionary trend towards the solemyoid life habit.

IN the animal kingdom the suspension-feeding lamellibranch bivalves are regarded as being the most successful exploiters of the almost inexhaustible primary biomass of the oceans, i.e. the plankton supply. The strikingly expanded ctenidia of these bivalves, which are used exclusively for food collecting, occupy most of the mantle cavity and the individual filaments are far more numerous than the protobranch ctenidia of deposit-feeders (nuculoids). Each filament is considerably longer than the short protobranch filament and is thus by far more efficient. In contrast to the lamellibranch ctenidia the protobranch ctenidia are used mainly for respiration.

The affinities of *Solemya* have always been controversial. Gross soft-part morphology points to a relationship with the nuculoids (e.g. Yonge 1941, 1959) but specialization along different lines makes its systematic position uncertain (e.g. Purchon 1978). The life habit of *Solemya* is poorly understood, considered by some to be intermediate between the deposit- and suspension-feeding mode of life (e.g. Yonge 1941) and by others as a suspension-feeder (e.g. Stanley 1970). However, recent discovery of procaryotic symbionts in *S. velum* (Cavanaugh *et al.* 1981) in combination with the fact that the gut of solemyoids is extraordinarily minute, and in some species even completely absent (Reid and Bernard 1980), suggests that these bivalves obtain nutrient mainly through symbiosis with chemoautotrophic bacteria.

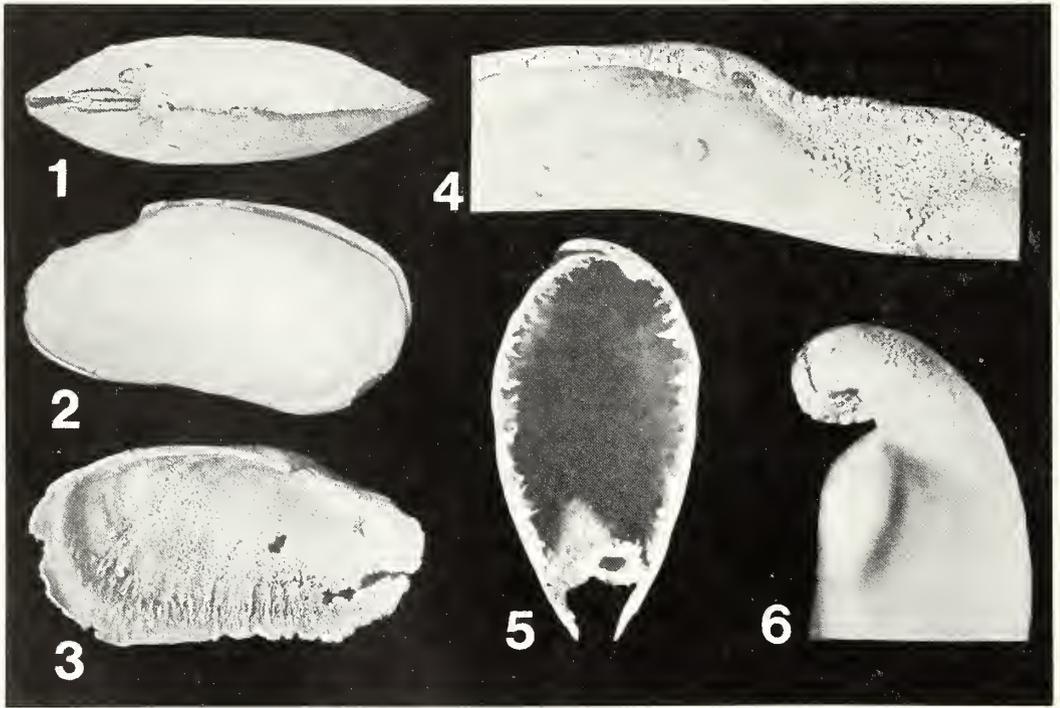
Morphological comparison of Janeia silurica with nuculoids and solenyoids

The silicified Wenlock fauna at the locality Möllbos 1, Gotland, Sweden contains eleven bivalve species, one of which is *J. silurica* Liljedahl, 1984 (see Liljedahl 1983, 1984 (in press)). This species is represented by more than 500 valves containing extraordinarily well-preserved specimens, some of which exhibit traces of the soft parts.

The discovery of *J. silurica* extended the known stratigraphical range of the solemyoids to the late Early Silurian, the oldest previously known representative being of mid Devonian age (Newell 1969). Pojeta (1978, p. 231, fig. 4) considered an Ordovician nuculoid as showing solemyoid characters (described by Eichwald 1880, p. 991, pl. 39, fig. 10, as *Nucula aedilis*) with the expanded anterior part of the shell and the enlarged anterior adductor muscle scar being the most typical features. I agree that the lateral outline of this species is possibly reminiscent of the solemyoid form (but see also the close similarity in shape with the nuculoid? *Dystactella subnasuta* Hall and Whitfield; see McAlester 1968, p. 27, pl. 5). However, since dentition and other internal features are unknown, it is necessary to await the discovery of better-preserved material to understand its systematic position. Pojeta's (1978)

second example of a nuculoid showing solemyoid features is *Ctenodonta nasuta* (Hall). It is elongate, has a slightly expanded anterior part but a posterior end which is longer than the anterior one (see Salter 1859, pl. 8, fig. 2 and Pojeta 1971, pl. 4, fig. 10).

J. silurica shows certain similarities to the solemyoids combined with a number of primitive features characteristic of extant Nuculoida. The shell of *J. silurica* is thin, as in the extant *Solemya*, and elongate with an extended anterior part (text-fig. 1:1, 2, 3). It is not, however, as strictly cylindrical as that of the extant *Solemya*. The shell of *Solemya* gapes at both ends while in *J. silurica* the valve margins fit together except for the dorsal margin, the left valve overlapping the right (text-fig. 1:5 and 3). Like the extant *Solemya*, the ligament of *J. silurica* consists of a posterior internal/external part and an anterior external part (text-fig. 1:1, 4, 6). The ligament construction was probably strong to judge by the unusually large ligament area (text-fig. 2B).

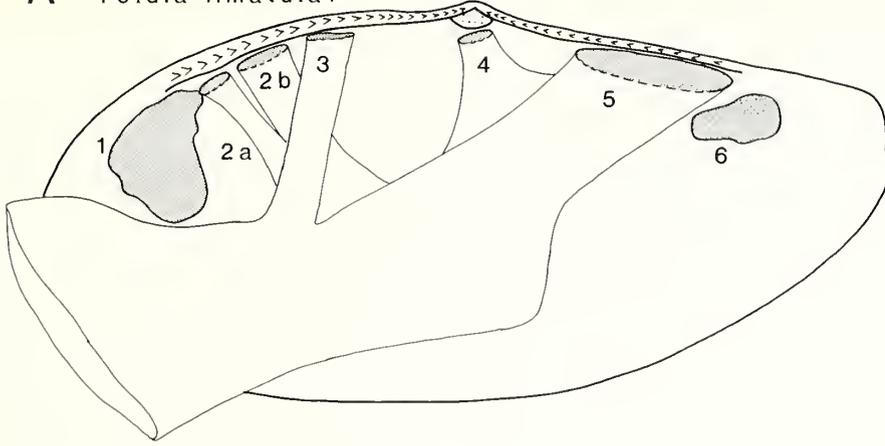


TEXT-FIG. 1. *Janeia silurica* Liljedahl, 1984.

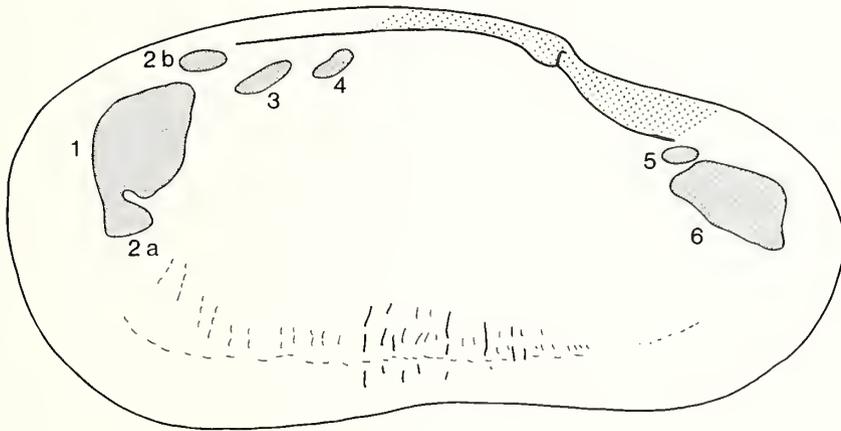
- 1, External dorsal view of articulated specimen, anterior to the right. SGU 3426/3427, $\times 1.8$, sample G77-29LJ.
- 2, External lateral view of articulated specimen, anterior to the right. Note overlapping left valve, same specimen as in 1, $\times 1.8$.
- 3, Internal lateral view of a right valve (holotype). Note conspicuous traces of pallial muscles. SGU 3608, $\times 2.4$, sample G79-79LJ.
- 4, Internal lateral view of umbonal part of a right valve. Note chondrophore extending above beak. SGU 3318, $\times 6.1$, sample G77-28LJ.
- 5, Vertical section of an articulated specimen. Note silicified possible folded in ventral margin of the mantle, SGU 3592/3593, $\times 4.4$, sample G79-78LJ.
- 6, Posterior view of beak and chondrophore, same specimen as 4, $\times 7.8$.

All specimens are in the Type Collection of the Geological Survey of Sweden. The material was coated with ammonium chloride prior to photography.

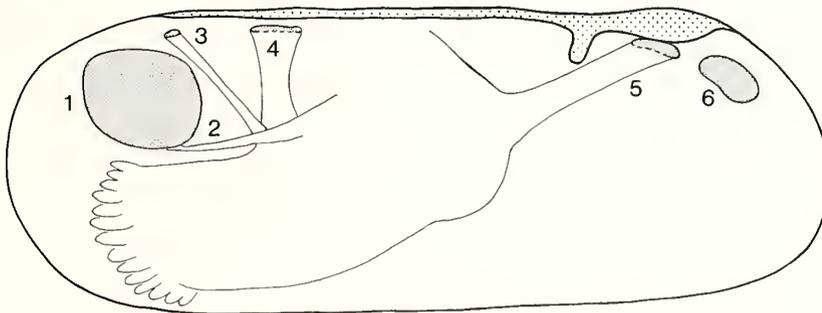
A *Yoldia limatula?*



B *Janeia silurica*



C *Solemya togata*



TEXT-FIG. 2. Muscular impressions (densely stippled) and ligament area (loosely stippled). A, *Yoldia limatula?*: 1 = anterior adductor muscle. 2a, 2b = anterior pedal protractor muscles. 3 = anterior pedal retractor muscle. 4 = pedal elevator muscle (dorsomedian muscle). 5 = posterior pedal retractor muscle. 6 = posterior adductor muscle; note conspicuously large posterior pedal retractor muscle (No. 5). After Heath 1937, pl. 10, fig. 83. B, *Janeia silurica* Liljedahl: 1 = anterior adductor muscle scar. 2a, 2b = anterior pedal protractor muscle scars. 3 = anterior pedal retractor muscle scar. 4 = pedal elevator muscle scar. 5 = posterior pedal retractor muscle scar. 6 = posterior adductor muscle scar. C, *Solemya togata* Poli: 1 = anterior adductor muscle. 2 = anterior pedal protractor muscle. 3 = anterior pedal retractor muscle. 4 = pedal elevator muscle. 5 = posterior pedal retractor muscle. 6 = posterior adductor muscle. After Pelseneer 1891, pl. 9, fig. 15, ligament extension after Owen 1959, p. 217, fig. 3c.

The muscular impressions of *J. silurica* (text-fig. 2B; see also Liljedahl 1984, fig. 15) are deeply incised, their distribution much resembling that of extant nuculoids (text-fig. 2A; cf. Heath 1937), similarities with *Solemya* also being evident (text-fig. 2C; cf. Pelseneer 1891). The adductor muscle scars are almost equal in size (cf. reduced posterior adductor muscle in extant *Solemya* in Newell 1969, p. N242). The anterior pedal protractors are absent or minute in *Solemya* (2 in text-fig. 2C) but well developed in *J. silurica* (2a in text-fig. 2B). Scar 2b of *J. silurica* possibly also indicates a pedal protractor muscle since it has a position similar to the most anterior pedal muscles in nuculoids which function as pedal protractors (2a, 2b in text-fig. 2A). Scar 3 in text-fig. 2B of *J. silurica* may be homologous with the anterior pedal retractor in nuculoids (3 in text-fig. 2A) while scar 4 in text-fig. 2B of *J. silurica* probably corresponds to the pedal elevator in both nuculoids and solemyoids (4 in text-fig. 2A, C). The posterior pedal retractor muscle scar of *J. silurica* (5 in text-fig. 2B) is minute as in solemyoids (5 in text-fig. 2C) in contrast to the extremely large posterior pedal retractor muscle of the nuculoids (5 in text-fig. 2A).

Thus the pattern of pedal muscle scars and the greatly extended anterior part of the shell of *J. silurica* together suggest that the foot was correspondingly enlarged occupying more than half the mantle cavity, and that it protruded from the anteroventral part of the shell. Accordingly it must have had a function similar to that in *Solemya* (cf. Drew 1900; see also Liljedahl 1984, fig. 15 showing a reconstruction of the foot of *J. silurica*).

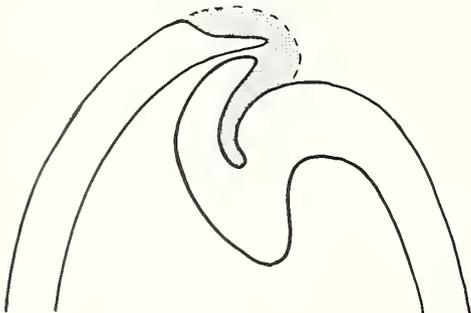
The conspicuously deep and broad traces of the pallial muscles of *J. silurica*, which are less accentuated in the posterior and anterior extremities, indicate that the radial muscles of the mantle edge were unusually strong (text-fig. 1:3). Because of their uneven impression these scars also suggest partially fused mantle edges (cf. *Solemya* in Drew 1900, p. 264, figs. 9, 10, 11, 12) with one anterior and one posterior opening. If these assumptions are true, then this species was probably able to withdraw the ventral margins of the mantle with great force, perhaps as in *Solemya* (see silicified possible replica of an infolded ventral margin of the mantle in text-fig. 1:5; cf. Drew 1900, pp. 264, 265).

The anteriorly extended shell and the distribution and size of the impressions of the pedal muscles of *J. silurica* indicate that the foot occupied more than half the mantle cavity, thus leaving about a third of the cavity for the ctenidia (cf. ctenidia of solemyoids occupying about half the mantle cavity in Yonge 1941, p. 93). If this assumption holds, then the ctenidia of *J. silurica* were probably not involved in ingestion (as they are to some extent in *Solemya*; Yonge 1941, p. 116) but were used for respiration only, as in nuculaceans (Yonge 1941, pp. 115, 143).

The shape of the shell with its posterior umbonal slope and with the position of the posterior adductor muscle scar, make a strictly posterior exhalant current, as in *Solemya*, improbable in *J. silurica*, the direction presumably being ventroposterior. Thus, unlike *Solemya* it probably did not have free-swimming ability (cf. Drew 1900).

Ecology of extant nuculoids and solemyoids

Extant nuculoids live in soft muddy to sandy bottoms, moving about only sparingly (Yonge 1941, pp. 81, 82). They collect food by means of the extended labial palps, or proboscides, which when



TEXT-FIG. 3. Vertical section of umbonal region of *Janeia silurica* showing chondrophore of right valve and reconstructed ligament (stippled).

protruded between the opened valves collect and guide food particles from the sediment to the mouth (Yonge 1941, p. 114). The protobranch ctenidia, the main function of which is respiration, are fairly small, and though they may possibly be involved in feeding they cannot be compared with those of the lamellibranch bivalves in this respect (Yonge 1941, p. 115).

Extant *Solemya* thrives in rather firm, sandy mud in which it digs itself down in a Y-shaped burrow (Stanley 1970) where it usually stays for the greater part of its time (Yonge 1941, p. 96). The protobranch ctenidium of this genus has a surface comparable with that of a lamellibranch ctenidium and the labial palps are small, not reaching beyond the mantle margins, i.e. they are not able to collect food outside the shell (Yonge 1959, p. 213). *Solemya* inhales water anteriorly by the actions of muscles. The water is heavily laden with suspended sediment, and food particles are transferred by the labial palps from the ctenidium to the mouth (Yonge 1959). The gut of *Solemya* is of such extremely reduced size that it alone cannot possibly provide enough nutrient material (Allen and Sanders 1969, p. 388). However, as mentioned above its paradoxically small gut (absent in some species) is probably compensated by its symbiosis with chemoautotrophic bacteria in sulphide-rich levels of the sediment. Possibly *Solemya* uses the lower part of its Y-shaped habit as a connection with its symbionts (suggested by L. Jeppsson).

Autecology of Janceia silurica

The bivalve fauna at Möllbos is dominated by deposit-feeders (90%, Liljedahl 1984) probably reflecting the high silt-clay content of the carbonate sediment (cf. Sanders 1958, 1960). *J. silurica* comprises approximately 20% of all deposit-feeding bivalves and is the third commonest species.

There are facts in favour of niche diversification between the different deposit-feeders at this locality (Liljedahl in press). *J. silurica* is believed to have inhabited a somewhat deeper level in the sediment than the remaining deposit-feeders (Liljedahl 1984, fig. 34). It may have lived symbiotically with chemoautotrophic bacteria at a sulphide-rich level of the bottom (like *S. velum*, see Cavanaugh *et al.* 1981) where it did not have to compete for food with other species (cf. discussion above of extremely reduced size and absence of gut in *Solemya*).

The hypothesis that *J. silurica* was not as specialized a passive suspension-feeding deposit-feeder as the extant *Solemya* but instead was an active burrower, is supported by the assumed differences in the size of the foot and ctenidia of this species and *Solemya*. The absence of a gape in *J. silurica* would have given this species an advantage while burrowing, in preventing excessive sediment from entering the mantle cavity. The almost stationary *Solemya*, on the other hand, has no need of completely closed shell margins. Instead the valves gape at each end, which is advantageous since it can inhale and exhale with the valves closed.

The assumed robust ligament construction of *J. silurica*, in combination with the edentulous hinge and deeply incised, large, subequal adductor muscle scars, may have made it possible for this species to close the valves quickly and vigorously as in *Solemya* (cf. Yonge 1941, p. 115) and with greater force and speed than in nuculoids. These have interlocking hinge teeth which are considered a hindrance to such rapid contraction.

The conspicuous impressions of the pallial muscles, as well as the inferred morphology of the foot and accessory muscles, suggest that *J. silurica* could infold the (fused?) ventral margin of the mantle and simultaneously withdraw the foot, possibly in much the same way as in *Solemya* (see Yonge 1941, p. 136). Thus, *J. silurica* probably had a system for removing indigestible matter from the mantle cavity, perhaps more effective than in extant nuculoids (cf. living nuculoids; Yonge 1941, p. 83).

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AUTECOLOGY AND DISTRIBUTION OF THE SILURIAN BRACHIOPOD *DUBARIA*

by BRIAN JONES *and* JOHN M. HURST

ABSTRACT. Smooth-shelled atrypoid brachiopods, *Dubaria varians* (Poulsen, 1943) and *Dubaria* sp. nov., occur in Llandovery strata of western North Greenland in cryptic habitats associated with biostromes and reefs. This ecological preference probably explains their patchy spatial and temporal distribution. It may explain the stratigraphic distribution of *Dubaria* since other species in the genus also occur in association with reefs. External morphological features of *Dubaria* are comparable with the morphological adaptations of a species of *Atrypodea* which lived in direct association with reefs in the upper Silurian of Arctic Canada.

AUTECOLOGY can be important to biostratigraphy since the interactions between single species and their environments may ultimately control their stratigraphic distribution. Inherent to the topic is the establishment of the environment in which the species lived, for without that knowledge it is impossible to examine the autecology of the species concerned. In some instances the nature of the environment has been inferred from the fossils themselves, a practice that ultimately leads to circular arguments once the autecology of the species is considered. The Silurian-Devonian brachiopod *Dubaria* provides an excellent example of how the knowledge of autecology assists in the understanding of the stratigraphic distribution of a genus or a species.

Boucot and Perry (1981, p. 212) argued that the low diversity *Dubaria* Community inhabited a quiet-water environment since the brachiopod shells are virtually always articulated and show no sign of abrasion. Thus, it might be expected that *Dubaria* would be a common element of Silurian-Devonian faunas for there is ample evidence that quiet-water environments were common in that time period. This is especially true in the light of the comment by Johnson *et al.* (1978, p. 803) that '. . . *Dubaria* is more of a biofacies indicator than a biochronological tool . . .'. However, as demonstrated in this paper, *Dubaria* evidently had particular ecological needs that served to restrict its occurrence to a well-defined ecological niche.

This paper utilizes occurrences of *Dubaria* on a world-wide basis (Table 1) and from western North Greenland (Table 2) to outline the ecological factors that controlled the distribution of the genus.

DUBARIA IN NORTH GREENLAND

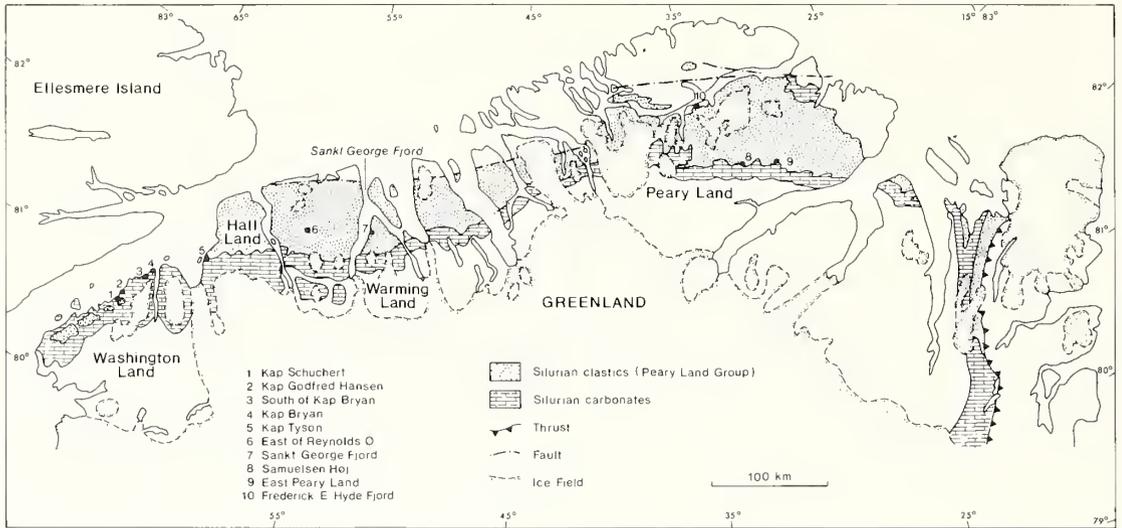
Spatial and temporal distribution

Dubaria were found at ten localities in North Greenland (text-fig. 1 and Table 2). Although strata between these localities were examined in detail, no further specimens of *Dubaria* were found. The stratigraphic distribution of *Dubaria* is similarly patchy; although it has been recorded at five different horizons in the Llandovery of North Greenland, strata between those horizons apparently contain no specimens of the genus (text-fig. 2 and Table 2).

This patchy spatial and temporal distribution suggests that other factors such as ecological requirements probably controlled the distribution of *Dubaria*.

Ecological distribution

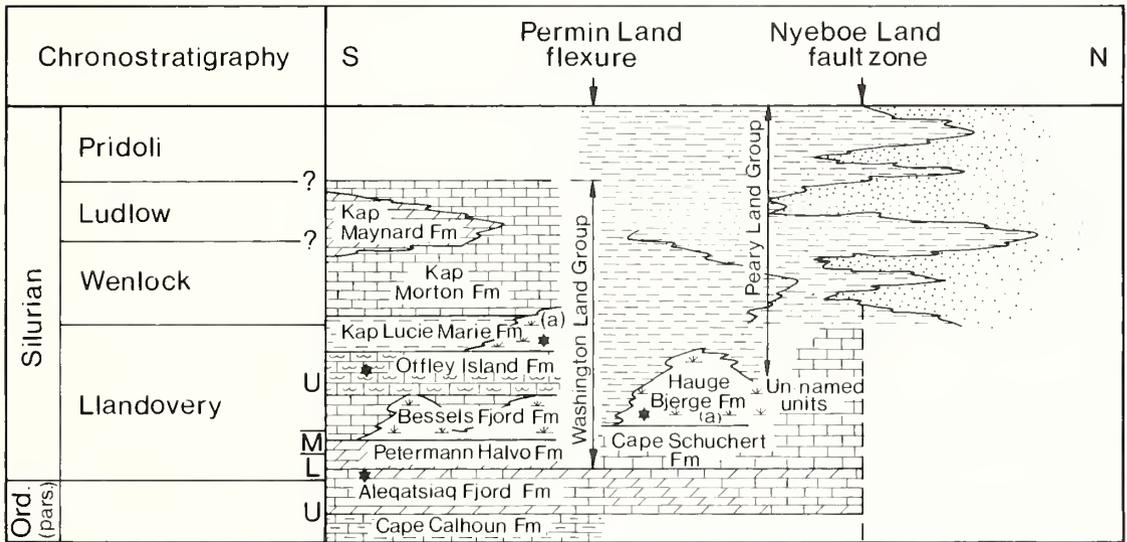
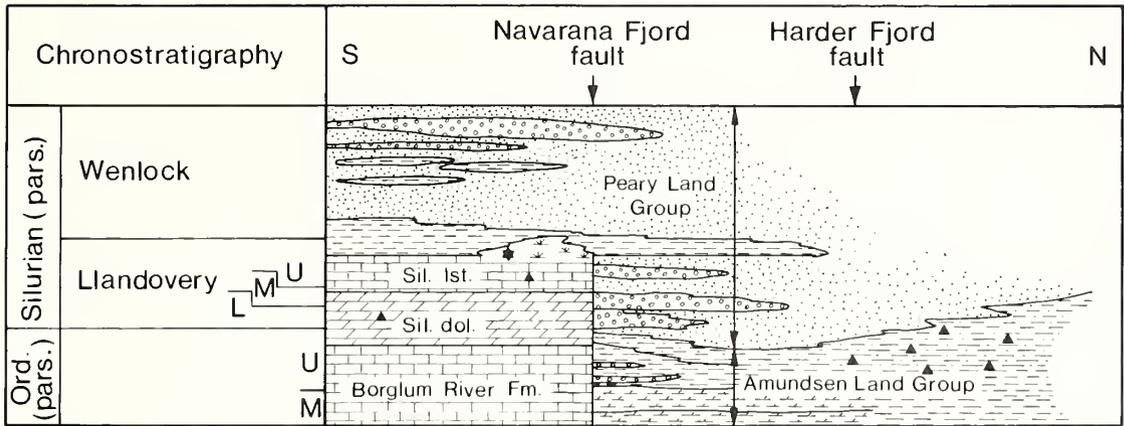
At Kap Schuchert, *D. varians* and *Dubaria* sp. nov. occur in the uppermost part of the Alegatsiaq Fjord Formation in direct association with small, localized biostromes that are surrounded by



TEXT-FIG. 1. Distribution of Silurian platform carbonates (Hurst 1980) and deep-water basin clastic sediments (Hurst and Surlyk 1982) on North Greenland. Localities 1 to 10 indicate where *Dubaria* were collected (Table 1).

TABLE 1. Recorded occurrences of *Dubaria*. Note the patchy spatial and temporal ranges of the genus as well as the species. * indicates species for which material has been studied.

Species	Reference	Geographic location	Stratigraphic level
<i>D. varians</i>	This paper	NW Greenland	Llandovery*
<i>D. reclinis</i>	Rubel 1970	Estonia	Llandovery*
<i>D. sp. nov.</i>	This paper	NW Greenland	Llandovery*
<i>D. legrinus</i>	Ivanovskii and Kulkov 1974	Altai-Sajan	Upper Llandovery
<i>D. tenera</i>	Nikiforova and Modzalevskaya 1968	Siberia	Llandovery
<i>D. rongxiensis</i>	Wan 1978	Tsuei-shan Yung Tzi Province, China	Middle Silurian
<i>D. sp. D</i>	Johnson <i>et al.</i> 1976	Central Nevada	Lower-middle Ludlow
<i>D. sp.</i>	Johnson <i>et al.</i> 1976	Central Nevada	Lower-middle Ludlow
<i>D. lentenoisi</i>	Termier 1936	North Africa	Lower Ludlow*
<i>D. megaeroides</i>	Johnson <i>et al.</i> 1973	Central Nevada	Upper Pridoli
<i>D. sp.</i>	Johnson and Boucot 1970		
<i>D. sp.</i>	Johnson, 1973	Central Nevada	Middle Lochkovian
<i>D. thesis</i>	Johnson, 1975	Arctic Canada	Upper Lochkovian
<i>D. sp.</i>	Smith 1980		
<i>D. sp.</i>	Johnson and Boucot 1970	Carnic Alps	Budnanian (Ludlow and Pridoli)



- | | | | | | |
|--|------------|--|------------------------------|--|---------------------------|
| | Limestone | | Sandy turbidites | | Black chert |
| | Dolomite | | Mudstone and thin turbidites | | Resedimented conglomerate |
| | Biostromes | | Mudstone | | |
| | Reefs | | Green chert | | |

TEXT-FIG. 2. (Above) Stratigraphic scheme for Peary Land, North Greenland (from Surlyk *et al.* 1980 and Surlyk and Hurst 1984). (Below) Stratigraphic scheme for western North Greenland based on Washington Land and Hall Land (Surlyk and Hurst 1984). Asterisks indicate stratigraphic location of *Dubaria* (Table 2).

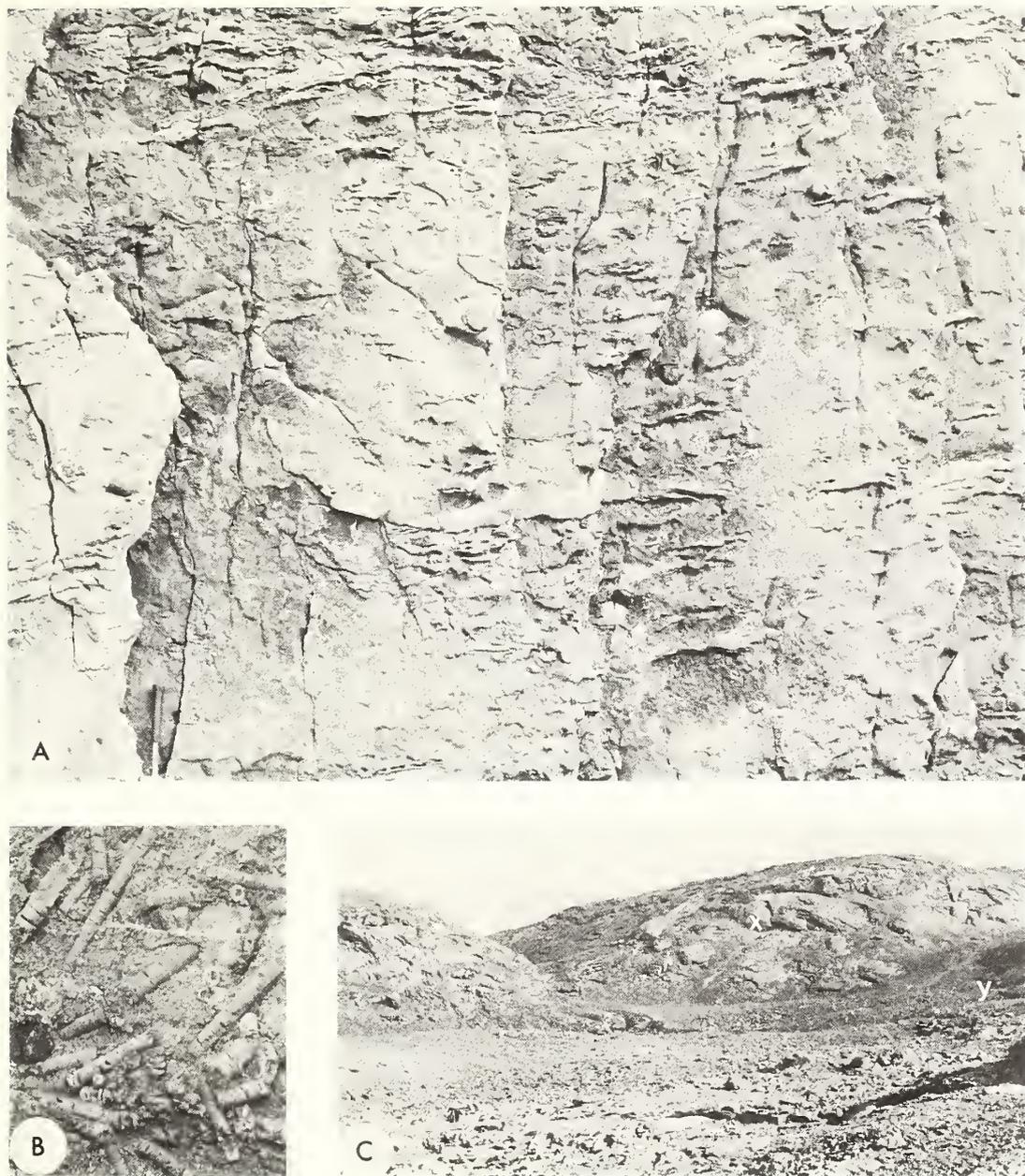
crinoidal rudstones (text-fig. 3). The poorly sorted nature of these rocks and the abundant coral and stromatoporoid colonies, many of which are overturned, suggests accumulation in relatively high-energy, shallow-water carbonate shelf environments. The isolated pockets of skeletal sands, which occur as isolated pockets up to 10 m thick and several tens of metres long, may represent the remains of skeletal sand shoals (Hurst 1980).

The Offley Island Formation represents a carbonate shelf, biostromal unit consisting of level-bedded stromatoporoid floatstones and skeletal, crinoidal, and stromatoporoid rudstones (text-fig. 3) associated with small reefs (Hurst 1980). The biostromes probably represent skeletal sand shoals that accumulated in an agitated, shallow-water subtidal carbonate platform environment. An undulatory sea-floor topography is reflected by the complex vertical and lateral relationship of the facies. The rare laminated pellet lime mudstones probably accumulated in the lower energy environments, that existed in the topographic lows between the sand shoals. *Dubaria* occurs only in the higher energy skeletal sand shoals, never in the low-energy pelletal lime mudstones. Large *D. varians* from upper Llandovery reefs (text-fig. 3c) also occur in pockets and as skeletal components in debris beds, suggesting that they inhabited high energy environments.

Dubaria occurrences in North Greenland are associated with high-energy biostromes and/or reef environments. Contrary to this opinion, Boucot and Perry (1981, p. 212) argued that the low diversity *Dubaria* Community inhabited a quiet-water environment. This dichotomy may reflect the scale at which environmental factors are viewed. Clearly, on a large scale the environment is a high energy one. However, even modern day, high-energy reefal environments encompass quiet, cryptic habitats that on a local scale are quite different in character. For example, Logan (1977) demonstrated that the modern brachiopods *Thecidellina barretti*, *Argyrotheca* sp., and *Platidia* sp. inhabit deep recesses in Eden's Rock, a large patch reef off the coast of Grand Cayman Island. Such recesses typically have little light and little water movement (Logan 1977, p. 91). Logan argued that intense predation pressures and severe competition for space forced the brachiopods to inhabit such cryptic habitats. The analogy with *Dubaria* is striking.

TABLE 2. Summary information on *Dubaria* from west North Greenland. * Geological Survey of Canada locality number. *Dv* = *Dubaria varians*; *D* = *Dubaria* sp. nov.

Locality	Species	Locality on Text-fig. 1	Collector	Formation	Age	Number of Specimens
256354	<i>Dv</i>	10	Mabillard	Unnamed Carbonate Reefs	Llandovery to early Wenlock	10
256357	<i>Dv</i>	10	Mabillard		Wenlock	57
82370	<i>Dv</i>	7	Dawes	Unnamed Carbonate Reefs	?	2
82368	<i>Dv</i>	7	Dawes		?	4
82367	<i>Dv</i>	7	Dawes		?	5
184128	<i>Dv</i>	9	Peel	Unnamed Carbonate Reefs	Llandovery to early Wenlock	1
211789	<i>Dv</i>	2	Norford	Aleqatsiaq Fjord Fm.	early Llandovery	2
211765	<i>D</i>	6	Norford	Offley Is. Fm.	Llandovery to early Wenlock	4
216887	<i>D</i>	2	Hurst	Aleqatsiaq Fjord Fm.	early Llandovery	1



TEXT-FIG. 3. A, biostrome of laminar stromatoporoids and bioclastic debris, Offley Island Formation, Hall Land. B, crinoidal rudstone, Offley Island Formation, Hall Land. C, carbonate buildup (x) surrounded by off-reefal sediments (y) in Peary Land. *Dubaria varians* occurs in both reefs and biostromes. See text-figs. 1 and 2 for location and stratigraphy.

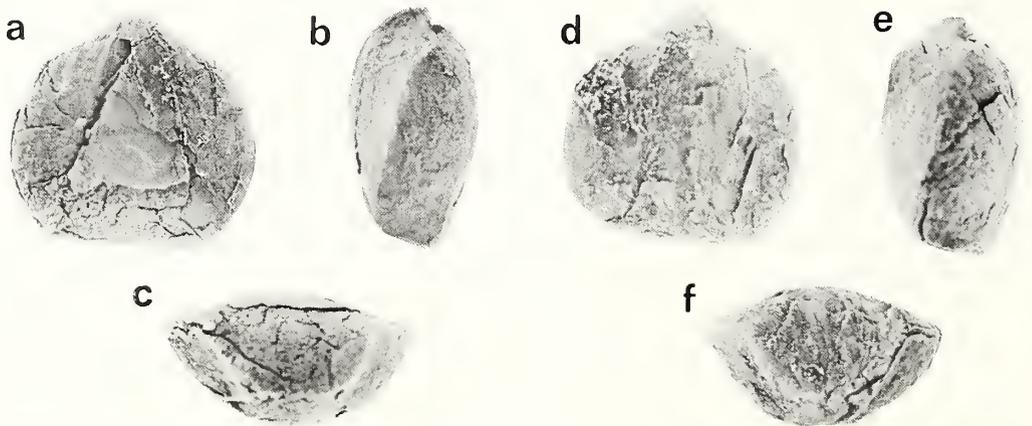
WORLDWIDE DISTRIBUTION OF *DUBARIA*

Dubaria occurs at many different, widely separated localities throughout the world (Table 1). As on Greenland, the stratigraphic distribution of *Dubaria* on a world-wide basis is also patchy (Table 1). For example, *Dubaria* is found in Llandovery strata but only rarely in the Wenlock (Table 1). These patchy spatial and temporal distributions also suggest that ecological factors may have controlled the occurrences of this brachiopod on a wide scale. Unfortunately, this suggestion cannot always be verified because the sedimentological setting of *Dubaria* is commonly not documented.

Atryopsis reclinis Rubel (= *D. reclinis*) is common in the Llandovery strata on the Estonian island of Hiiuma in the northern Baltic. Rubel (1983 written comm.) states that 'the known distribution of *Atryopsis reclinis* in the North Baltic is really restricted to the bioherms or related rocks'. *D. lantenoisi*, the type species of the genus, occurs in the Ludlow of Morocco (Termier 1936). Termier and Termier (1960, fig. 390) illustrated a series of reefs surrounded by shale and indicated that *Dubaria* occurred in direct association with the reefs. Other illustrations (Termier and Termier 1960, figs. 391 and 394) show *Dubaria* associated with algal limestone from the reefs. Johnson (1975, p. 16) inferred that *Dubaria* from the upper Lochkovian of Bathurst Island was also associated with reefs. Elsewhere the ecological setting of the genus cannot be ascertained from the available data.

COMPARISON OF ECOLOGICAL SETTINGS OF *DUBARIA* AND *ATRYPOIDEA*

Atrypoidea Mitchell and Dun, 1920 which is very common in the Ludlow strata of Arctic Canada, is morphologically similar to *Dubaria*. *Atrypoidea* differs, however, in not having dental lamellae in the pedicle valve. Most *Atrypoidea* appear to have inhabited a soft-substrate in quiet-water, subtidal environment (Jones 1982) and thus occupied a different ecological niche than that proposed for *Dubaria*. However, one species of *Atrypoidea* did develop the ability to inhabit reefs and/or the skeletal sands surrounding the bioherms (Jones and Narbonne 1984). In the areas between the reef only *A. foxi* occurs (Jones 1974). *Atrypoidea bioherma* has an external morphology directly comparable with that of *D. varians*. Both have a similar overall shell form, both apparently had functional pedicles, and both developed rectangular-shaped deflections of the anterior commissure.



TEXT-FIG. 4. Pedicle, lateral and anterior views of *Dubaria varians*, $\times 1.5$, specimens are from sample 256367 (Table 1) and are deposited in the Geologisk Museum, Copenhagen. A-C, MGUH 16097; D-F, MGUH 16098.

CONCLUSIONS

Dubaria and *A. bioherma* sp. nov. both inhabited quiet-water, cryptic habitats associated with reefs. The similarity in the external morphology of the *Dubaria* species and *A. bioherma* strongly suggests that this general morphological scheme was adapted specifically for such a habitat. In particular, the rectangular form of the anterior deflection of the commissure appears to have been a necessity, presumably in some way assisting the feeding process. Comparison with similar modern reef-dwelling brachiopods suggests that predation or more likely competition from other organisms restricted their occurrence to such cryptic habitats. This may explain why *Dubaria* apparently does not occur in quiet-water environments of a more open aspect (for example, in quiet-water lagoonal deposits). The result of such spatial restriction is that brachiopods such as *Dubaria* have a very patchy stratigraphic occurrence.

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A REAPPRAISAL OF THE LOWER CARBONIFEROUS LEPIDOPHYTE *ESKDALIA* KIDSTON

by B. A. THOMAS and S. V. MEYEN

ABSTRACT. Two new species of *Eskdalia* are described from the Lower Carboniferous of Siberia. *Eskdalia* has been thought to possess true leaf scars produced as a result of leaf abscission. The new specimens similarly have misleading oval areas thought to indicate leaf abscission. However, closer examination and consideration of sedimentary effects upon preservation, shows that leaves are still attached although their preservation is poor. The genus is rediagnosed and compared with other similar lepidophytes.

ESKDALIA was originally thought to be a fern rachis by Kidston (1883), but was later clearly shown to be a ligulate lycopod shoot (Chaloner 1967; Thomas 1968). Such specimens have very distinct longitudinally elongated oval areas which have been interpreted as leaf scars by comparison with other genera and because they lack maceratable cuticle. Stem cuticle can be prepared, but perforations are present at the sites of the ovals. Small depressions can be seen in the upper margins of many of the ovals and macerations showed them to be the remains of ligule pits. Similar cuticle with perforations and ligule pit tubes have been described many times from the Russian paper coal of the lower Carboniferous of the Moscow basin. They were originally described as species of *Lepidodendron* by Eichwald (1860), Auerbach and Trautschold (1860), and Göeppert (1861) or of *Bothrodendron* by Zeiller (1880, 1882). Zalessky (1915), however, named them as species of a new genus *Porodendron* and was followed by most Russian authors until they were referred to *Eskdalia* (Thomas 1968; Meyen 1972, 1976). Meyen (1976), however, also remarked that there is a similarity between *Eskdalia* and certain other Angaran lepidophytes, notably *Tomiodendron varium* (Radcz.) Meyen and those described as *Lepidodendron* (?) cf. *planum* by Rasskazova (1962) (now *Tunguskadendron borkii* Meyen and Thomas *in press*). Also, in comparison with *Angarodendron* and *Ulodendron*, Meyen made the suggestion that the perforations seen in such stem cuticles may possibly be the result of cuticle being absent from persistent leaves, rather than the leaves having been shed by means of definite abscission layers located at the levels of the stem cuticle perforations. There are other genera which similarly show cuticles with perforations but no ligule pits, even though they are leafy and probably heterosporous. So suggestions have been made about leaves having no cuticle, ligules being either short or situated on unclear or unpreserved leaves, or such axes being remnants of cones that have lost their sporophylls and sporangia.

There is an obvious need for much more information on this topic. It was therefore thought to be highly desirable to reinvestigate *Eskdalia* and certain similar forms in an attempt to clarify this situation.

LOCALITIES AND STRATIGRAPHY OF NEW MATERIAL

Two new collections were available for study, each with several specimens. Both are housed in the collections of the Geological Institute of the Academy of Sciences in Moscow. Collection 1 constitutes specimen nos. 3779/81-92 and 4034/2-5. They are preserved on a blue green siltstone from 'Kyutyungde' locality, the right bank of the Kyutyungde River in Eastern Siberia, 12 km from its mouth and 2 km below the mouth of the Khalomalokh (70° 43' North, 123° East). The sediments have been dated by associated marine fauna as Tournaisian (it is difficult to be more precise, but it is not equivalent to that part of the Tournaisian that is referred in W. Europe to the Devonian). Collection 2 Constitutes specimen nos. 4034/1 and 9. They are preserved

in grey shale from the number K-3 borehole (depth 930 m), between the Kempendyai and Namana Rivers, 65 km east of the village of Kempendyai, Eastern Siberia (roughly 62° North, 119° 48' East). It is dated as the upper part of the Kurunguryakh suite (Visean) of the Vilyui syncline (Kolodeznikov 1982). The miospores from 'Kempendyai' have been described by Pashkevich *et al.* (1978).

DESCRIPTION

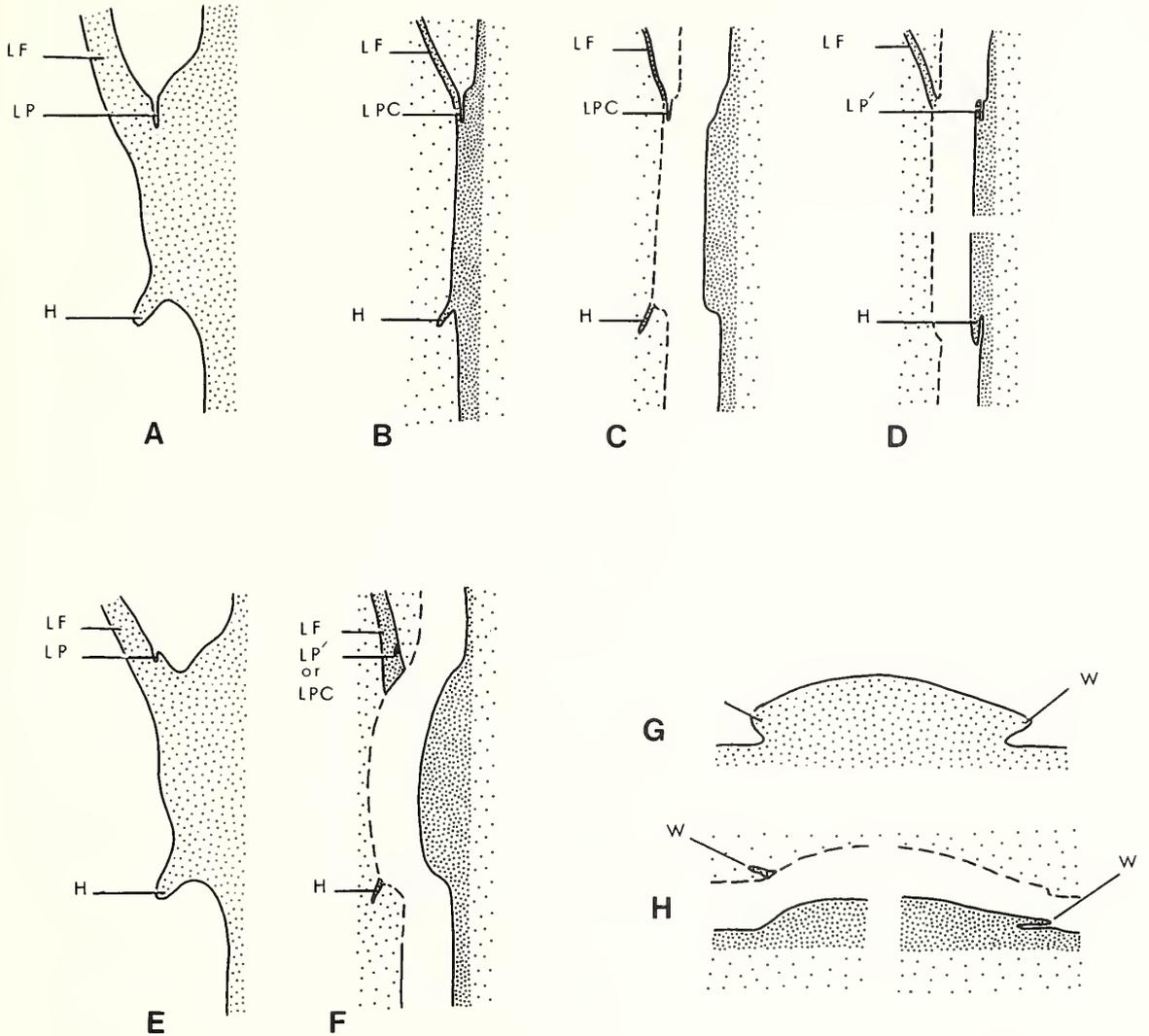
All the specimens clearly show the longitudinal elongated oval areas typical of *Eskdalia* and remains of ligule pits can be seen in their upper angles. One minor difference between the new specimens and those described previously by Zalessky (1915), Chaloner (1967), and Thomas (1968) is the manner of preservation of the pits. The earlier specimens had tubes of cuticle representing the inner linings of the actual pits. The new Russian specimens have their pits preserved as casts similar to those described by Meyen (1972, 1976) and Thomas and Purdy (1982).

Specimens from both collections were examined closely for details. This involved transferring portions of stems using Darrah solution (Darrah 1952), degaging around the edges of the ovals and at the sides of the stems, and macerating stem compressions using Schulze's solution followed by dilute ammonia solution. Both collections show some variation, but there appear to have been enough differences to treat them initially as new species.

The maximum size of the stem fragments is governed by the dimensions of the rock samples, but we have the first evidence of branching within this genus. Two specimens from the borehole each show an equal dichotomy even though these are amongst the smallest fragments of stem referable to this genus. Length of preserved axis is therefore not the controlling factor in showing whether the plants branched.

Leaf abscission producing oval leaf scars is one of the main diagnostic characters of *Eskdalia* as interpreted by Chaloner (1967) and Thomas (1968). The degaging and transfer techniques, however, have revealed a very suggestive fact. The longitudinally elongated ovals are outlined by a very thin line of compression which continues into the matrix. The extra compression revealed by degaging and transferring clearly shows that there was a narrow band of compression extending into the matrix around the oval. This compression can be traced upwards into what must have been a persistent leaf and downwards into a distinctive heel. The ovals cannot therefore be true abscission scars. Instead, they must be artificial scars produced by the splitting of the carbon compression during the fracturing of the rock. Such breakage is similar to that described in *Angarophloios* Meyen (1976) and in *Tomiodendron* Radezenko by Meyen (1976) and Thomas and Purdy (1982). It also parallels the artificial loss of leaves shown by Chaloner (1967) and Mensah and Chaloner (1971).

With this new concept of leaf cushion in mind, we can interpret other features shown on the stems. The central ridges shown on the ovals are most probably the very basal expressions of laminae midribs (keels) rather than any features formed by abscission. Some stems have ovals which seem to extend downwards into tails (4034/3-2). This would originally have suggested different-shaped scars, but now they can be interpreted as being the result of heel impressions extending the more normal oval leaf cushion impressions. In this case the heels were closely pressed to the stem and were not separated by rock matrix (text-fig. 1D). This formation of an apparently different character by sedimentary effects is paralleled by similar effects on the ligule pit. The pits can sometimes become filled with sediment producing a pit cast. Meyen (1972, 1976) has clearly shown this to happen in *Tomiodendron* Radezenko, *Ursodendron* Radezenko, and *Angarodendron* Zalessky (see also Thomas and Purdy 1982). If a ligule pit cast is formed in the impression, the corresponding stem compression will obviously have no ligule pit cuticle (text-fig. 1C). Cuticle preparation from the upper angle of such ovals will never reveal the plant to be ligulate. If the ligule pit does not become filled with sediment, it will separate with the main part of the stem compression during the fracturing of the rock (text-fig. 1D). Maceration will then reveal a cutinized ligule pit as described by Chaloner (1967) and Thomas (1968). Such effects of sedimentary infillings on the resultant fossils are all summarized in text-fig. 1. Both collections showed sedimentary infillings of the ligule pits, so no cuticular linings could be prepared as was achieved with *Eskdalia minuta*.



TEXT-FIG. 1. Diagram to illustrate the interrelationships of sedimentation and rock fracture upon the *Eskdalia* type of leaf cushion. A, E, and G represent plant tissues seen in section before fossilization (leaf = LF, ligule pit = LP, heel = H, and lateral Wings = W). The others represent compressed plant material (dark stippling) embedded in rock matrix (light stippling). A, B, and C represent successive stages of plant compression and rock fracture as seen in longitudinal section. In C, the ligule pit cast is formed (LPC) and the leaf and heel are lost. D represents an alternative situation to C after rock fracture. Here there is no ligule pit cast although the pit is retained as a compression (LP') and the heel is pressed against the stem. Either may occur independently so there are four possibilities of preservation. E and F represent similar stages to A and C except that a ligule pit compression or cast is formed further up the leaf lamina and is never seen. The heel may also be visible as in D. G and H are similar stages seen in transverse section. Here the lateral wings may be lost or shown as side extensions to the cushion.

One other sedimentary effect is also of interest to us here. Both types of stem can be seen in transverse section either on the cut side of the core or on the fracture surface of the rock. In both cases there is a compressed central core of coaly plant material inside the matrix of the stem. This is almost certainly the remains of the protostele even though no tracheids can be seen or prepared by maceration.

Stem cuticle was prepared from both collections by maceration with Schulze's solution. Both showed a simple epidermal arrangement with polygonal equal-sided to longitudinally elongated cells. The anticlinal walls are straight and the periclinal walls are flat, smooth, and without the cuticular lumps described from *E. minuta* by Thomas (1968). No cuticle could be prepared from the ovals, although cell outlines were clearly visible and similarly none was obtained from the leaves uncovered from the matrix.

DISCUSSION

The available information therefore allows us to rediagnose the genus *Eskdalia* and to name the two new species *E. kidstonii* and *E. siberica*. The morphological and cuticular characters of the two new species together with those of *E. minuta* Kidston, are summarized in Table 1. There are differences in leaf cushion and ligule pit sizes, although these two are not directly related. *E. kidstonii* shows much more regularity in cushion size and cushion spacing than the other species, whereas *E. siberica* shows the greatest variation. The latter species also differs in having longitudinal furrows running between the leaf cushion on some of the stems. Stem epidermal details are not sufficiently distinctive to separate the species, although the ranges of cell sizes are not identical. The epidermal lumps described from *E. minuta* are not, however, found in the other two species. *E. kidstonii* alone shows occasional dichotomies, although, as mentioned earlier, this feature is not related to the comparative lengths of the specimens. The other species include large stems but show no evidence of branching. Leaf, heel, and stele sizes are unfortunately not known for all the species.

COMPARISON

Eskdalia in its new concept is a sparsely branched ligulate lycopod shoot. It has persistent leaves borne on leaf cushions which also possess distinct heels at their lower ends. There are many other similar genera and doubtfully placed specimens which now need to be reconsidered in the light of this new interpretation of *Eskdalia*. Some are clearly better understood than others and some may never

TABLE 1. Comparison of *Eskdalia kidstonii* sp. nov. and *E. siberica* sp. nov. with the type species of the genus, *E. minuta*

	<i>E. minuta</i>	<i>E. kidstonii</i>	<i>E. siberica</i>
Size of leaf cushions (mm)	4.5-5.5 × 3.4	2 × 1.2	1.2 × 0.6-1.3
Ligule pits (μm)	flask shaped 400 × 150	cylindrical 200 × 100	globular 300 × 150
Heels (mm)	?	0.7	?
Leaves (mm)	?	4	4
Stem epidermal cells (μm)	130 × 25-35 with lumps	60-125 × 25 no lumps	90-150 × 25 no lumps
Observed stem sizes (mm)	110 × 4-25	75 × 4	130 × 13
Branching	none	occasional dichotomies	none
Stele/axis ratio	?	1:3	1:4

TABLE 2. Comparison of *Eskdalia* and other genera of ligulate lycophytes

	Meyen (1976)	<i>Eskdalia</i> (1903)	<i>Lepidodendron perforatum</i> Lacey (1962)	<i>Lepidostigmaria</i> Kräusel and Weyland (1949)	<i>Forondron</i> Zalesky (1915)	<i>Psudolepidodendron</i> V. Ananiev (1974)	<i>Tomiodendron</i> Radezenko emend. Meyen (1972)	<i>Ursodendron</i> Radezenko (1960)	<i>Ulodendron</i> L & H emend. Thomas (1967)	<i>Lycopodiopsis Renauli</i> emend. Lemoigne and Brown (1980)	<i>Vahneryodendron</i> Jennings (1972)
Leaf cushion/base shape	transversely elongated, lenticular, rhombical to nearly square	elongated oval	elongated oval	elongated oval	elongated oval or cordate	elongated oval	elongated oval, rhomboid, or sagittate	transversely elongated	rhomboidal	rhomboidal to transversely elongated	quadrangular to hexagonal
Leaf abscission	-	+	+	+	+	+	+	+	+	+	+
Axillary fold	+	+	+	+	+	+	+	+	+	+	+
Heel	+	+	+	+	+	+	+	+	+	+	+
Corner folds	+	+	+	+	+	+	+	+	+	+	+
Vascular scar	-?	+	+	+	+	+	+	+	+	+	+
Infrafoliar bladder	+	-	-	-	-	-	+	+/-	-	+	+?
Phyllotaxis	lepidodendroid	lepidodendroid	lepidodendroid	sigillarioid and parichnos	lepidodendroid	lepidodendroid	sigillarioid or lepidodendroid	lepidodendroid	lepidodendroid	lepidodendroid	lepidodendroid
Leaf shape	?	linear	slender	short, narrow, Lax	linear	?	?	?	long and linear	long and linear	nearly triangular
Branching	?	rarely dichotomous	frequently dichotomous	?	?	occasionally dichotomous	+/-	repeatedly forked	frequently dichotomous	?	frequently dichotomous (often equally)

be satisfactorily included in any well-defined genus. The apparent lack of leaf cuticle is an important feature which deserves careful consideration. Rock fragmentation can give an illusion of leaf abscission, and maceration will not reveal the presence of leaves. Therefore, we must be very cautious when interpreting similar specimens and in making generic comparisons.

We believe there are three taxa which are better included as *Eskdalia*. They are *Porodendron*, which has already been described as a synonym of *Eskdalia* by Thomas (1968), *Tomiodendron varium* (Radcz.) Meyen, and *Pseudolepidodendropsis igrischense* (A. R. Ananiev) V. A. Ananiev. Those other taxa which are thought to be better kept distinct from *Eskdalia* are compared in Table 2.

Porodendron was originally described by Zalesky (1909) for specimens from Mugaoda. He included other specimens of Auerbach and Trautschold that were preserved rather differently as cuticles. Zalesky later (1915) described these cuticles together with some compression-impression specimens as species of *Lepidodendron*, although Bode (1929) retained them in *Porodendron*. Zalesky's original *Porodendron* specimens are very poorly preserved and we see no characters to distinguish them from *Eskdalia*. The specimens described by Zalesky in 1915 have been referred to *Eskdalia* by Thomas (1968) because of the very great similarity between their cuticles. Both stems have simple epidermal cells which are either isodiametrical or elongated and neither have stomata. The stem cuticles all possess regular perforations which have been described as leaf scars and many have their ligule pits preserved in the upper angles of the perforations. If the illustrations of Zalesky are carefully examined, certain other features are apparent. His plate 2, figs. 5 and 5a, illustrates a leafy specimen, while plate 6 shows a further specimen with indications of heels. Unfortunately, we have no idea of the whereabouts of his specimens, for they have either been destroyed, lost, or mislaid. The lack of leaf and heel cuticles in the paper coal cuticles was originally explained as leaf abscission, but it could equally well be the result of their having a very thin cuticle which was not preserved. Evidence for this alternative view has been provided by Wilson (1931) who described some of the Russian paper coal cuticles that had fragments of thinner cuticle attached to the basal angles of some ovals. The stomata present in these thinner cuticles suggest that they were fragments of the basal parts of leaves.

Zalesky's material clearly shows variation but, without examining the original material or additional stem specimens, it is impossible to decide if such variation is gradual or not. We cannot therefore be certain if it suggests intraspecific variation or whether there is more than one species present within the collection. Leaving apart this question of specific independence of these varieties we believe that they can all be included within *Eskdalia*.

Meyen (1972, 1976) has reinvestigated the type of material of *Prelepidodendron varium* Radzenko and come to rather a different conclusion the generic identification. The specimens were shown to have persistent leaves and axillary-positioned ligule pits, so for these reasons the species was transferred to *Tomiodendron* (Radzenko, 1955) 1956 emend. S. Meyen 1972. It was noted, however, that the specimens differed from other *Tomiodendron* species by having dichotomizing axes and much small leaf cushions. No wings have been shown on its leaf cushions and infrafoliar bladders are not convincingly shown. Also, the cushions have asymmetrically attenuated lower parts unlike the other species which have more oval cushion outlines. We are now suggesting that the species is better included within *Eskdalia*. Its persistent leaves and axillary ligule pits indicate eskdalian affinity. The

EXPLANATION OF PLATE 62

Eskdalia kidstonii sp. nov.

Figs. 1-3. Holotype, no. 4034/1a-1. 1, core sample 4034/1a with holotype, $\times 1$. 2, 3, enlargements of same, $\times 10$.

Fig. 4. No. 4034/1a-3, $\times 10$.

Figs. 5, 6. No. 4031/1-b(g). Transfer preparation on cellulose acetate film. Stereopair, $\times 10$.

Fig. 7. No. 4034/1a-4. Broken end of axis. Enlargement of the lower of the two fractured axes seen on the right-hand side of fig. 1, $\times 10$.



THOMAS and MEYEN, *Eskdalia*

pits are flask-shaped as in *Eskdalia*, whereas those of other *Tomiodendron* species are much more massive and do not have narrowed necks. *Eskdalia* has distinct heels which could be preserved in two different ways, which would give two rather different results when the rock was split (text-fig. 1C, D). When flattened against the stem such heels would appear as attenuated lower ends of the leaf-base oval areas. Therefore the new combination of *E. varia* (Radcz.) Thomas and Meyen is proposed here.

The third probable member of *Eskdalia* is the lepidophyte originally described by A. R. Ananiev (in Ananiev and Graizer 1957) as *Sublepidodendron igrischense* and subsequently referred by V. A. Ananiev (1974) to his monotypic genus *Pseudolepidodendron*. The only evident difference between *Eskdalia* and *Pseudolepidodendron* is the presence in the latter of vertical leaf cushion fusion, with the corresponding lack of heels, and rather deep grooves between the orthostichies. Variation in *P. igrischense*, as shown by Ananiev, is similar to that of Zalesky's material mentioned earlier. Usually the cushions are fused into orthostichies, but sometimes they are very clearly not. Another lepidophyte showing the same type of stem relief is *Lepidodendron concinna* Radczenko, 1960. However, this species shows denticulate leaves (Meyen 1976) and there is no evidence of a ligule. Although the leaf structure of *P. igrischense* is unknown, it seems possible that *L. concinna* might be a younger synonym of *P. igrischense*. Such a synonym must be supported by a more detailed study of both species. Meanwhile, in spite of the lack of data on leaf structure, it seems reasonable to include *P. igrischense* within *Eskdalia*. The new combination *E. igrischensis* (A. R. Ananiev) is therefore proposed.

The other taxa included in Table 2 are other ligulate lycophytes, but they all differ in sufficient ways to remain distinct from *Eskdalia*. *Valmeyrodendron* was described by Jennings (1972) for dichotomously branching lycopod systems with eligulate leaf cushions. However, we believe the genus to be ligulate because some of the Jennings's figures (notably figs. 4, 5, 9, 10, and 22) show structures in the upper angles of the leaf cushions comparable to the ligule pits described by Thomas (1968) and Meyen (1972, 1976). However, it is clear that no single character is consistently important for this purpose. All seem to have some characters of the other genera which makes their separation more difficult. Indeed, we are inclined to believe that *Angarodendron*, *Lycopodiopsis*, and *Valmeyrodendron* are synonyms, even though we are leaving them separate here. Future work might well reveal new synonyms or characters that will precipitate a whole new approach to naming such genera.

SYSTEMATIC PALAEONTOLOGY

Genus *Eskdalia* Kidston 1903

Synonymy. *Eskdalia* Kidston 1903. *Porodendron* Zalesky 1909. *Porodendron* Zalesky; Nathorst (1914, p. 68). *Porodendron* Nathorst (*non* Zalesky); Bode (1929, p. 134). *Eskdalia* Kidston; Thomas (1968, p. 442).

Type species. *E. (Caulopteris) minuta* Kidston; (Kidston 1883, p. 541, pl. 31, figs. 1, 1a).

Emended diagnosis. Leafy lycopod shoot. Leaves in low angle spirals. Basal attachment areas of leaves (leaf cushions) with heels and sometimes shoulders. Ligule pit at apex of leaf cushion, often appearing as a ridge. One simple vascular trace slightly above middle of false leaf scar. No parichnos present.

EXPLANATION OF PLATE 63

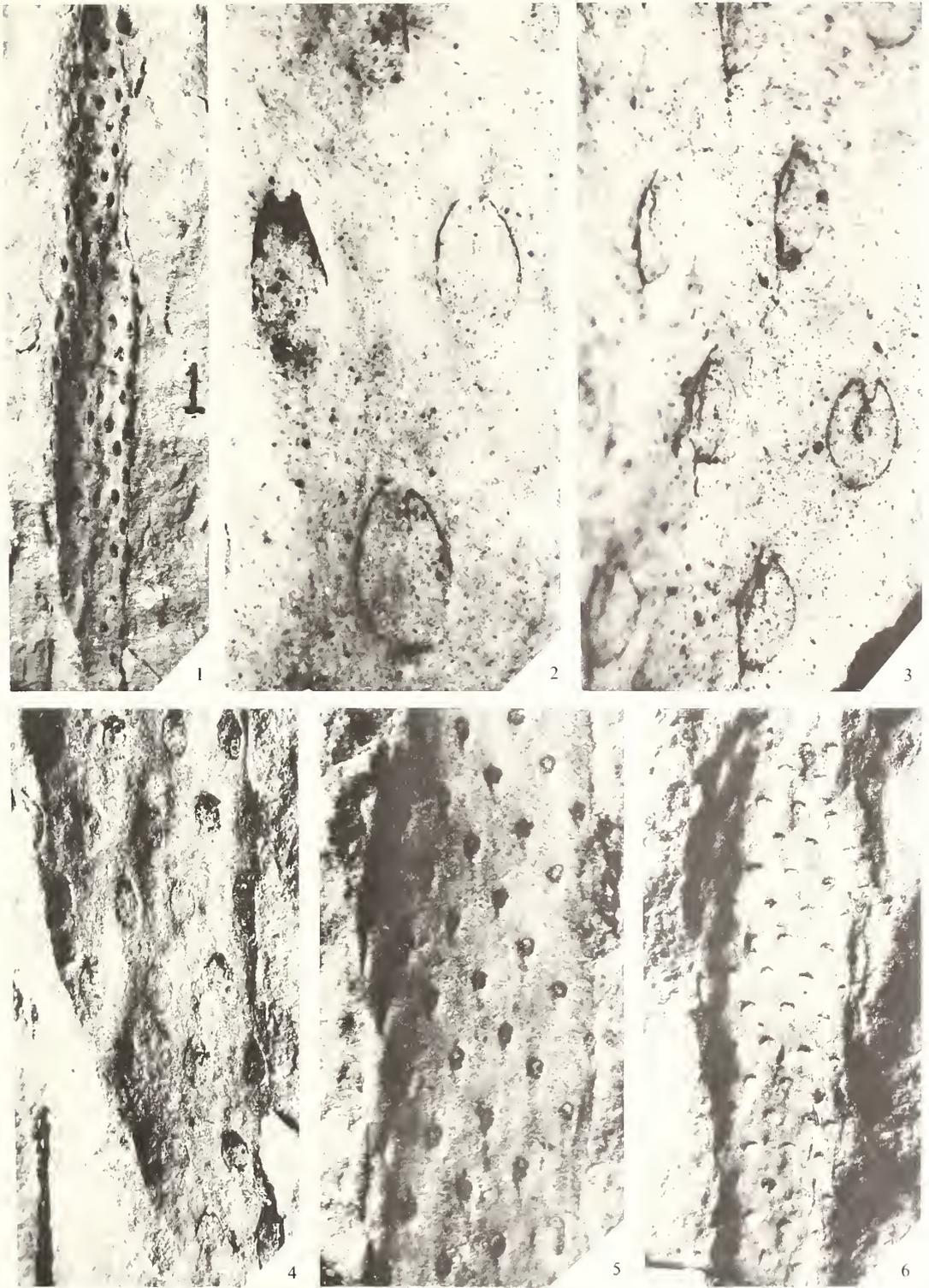
Eskdalia siberica sp. nov.

Figs. 1-3. Holotype, no. 4034/4-1. 1, $\times 1$. 2, $\times 10$. 3, photographed under alcohol, $\times 8$.

Fig. 4. No. 4034/32, $\times 3$.

Fig. 5. No. 3779/88-1, photographed under alcohol, $\times 3$.

Fig. 6. No. 3779/82, $\times 3$.



THOMAS and MEYEN, *Eskdalia*

Eskdalia kidstonii sp. nov.

Plate 62, figs. 1-7

1972 *Eskdalia* sp. Meyen, p. 154, pl. 1, figs. 3-6; text-fig. 4.*Type specimen.* Geological Institute of the Academy of Sciences, Moscow, no. 4034/4.*Locality.* 'Kyutyungde', Eastern Siberia (70° 43' North, 123° East).*Horizon.* Tournaisian.*Derivation of name.* For the late Dr. Robert Kidston.

Diagnosis. Stems up to 4 mm broad, with occasional dichotomies. Leaves in spirals, sometimes in nearly horizontal rows. Leaves linear and tapering up to 4 mm long, heels 0.7 mm long. Leaf cushions oval, 2 mm long, 1.2 mm broad, separated vertically by 2.0-2.5 leaf cushion lengths and horizontally by 1.0-1.5 leaf cushion breadths. Stem surface epidermal cells rectangular to polygonal, 60-125 μm long and 20-25 μm broad. Anticlinal walls straight, periclinal walls flat and smooth. Ligule pits linear, about 200 μm long.

Eskdalia siberica sp. nov.

Plate 63, figs. 1-6

Type specimen. Geological Institute of the Academy of Sciences, Moscow, nos. 4034/1-2, 1a-2 (counterpart).*Locality.* 'Kempendyai', Eastern Siberia (62° North, 119° 48' East).*Horizon.* Visean (Upper part of the Kurunguryakh suite).*Derivation of name.* From Siberia.

Diagnosis. Stems up to 13 mm broad. Leaves in spirals, sometimes in nearly horizontal rows. Leaves linear and tapering up to 4 mm long. Leaf cushions oval, 2 mm long and 1.3 mm broad, separated vertically by 1.0-1.5 cushion lengths and horizontally by 0.5-1.0 cushion breadths. Stem surface cells rectangular and polygonal, 90-150 μm long and 25 μm broad. Anticlinal walls straight, periclinal walls smooth. Ligule pits globular, about 340 μm long.

Eskdalia varia (Radcz.) comb. nov.1960 *Prelepidodendron varium* Radczenko, p. 18, pl. 4 (figs. 1, 1a, 2-4).1972 *Tomiodendron varium* (Radczenko); Meyen, p. 150, pl. 1 (fig. 2), text-fig. 2.1962 ?*Lepidodendropsis hirmieri* A. R. Ananiev and Mikhilova, p. 222, pl. C-32 (fig. 5).*Eskdalia igrischense* (A. R. Ananiev) comb. nov.1957 *Sublepidodendron igrischensis* A. R. Ananiev in Ananiev and Graizer, p. 999, figs. 2-4.1974 *Pseudolepidodendron igrischense* (A. R. Ananiev); V. A. Ananiev.

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A NEW CONIFER GENUS FROM THE LOWER CRETACEOUS GLEN ROSE FORMATION, TEXAS

by JOAN WATSON *and* HELEN L. FISHER

ABSTRACT. A new genus, *Glenrosa*, is erected to include two species of fossil conifer shoots, *G. texensis* (Fontaine) comb. nov. (the type species) and *G. pagiophylloides* (Fontaine) comb. nov. which are found interspersed with conifer species belonging to the family Cheirolepidiaceae. The stomatal arrangement of the new genus, which is similar to that of the extant angiosperm *Nerium oleander* L. of the Apocynaceae but unlike any other gymnosperm, shows extreme xeromorphy and is probably an adaptation to an arid environment.

THE flora of the Lower Cretaceous Glen Rose Formation in central Texas, which was first described by Fontaine (1893), comprises some five or six well-characterized conifers together with two or three bennettitalean species and a number of cones which have not yet been satisfactorily attributed to parent plants. The original collection on which Fontaine worked was made by Mr. J. W. Harvey of Glen Rose and is now housed in the Smithsonian Institution. The specimens are few in number and mostly fragmentary but the cuticles are exquisitely preserved in the fine dolomitic limestone. This small but important flora is currently being revised and continues to yield surprising results. Two of the conifers which have already been redescribed (Watson 1977) proved to be members of the extinct family Cheirolepidiaceae. Both species, *Frenelopsis alata* (K. Feistmantel) Knobloch and *Pseudofrenelopsis varians* (Fontaine) Watson have a most unusual jointed, xeromorphic appearance and *P. varians* has an extraordinary cuticle well over 100 μm thick. The two conifers redescribed below, whilst not unusual in morphology, have proved to possess a stomatal arrangement unique amongst conifers.

SYSTEMATIC PALAEOLOGY

The microscope preparations are housed with their parent specimens in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Hunterian Museum, Glasgow. A duplicate set of preparations has been deposited in the British Museum (Natural History) (numbers V58652-V58653).

CONIFERALES *incertae sedis*
Genus *Glenrosa* gen. nov.

Type species. Brachyphyllum texense Fontaine, 1893, p. 269.

Diagnosis. Coniferous tree or shrub with spirally arranged leaves, adpressed or falcate. Stomata occurring in groups, each group confined to sunken chamber which forms communal stomatal pit narrowing towards rim.

Glenrosa texensis (Fontaine) comb. nov.

Plate 64; text-figs. 1, 2, 4A

1893 *Brachyphyllum texense* Fontaine, p. 269, pl. 38, fig. 5; pl. 39, figs. 1, 1a.

Emended diagnosis. Branched shoots bearing leaves in a simple helix with 1 + 2 parastichies. Leaves scale-like, adpressed, arising from centre of rhomboidal leaf-base cushion; leaf and basal cushion combined typically 3 mm long and 2.5 mm wide. Free part of leaf up to one fifth of total length. Leaf margins converging at up to 70° towards bluntly pointed apex; fimbriate, hairs up to 65 μm long. Leaf biconvex in section with prominent median keel on abaxial surface continuing onto cushion. Stomatal chambers oval, occurring on both surfaces; four to eight stomata per chamber; long finger-like processes interdigitating across opening of chamber. Abaxial chambers scattered over whole surface, up to eight per square mm; typically 112 μm long and 69 μm wide. Adaxial chambers smaller, arranged in well-spaced curving row, inset from but following leaf margin; typically 90 μm long and 66 μm wide. Stomatal apparatus commonly 75 μm long and 50 μm wide with four to six subsidiary cells, sometimes shared between adjacent stomata. Ordinary epidermal cells of both surfaces rectangular, arranged in longitudinal files converging at apex; average size 38 μm long and 16 μm wide. Anticlinal walls straight, pitted, up to 5 μm wide. Well-developed cutinized hypodermis of elongated cells present under non-stomatal areas.



TEXT-FIG. 1. *Glenrosa texensis* (Fontaine). A, USNM 326800, lectotype, $\times 1$. B, USNM 326801, the other branched specimen previously figured by Fontaine, $\times 1$. The leaf outlines on both of these specimens are now known to be indian ink.

EXPLANATION OF PLATE 64

Figs. 1-7. *Glenrosa texensis* (Fontaine). 1, 4-6 are scanning electron micrographs. 1, USNM 192358, single leaf showing scattered stomatal chambers on inside of abaxial surface and the outside of part of the adaxial surface, $\times 25$. 2, USNM 192384, light micrograph of similar leaf, $\times 25$. 3, Pb 2093, part of adaxial cuticle showing curving row of stomatal chambers, $\times 100$. 4, USNM 192358, part of fig. 1 showing the fimbriate margin and the stomatal chambers, $\times 100$. 5, USNM 326800, outside of abaxial surface showing interdigitating papillae sealing stomatal chamber, $\times 200$. 6, USNM 192358, outer view of single adaxial stomatal chamber showing details of finger-like papillae, $\times 400$. 7, Pb 2093, light micrograph of single abaxial stomatal chamber showing papillae arising around rim; stomata missing, $\times 400$.



1



2



3



4



5



6



7

Material and occurrence. The lectotype USNM 326800 was figured by Fontaine (1893, pl. 38, fig. 5). *G. texensis* (Fontaine) is known from two localities in the U.S.A.: Glen Rose, Texas, the type locality which yielded excellent specimens, and Trent's Reach, Virginia, from where very short lengths of shoot have been identified. The Glen Rose Limestone in the Trinity Group (Lower Cretaceous) is considered to be late Aptian to earliest Albian. The Trent's Reach locality has been dated as Barremian to Aptian. The total Smithsonian collection of this species numbers only five specimens, plus a number of cones which could prove to belong to it. All the cones are from Glen Rose. Specimen Pb 2093 from Trent's Reach is in a small collection of fossil plants bearing old Smithsonian numbers in the Hunterian Museum, Glasgow (see Watson 1977, p. 718).

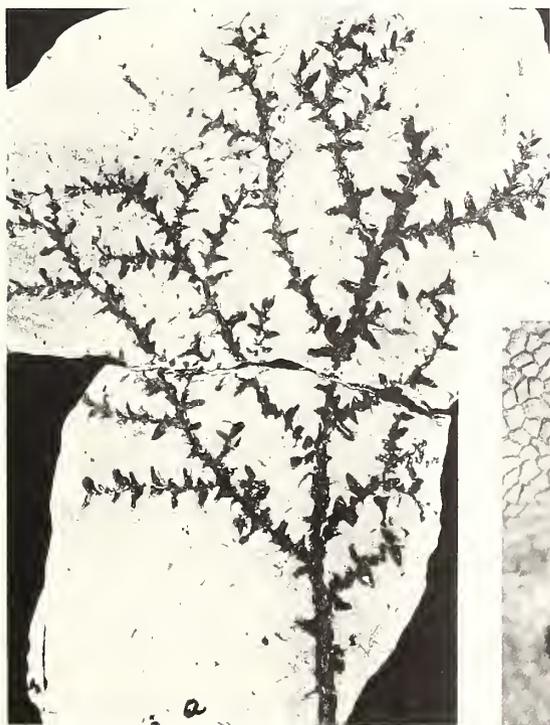
Description. It should be pointed out that the leaves showing only as black outlines, previously figured by Fontaine (1893) and refigured here as text-fig. 1, were at first assumed to have rims of cuticle remaining, and the diagnosis was made on this assumption. It is now clear, however, that they are drawn in, probably in indian ink and presumably by Fontaine. There is no reason to suppose that they are not accurately drawn, as the impressions left by the bulging leaves and bases are very clear. The persistent leaves have cuticle which is thick, beautifully preserved and macerates easily and quickly; as a result several preparations of whole leaves could be obtained without difficulty. Plate 64, fig. 1 clearly shows the stomatal chambers of *G. texensis* scattered over the whole of the abaxial surface and ordered in a well-spaced curving row following the leaf margins on the adaxial surface. The outside surface of the cuticle viewed with the SEM (Pl. 64, figs. 4–6) shows papillae around the rim of the stomatal chamber interdigitating and effectively sealing the opening. It is clear from Plate 64, fig. 7 that some of these finger-like protuberances are borne by certain epidermal cells around the rim of the chamber. In this preparation the inner parts of the chamber, including all the stomata, are missing. In preparations with complete chambers it was much more difficult to establish that at least some of the subsidiary cells also bear these



TEXT-FIG. 2. *Glenrosa texensis* (Fontaine). A, USNM 326800, inside of abaxial cuticle showing details of a single group showing four stomata, $\times 400$. B, USNM 192358, the longest hairs seen on the leaf margin, $\times 400$.

EXPLANATION OF PLATE 65

Figs. 1–5. *Glenrosa pagiophylloides* (Fontaine). 3, 4 are scanning electron micrographs. 1, USNM 326803, one of Fontaine's figured specimens showing particularly large and well-shaped leaves, $\times 1$. 2, USNM 326802A, lectotype showing branching pattern, $\times 1$. 3, USNM 326802A, distal portion of leaf showing strongly papillate surface; openings of stomatal chambers are just visible scattered over surface, $\times 50$. 4, USNM 192377, light micrograph showing long pointed hairs on ordinary epidermal cells, $\times 400$. 5, USNM 192377, light micrograph showing distribution of stomatal chambers, some with stomata present, some without; cutinized hypodermis can be seen top left, $\times 100$.



WATSON and FISHER, *Glenrosa*

papillae. This was done by viewing cut edges of cuticle at very high angles of tilt in the SEM. Text-fig. 4A is a reconstruction of a stomatal chamber in vertical section compiled from several of these SEM views.

The specimens from the two known localities show minor differences in that the Glen Rose specimens have slightly darker cuticle and a higher stomatal density. The shoots of *G. texensis* on the Trent's Reach blocks, particularly USNM 192358, are present as very short lengths amongst larger shoots of the conifer *Pseudofrenelopsis parceramosa* (Fontaine) Watson. Fontaine (1889, p. 220) stated in his description of *P. parceramosa* that it is found in close association with *Brachyphyllum crassaule* Fontaine with few other species present. Clearly Fontaine considered all the small fragments to be *B. crassaule*, not surprisingly since *G. texensis* was detected initially only in cuticle preparations. The Trent's Reach *G. texensis* has been used to illustrate cuticle features on Plate 64. The cuticle of *B. crassaule* is clearly distinct and will be described elsewhere.

Glenrosa pagiophylloides (Fontaine) comb. nov.

Plate 65; text-figs. 3, 4B

1893 *Sequoia pagiophylloides* Fontaine, p. 276, pl. 42, figs. 1–3a.

Emended diagnosis. Branched twigs bearing falcate leaves diverging radially, standing away from axis at 80° or less. Free leaf up to 3 mm long, 2 mm wide at base tapering to acute, rounded apex, triangular in cross section; lower angle forming median keel continuing onto cushion, upper surface flat, leaf margins sharp, entire. Cuticle of all surfaces up to 10 µm thick. Stomatal chambers scattered over all surfaces, up to four stomata per chamber. Subsidiary cells of adjacent stomata often shared, some bearing long pointed papillae. Stomatal chambers having more or less circular rim, averaging 78 µm diameter, up to seven per square mm. Ordinary epidermal cells of both surfaces small, polygonal, randomly arranged; each bearing a small papilla. Average cell size 28 µm long and 23 µm wide. Anticlinal walls straight, pitted, up to 5 µm wide.

Material and occurrence. The lectotype USNM 326802A was figured by Fontaine (1893, pl. 42, fig. 1). *G. pagiophylloides* (Fontaine) is known only from the Glen Rose Limestone in the Trinity Division of the Lower Cretaceous at Glen Rose, Texas. The stratigraphic horizon is probably late Aptian to earliest Albian. The Smithsonian collection comprises some ten specimens of *G. pagiophylloides* including both part and counterpart of the lectotype.

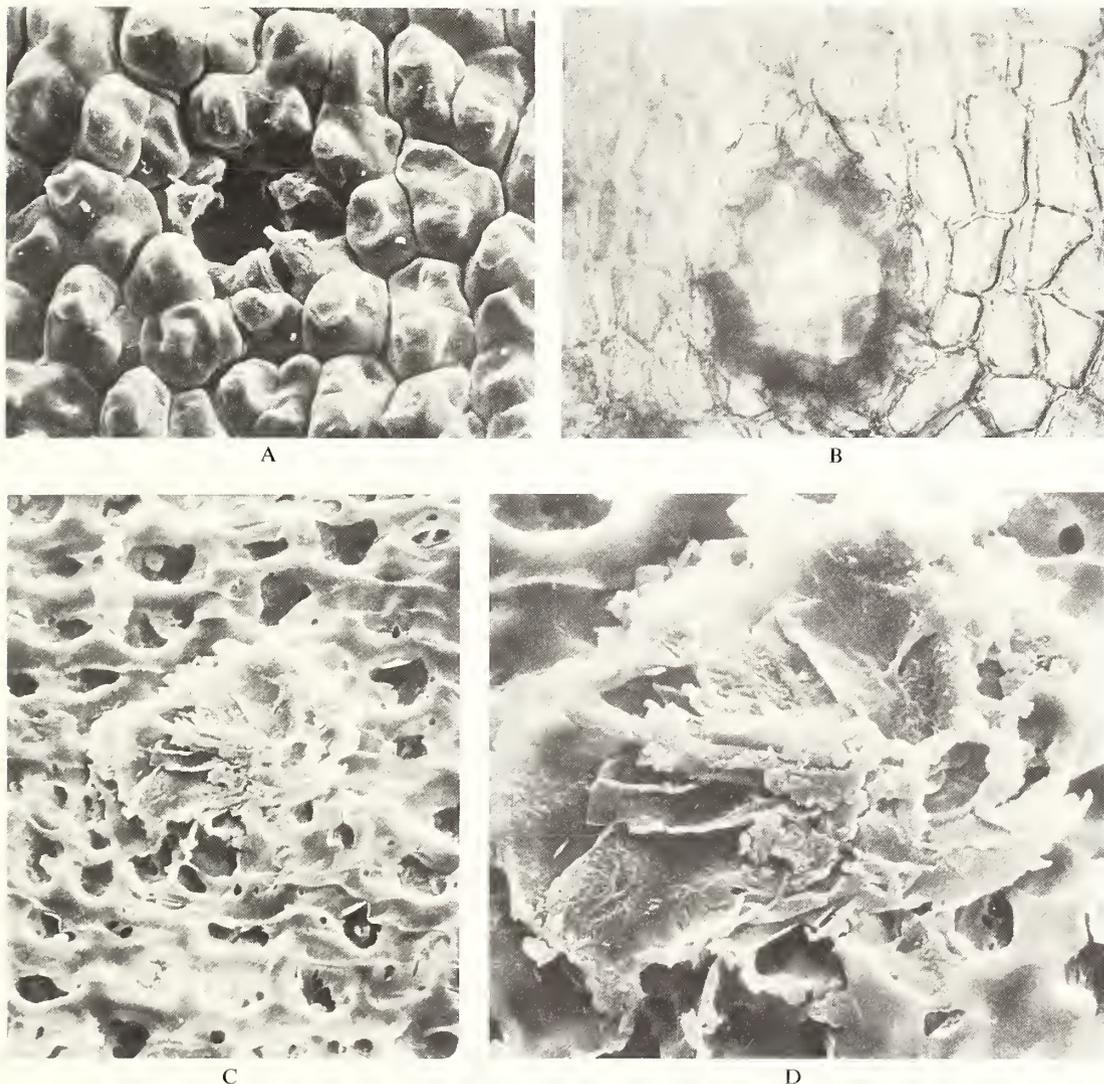
Description. The lectotype of *G. pagiophylloides* shows three orders of branching which appear alternate in one plane but we cannot say whether the shoots are truly complanate; nor are we able to determine the phyllotaxy. Fontaine (1893, pl. 42, fig. 1a) speaks of and illustrates inconspicuous facial leaves and much larger lateral leaves but we have been unable to confirm this. The axial parts of the shoots are rather crumbly and the facial leaves appear to us only as split and worn remnants. One would need to reveal the other side of a shoot by the transfer technique to be absolutely certain on this matter. Fontaine (1893, pl. 42, fig. 2a) also illustrates a double lateral keel on the leaves seen in side view, shown here in Plate 65, fig. 3. This is, however, an inconsistent feature which may well be a preservational effect.

The cuticle of *G. pagiophylloides* is very tough and easy to prepare though requiring a lengthy maceration time (up to twenty four hours). The surface of the leaf is extremely uniform, each cell bearing a short blunt papilla, but in one preparation some of the ordinary epidermal cells (Pl. 65, fig. 4) bear rather longer pointed hairs like those borne around the stomatal chamber. As with *G. texensis*, the exact configuration of the various cells and papillae within the stomatal chamber was very difficult to determine. The same technique of viewing cut edges in the SEM was used to draw up the reconstruction of a chamber in vertical section (text-fig. 4B).

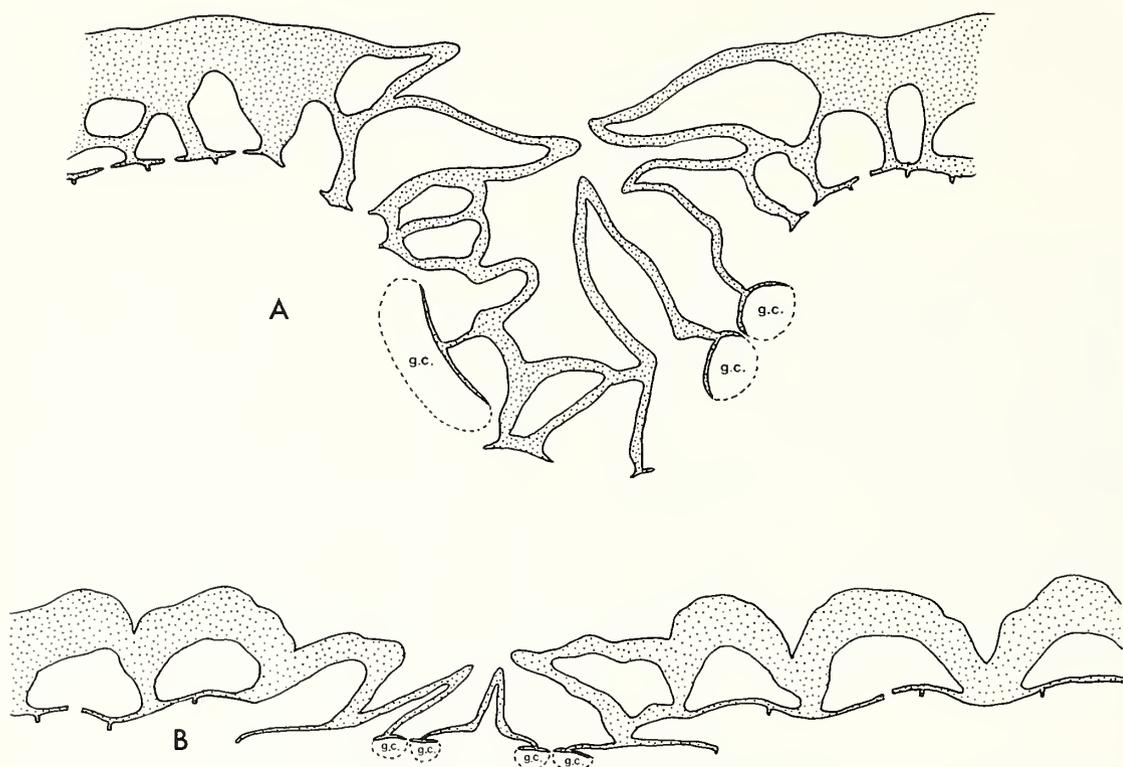
DISCUSSION AND COMPARISON

This interesting and unusual stomatal arrangement shown by *G. texensis* and *G. pagiophylloides* is unknown in any other conifer, fossil or living, and hence they can only be compared with each other. Confronted by two species of such a genus in the same flora, the possibility has not eluded us that they may represent adult and juvenile foliage of the same plant. All available specimens, however, are clearly distinct both in hand specimen and microscopically, and any such connection remains to be demonstrated.

The only other conifer we regard as even faintly reminiscent of *Glenrosa* is *Sphenolepis kurriana* (Dunker) Schenk from the Wealden of Germany and England which was recently revised by Fisher (1981). The stomatal chambers of *Glenrosa* could perhaps represent an extreme modification of the dense stomatal patches shown by *S. kurriana*. The *Glenrosa* form of stomatal distribution is most similar to that of the angiosperm *Nerium oleander* L. (Apocynaceae) but that species has much bigger stomatal chambers incorporating a larger number of specialized papillate epidermal cells than in the



TEXT-FIG. 3. *Glenrosa pagiophylloides* (Fontaine). A, C, D are scanning electron micrographs. A, USNM 326802A, outer surface showing papillae on ordinary epidermal cells and long hair-like papillae of subsidiary cells around opening of stomatal chamber, $\times 400$. B, USNM 192377, light micrograph showing subsidiary cell papillae in and around stomatal chamber, $\times 400$. C, USNM 326802, inner surface of cuticle showing cutinization of epidermal and hypodermal cells together with one stomatal complex, $\times 400$. D, detail of fig. C clearly showing two sets of guard cells, at least one other stoma obliterated, $\times 1000$.



TEXT-FIG. 4. A, *Glenrosa texensis* (Fontaine), reconstruction of vertical section of cuticle, $\times 700$. B, *Glenrosa pagiophylloides* (Fontaine), reconstruction of vertical section of cuticle, $\times 700$. Guard cells indicated by g.c.

conifer species. Thus the stomata of *N. oleander* are uncrowded and rarely share subsidiary cells. *N. oleander* is a classic textbook example of a species which has adapted to a hot, dry habitat. The stomatal spaces trap and contain still, humid air and in this way restrict the evaporation of trapped moisture. *G. texensis* shows further morphological adaptation to aridity by reduction to a scale-leaf whereas *G. pagiophylloides* has spreading leaves which potentially present a greater evaporation surface. This is compensated for by the papillae on the epidermal cells which would have contained the spread of trapped droplets of moisture on the surface, thus reducing the surface area available for evaporation.

The stomatal adaptation of *N. oleander* gives an indication of the type of habitat which *G. texensis* and *G. pagiophylloides* might have occupied. The *Glenrosa* species are found in association with the conifers *Frenelopsis alata*, *Pseudofrenelopsis parceramosa* and *P. varians* of the Cheirolepidiaceae; all five species showing extreme adaptation to arid conditions (Watson 1977). There is clear geological evidence (Daghlian and Person 1977) that the Glen Rose Formation represents an environment characterized by high salinity and high rates of evaporation.

The taxonomic position of *Glenrosa* can only be speculated upon at this stage but the family Cheirolepidiaceae must be a prime candidate. Research in recent years (Upchurch and Doyle 1981; Watson 1982) has shown that members of this family, characterized by the possession of *Classopollis* pollen, probably embraced a wide variety of habit and habitat with most species displaying extreme xeromorphic cuticle characters. It is possible that work about to commence on the dispersed cones in the Glen Rose flora will shed light on the affinities of *Glenrosa*.

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CRANE *GRUS* FOSSILS FROM THE MALTESE PLEISTOCENE

by E. MARJORIE NORTHCOTE

ABSTRACT. A coracoid (a syntype specimen) and a humerus, both of which are comparatively small, were formerly assigned to the large, extinct Pleistocene Maltese Crane *Grus melitensis*. They are reassigned to the much smaller extant Common Crane *G. grus*. This reidentification, supported by the discovery of additional Common Crane specimens from the Maltese Pleistocene, removes the evidence for maintaining, as previous authors have done, that the Maltese Crane had reduced flying power. This is the first record of Common Crane from the Maltese Pleistocene; it suggests that habitats with standing water existed on Malta c.125,000 years ago. The reassignment of the coracoid leaves the syntypal series for *G. melitensis* with two bones; from these a tarsometatarsus is chosen as lectotype and an emended diagnosis is given. This bone has splayed trochleae and a broad eminentia that is not clearly demarcated from the area intercondylaris.

LYDEKKER (1890, 1891), Harrison and Cowles (1977), Harrison (1979), and Northcote (1982a) have reported remains of the large extinct Maltese Crane *G. melitensis* Lydekker, 1890 from various Maltese Pleistocene sites. This crane was about the size of the Sarus Crane *G. antigone*, the largest living crane species (c. 8kg). Two bones appertaining to the forelimb, a coracoid and a humerus, have formerly been attributed to the Maltese Crane. Both of these bones are much smaller than those of the Sarus Crane. On account of this previous workers concluded that the Maltese Crane had reduced flying power. A purpose of this paper is to show that the coracoid and humerus do not belong to the Maltese Crane but to the much smaller extant Common Crane *G. grus* (c.6kg) that, as I will show here, was also present on Malta at that time. This necessitates a reconsideration of the Maltese Crane's flight ability. Lydekker did not designate a holotype for *G. melitensis* and his diagnosis for this crane cannot be substantiated. The coracoid is a syntype specimen; its reidentification leaves the syntypal series with two bones. From these it is important to select a lectotype upon which to base an entirely emended diagnosis for this species. Zoological nomenclature procedure follows the International Code (1961) (ICZN). Osteological nomenclature follows Baumel (1979).

DATE OF THE CRANE SPECIMENS

Maltese Pleistocene deposits are highly calcareous and no countable pollen that could be used for dating them has been found (Zammit-Maempel 1981, Northcote 1982b). Deposits that contain Maltese Crane remains such as those at Mnaidra, Tal Gnien, and Zebbug, also contain remains of the pygmy elephants *Elephas melitensis* Falconer, 1862 and/or *E. falconeri* Busk, 1867 (Adams 1870). These elephants were widespread on Sicily and Malta (Sondaar and Boekschoten 1967, p. 567) (the islands were connected by an isthmus at times during the Pleistocene, Zammit-Maempel 1977) and they flourished in the Upper Pleistocene during a period equivalent to the Ipswichian (Eemian) Interglacial Stage of more northern countries (Sondaar 1971). Gascoyne, Schwarcz, and Ford (1983) define this period by the interval 115–135 ka. This, then, is the date of the Maltese Crane and the associated crane remains that are the subject of this work.

IDENTIFICATION OF THE CRANE SPECIMENS FROM MNAIDRA

Material excavated by Adams (1870) from a Pleistocene fissure deposit at Mnaidra, Malta (Universal Transverse Mercator Grid VV 491651) is stored in the University Museum of Zoology, Cambridge

UMZC, Registered Number 252a. Fossilized bones were isolated from conglomerate using an electric mallet and drill and a clamped pin, then treated with 10–15% acetic acid, washed, dried, and laquered. As well as the Maltese Crane bones that I have described elsewhere (Northcote 1982*a*), the deposit yielded other crane specimens comprising a synsacrum fragment, the proximal extremities of both humeri, of the distal phalanx from a left digit majoris, of a right femur and of a left tarsometatarsus, and the distal extremity of a left tibiotarsus.

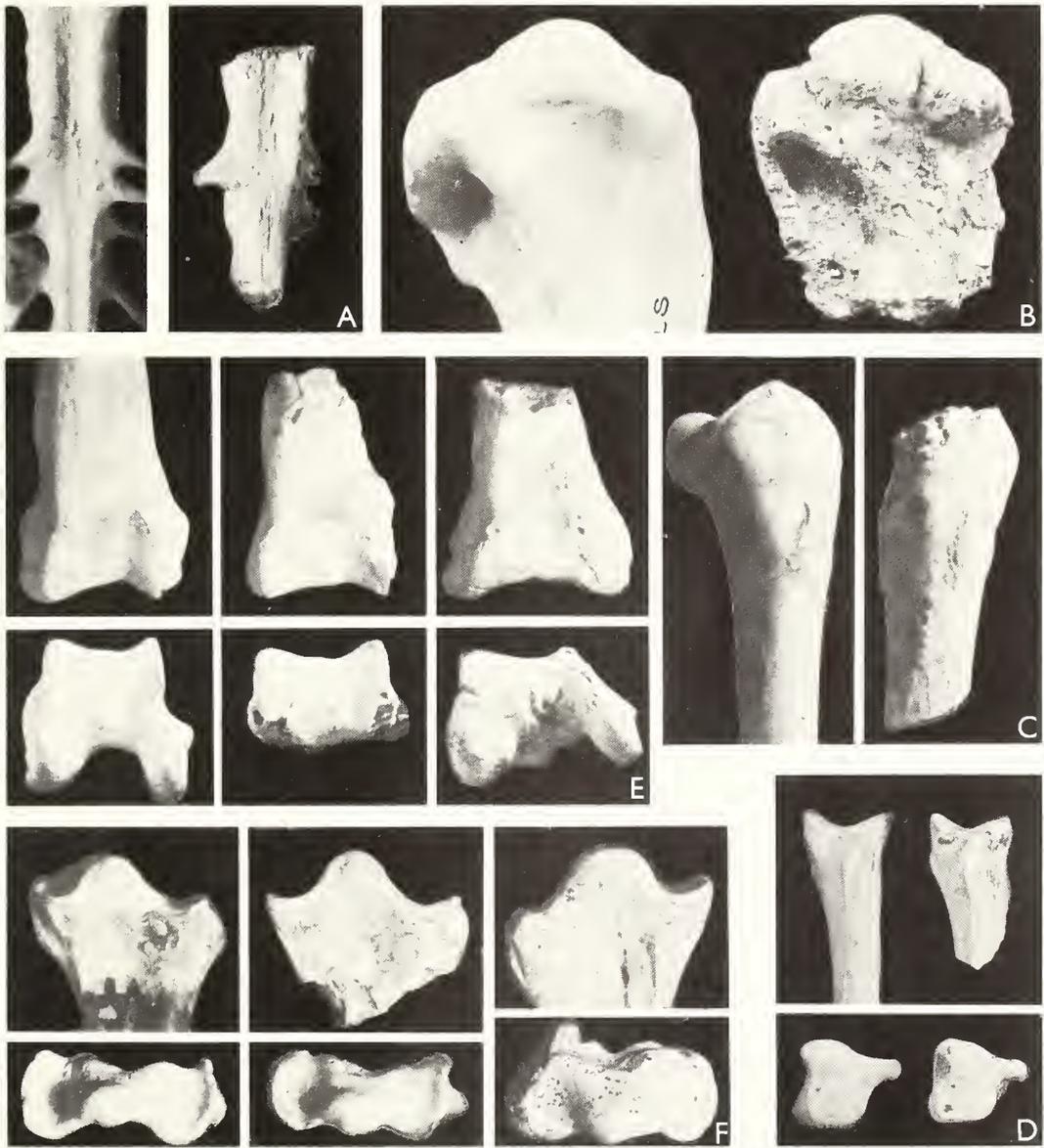
In size and proportions the fossil bones closely resemble the Common Crane (Reference Specimens: British Museum (Natural History) BM (NH) S/1972.152.4.3 and UMZC 344S); they are smaller than the Sarus Crane (Reference Specimens BM (NH) S/1952.2.149 and UMZC 344M). The only specimens among the new crane fossils for which comparable Maltese Crane specimens are available are the tibia and tarsus. The caudal width of the new fossil tibiotarsus extremity measures 21.0 mm; the Common Crane measures 20.0–22.2 mm, $n = 6$ (Harrison and Cowles 1977), Sarus and Maltese Cranes 23.9–28.6 mm, $n = 8$ (Northcote 1982*a*). The maximum width of the new fossil tarsometatarsus extremity measures 26.5 mm; the Common Crane measures 20.8–27.0 mm, $n = 11$ (Northcote 1979), Sarus and Maltese Cranes 27.1–33.3 mm, $n = 8$ (Northcote 1982*a*). Thus the new fossil tibia and tarsus are too narrow to belong to the Maltese Crane.

Text-fig. 1. shows features on the new fossils that are sufficiently intact for morphological comparison with the Common Crane: the sulcus ventralis of the synsacrum (text-fig. 1A), the impressiones obturatoriae of the femur (text-fig. 1C), the tuberculum ventrale, incisura capitis and caput of the humerus (text-fig. 1B), the dorsal and articular surfaces of the wing phalanx (text-fig. 1D), the sulcus cartilaginis and the condyles of the tibiotarsus (text-fig. 1E) and the eminentia intercondylaris and the cotyla of the tarsometatarsus (text-fig. 1F). In morphological structure the fossil bones closely resemble the Common Crane. Certain features of the newly prepared tibia and tarsus can also be compared with the Maltese Crane. On the tibiotarsus in both the new fossil and the Common Crane the condylus medialis is flattened medially and there is a high ridge where it meets the sulcus cartilaginis on the caudal surface. In contrast, the Maltese Crane has a more rounded condyle, the ridge is lower, and the sulcus is consequently more smoothly curved (text-fig. 1E, top). Another tibial characteristic concerns the disposition of the condyles. In the Common Crane the condylus medialis and the ridged medial edge of the sulcus lie parallel to the condylus lateralis and the lateral edge of the sulcus; there is an indication of this condition in the new fossil tibia—although the cranial parts of the condyles are missing, the edges of the sulcus lie parallel to one another. In contrast, the Maltese Crane tibia has the condylus medialis and the medial edge of the sulcus directed medially and away from the condylus lateralis (text-fig. 1E, bottom). On the tarsometatarsus in both the new fossil and the Common Crane the eminentia intercondylaris is attenuated and clearly demarcated from the area intercondylaris. In contrast, the Maltese Crane tarsus has a broad eminentia that is not clearly demarcated from the area behind it (text-fig. 1F). Thus, in morphological structure the new fossil tibia and tarsus differ from the Maltese Crane.

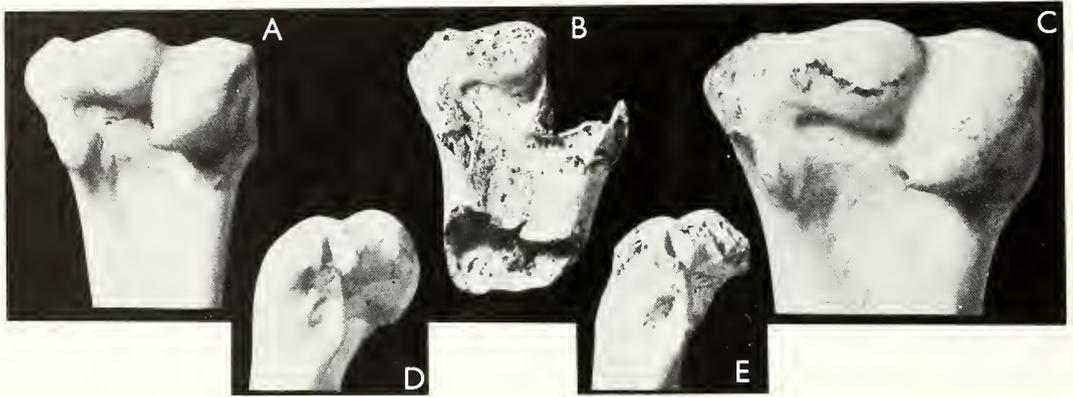
In summary, their size, proportions and morphological structure provide reasonable justification for assigning the newly prepared sacrum, fore- and hind-limb fossils to the Common Crane.

REASSIGNMENT OF THE HUMERUS BM (NH) A5162

Part of the distal extremity of a right humerus excavated by Bate *c.*1934 from a Pleistocene cave deposit at Tal Gnien, Malta (VV 421751) is stored in the British Museum (Natural History), Registered Number A5162. This humerus fragment is much smaller than the corresponding part of the Sarus Crane; in size and proportions it closely resembles the Common Crane (text-fig. 2). The size and proportions of this distal humeral extremity match those of the proximal humeral extremity shown in text-fig. 1 B. The caudal and dorsal surfaces of fossil A5162 are damaged but where it is sufficiently intact for morphological comparison it closely resembles the Common Crane. In particular, both have the epicondylus ventralis rounded ventrally and confluent with the condylus ventralis. In both, also, the condylus lies at right angles to the shaft of the bone and its bulbous dorsal part is symmetrically shaped. Also, the angle between the condylus and the tuberculum supracondylare



TEXT-FIG. 1. A-D, Common Crane, recent UMZC 344S (left) and Maltese Pleistocene UMZC 252a (right). A, ventral view of synsacrum, B, caudal view of proximal part of right humerus, C, caudal view of proximal part of right femur, D, dorsal view (above), articular surface (below) of distal phalanx of left digit majoris. E, F, Common Crane, recent UMZC 344S (left) and Maltese Pleistocene UMZC 252a (centre), Maltese Crane UMZC 252a (right). E, caudal view (above), articular surface (below) of distal part of left tibiotarsus. F, dorsal view (above), articular surface (below) of proximal part of left tarsometatarsus (left and centre) and right tarsometatarsus (right). D is figured $\times 2$; all the rest $\times 1$.



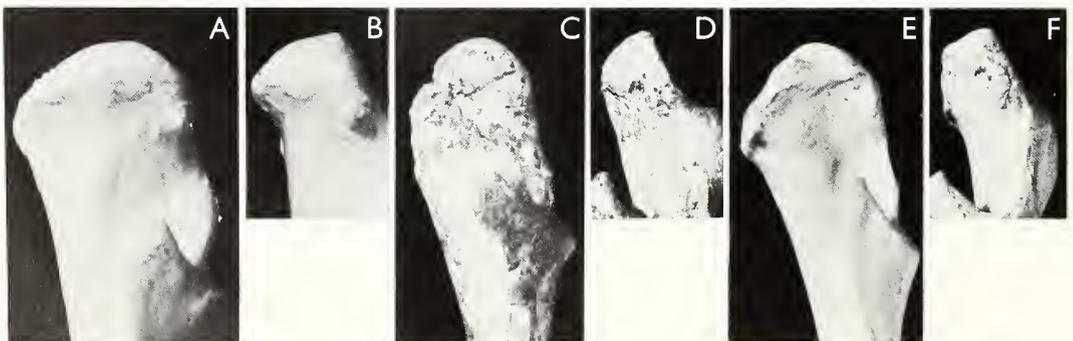
TEXT-FIG. 2. Distal extremity of right humerus. A-C, cranial view. A, Common Crane recent UMZC 344S, B, Maltese Pleistocene BM(NH) A5162, C, Sarus Crane UMZC 344M. D, E, ventral view. D, Common Crane recent UMZC 344S, E, Maltese Pleistocene BM(NH) A5162. All $\times 1$.

is of similar form on the fossil and on the Common Crane (text-fig. 2, A and B. The proximal part of the tuberculum of the fossil is missing (text-fig. 2B); its ventral surface compares well with that of the Common Crane text-fig. 2, D and E).

Harrison (1979, p. 14), too, observed the fossil humerus BM (NH) A5162 to be 'of similar size and character to that of the Common Crane', but, without illustration or further description, he assigned the bone to the much larger Maltese Crane. However, its size, proportions, and morphological structure provide reasonable justification for reassigning this humerus to the Common Crane.

REASSIGNMENT OF THE SYNTYPE CORACOID BM (NH) 49365

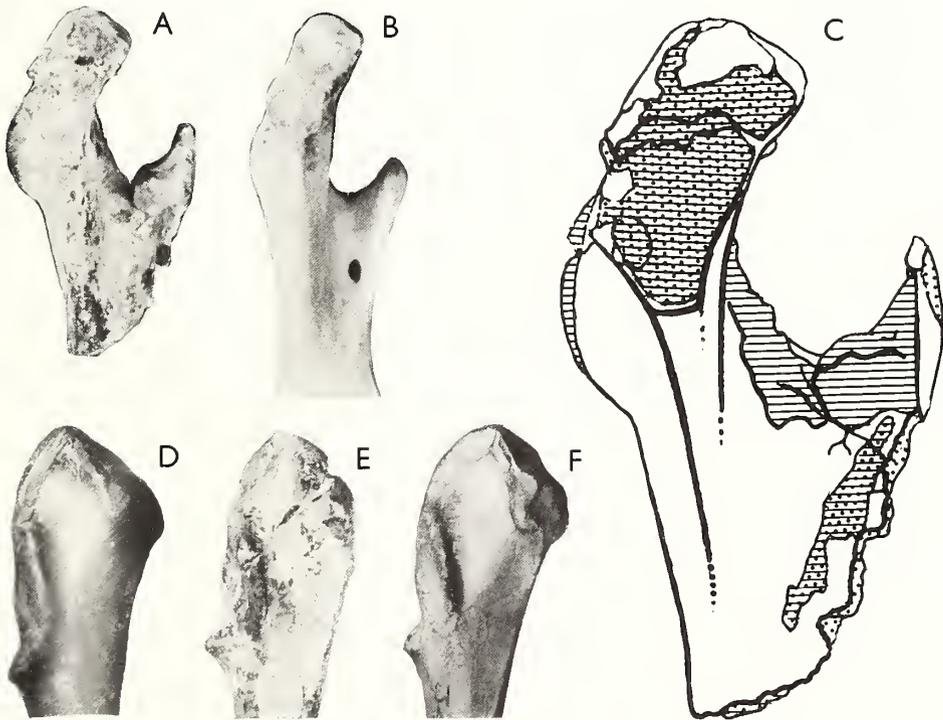
The dorsal half of a right coracoid excavated by Spratt *c.*1860 from a Pleistocene cave deposit at Zebbug, Malta (VV 497700) is stored in the British Museum (Natural History), Registered Number 49365. Lydekker (1890, 1891) described the 'head' (i.e. the dorsal tip) of this fossil as 'smaller and relatively narrower' compared to the Sarus Crane 'which affords a well-marked distinction from that species' (1890, p. 408). Harrison and Cowles (1977) considered the 'head' too eroded for such comment and it is, indeed, too damaged for accurate measurement (text-fig. 3). In general, bone



TEXT-FIG. 3. Dorsal part of right coracoid. A, C, E, medial view; B, D, F, dorsal view of 'head'. Sarus Crane UMZC 344M (left), Common Crane recent UMZC 344S (right) and Maltese Pleistocene BM (NH) 49365 (centre). All $\times 1$.

width is proportional to weight^{0.375} (Northcote 1982*b*). Text-fig. 3 shows that, not only the dorsal tip, but also the rest of the coracoid fragment is much smaller than the Sarus Crane; in size and proportions the bone closely resembles the Common Crane (text-fig. 3) that is *c.*2 kg lighter. A 'smaller and relatively narrower head' is, therefore, to be expected, Lydekker (1890) made no comment concerning the rest of the bone. He provided only an inaccurate sketch and assigned the coracoid to a new, very large extinct species he named the Maltese Crane *G. melitensis*.

Harrison (1979) noted the correspondence in size between the fossil coracoid and the Common Crane but considered they differed in their morphological structure; he provided no illustration. First (p. 14), he maintained that the processus procoracoideus is 'proportionately longer and more curved' on the fossil than on the Common Crane. However, the processus on the fossil has a length (10.3 mm) within the range (8.8–10.9 mm, *n* = 6) for Neolithic (UMZC and Sedgwick Museum, Cambridge SMC) and recent Common Cranes. It appears 'more curved' because the lateral edge is eroded and the tip is cracked and buckled; in addition, the whole processus seems to have become detached at some time, then replaced in an unnatural position with adherent matrix at its base and this has altered its appearance (text-fig. 4A–C). Secondly, Harrison (1979 p. 15) stated that the area between the facies articularis humeralis and the lateral edge of the processus acrocoracoideus is narrower and deeper on the fossil coracoid than on the Common Crane. However, matrix adheres to the eroded lateral edges of both the facies and the processus on the fossil and this results in an apparent narrowing and deepening of this area (text-fig. 4D–F). Thirdly, Harrison (1979, p. 14) considered the surface of the sulcus *m. supracoracoidei*, particularly at the level of the medial part of the facies articularis clavicularis, to be dorso-ventrally narrower on the fossil coracoid than on the Common Crane.



TEXT-FIG. 4. Dorsal part of right coracoid. A–C, ventral view. A, Maltese Pleistocene BM (NH) 49365, C, the same specimen to show matrix (hatched) and erosion (stippled), B, Common Crane recent UMZC 344S. D–F, lateral view. D, Common Crane Neolithic SMC 1912, E, Maltese Pleistocene BM (NH) 49365, F, recent UMZC 344S. C is figured $\times 2$; all the rest $\times 1$.

However, this area appears narrower on the fossil as a result of erosion of the ventral and medial corner of the sulcus and the adjoining part of the facies articulares claviculares (text-fig. 4). Harrison and Cowles (1977, p. 27) considered the fossil coracoid too 'slender' to belong to the Common Crane. However, only in ventral view does it appear to be more 'slender' and this results from erosion and chipping of the medial edge of the shaft at the base of the processus procoracoideus (text-fig. 4 A-C).

In summary, there is no evidence for assigning coracoid BM (NH) 49365 to the Maltese Crane. Features that have been used for doing so are the result of erosion, fossilization, and excavation. The size, proportions, and morphological structures of this bone provide reasonable justification for reassigning it to the Common Crane.

DISCUSSION

This is the first Common Crane record from the Maltese Pleistocene. (The proximal humeral extremity from Mnajdra and the dorsal coracoid extremity from Zebbug articulate satisfactorily with each other and with a recent Common Crane scapula; this confirms that all three belong to one species.) Evidently, two crane species, one very large, the other smaller, were sympatric on Malta. Today, Common Cranes are strongly associated with aquatic habitats (Cramp and Simmons 1980, pp. 616, 618). Their presence at various localities on Malta *c.* 125,000 years ago suggests that, unlike today, habitats with standing water existed on the island at that time.

There are many hind-limb bones of the Maltese Crane in existence but Harrison and Cowles (1977) and Harrison (1979) knew of no fore-limb bones large enough to support such a large crane in the air, nor hind-limb bones of a smaller crane that came from the Maltese Pleistocene. They, therefore, reasoned that the relatively smaller size of the two fore-limb bones that they regarded as belonging to the Maltese Crane, indicates that it had reduced wings and Harrison and Cowles (1977, p. 27) suggested that the bird was 'an insular form with reduced powers of flight'. Doubt is cast upon this reasoning as a result of the re-examination of the fore-limb bones. This doubt is reinforced by the presence in the Maltese Pleistocene deposit of Common Crane remains, especially as these include hind-limb bones. It is more reasonable to assign the comparatively small fore-limb bones to the comparatively small and contemporaneous crane they resemble than to assign them to a much larger crane and postulate reduced flight ability to explain the resultant size disparity.

Lydekker (1890) based the new species *G. melitensis* on three specimens—the coracoid BM (NH) 49365, a tibiotarsus BM (NH) 49361 and a tarsometatarsus BM (NH) 49358. (All occurred in one deposit; presumably that is why Lydekker (1890) assigned them all to one species.) All the specimens in this syntypal series are of equal value in nomenclature (ICZN, Article 73c). A year later, Lydekker (1891) designated as the 'types' (that is, the syntypal series) the coracoid from the original syntypal series plus a pelvic girdle fragment. Brodkorb (1967) followed Lydekker (1891). However, the syntypal series consists of the specimens on which the author based the species (ICZN, Article 72b) so that Lydekker's designation dated 1891 is invalid. Reassignment of the coracoid to the Common Crane, as recommended here, requires its removal from Lydekker's (1890) syntypal series of *G. melitensis*. Two specimens now remain—the tibiotarsus and the tarsometatarsus; both have been described and figured (Lydekker 1890, 1891; Northcote 1982a). With regard to the tibiotarsus, Lydekker (1890, 1891) and Harrison and Cowles (1977) stated that the smaller disto-proximal width of the supratendinal bridge distinguishes *G. melitensis* from *G. antigone* but Mourer-Chauviré, Adrover, and Pons (1975), Harrison (1979), and Northcote (1982a) showed this feature to be not diagnostic for *G. melitensis*. With regard to the tarsometatarsus, Lydekker (1891, p. 163) stated that 'the proportions and relationships of the three trochleae are precisely the same' on Maltese and Sarus Cranes and similar to those on the Australian Crane *G. ribicunda*. However, on both of the last-named species (as on other living cranes) the trochleae are close together and roughly parallel to one another, whereas on *G. melitensis* the intertrochlear notches are relatively wide and the trochleae for digits II and IV are curved away from that for digit III; compared to *G. antigone*, the incisura intertrochlearis medialis is greater in *G. melitensis* (*c.* 5 mm *cf.* *c.* 4 mm) and the trochlea for digit IV is more curved laterally (Northcote 1982a). Though undoubtedly gruiform, the tarsometatarsus of

G. melitensis, unlike the tibiotarsus, clearly differs from *G. antigone* in morphological structure. Lydekker (1890) considered the tarsometatarsus of *G. melitensis* to be larger than *G. antigone*, chiefly on account of its larger maximum medio-lateral width (32 mm *cf.* 26 mm) but this larger width results from the splaying of the trochleae. Lydekker did not designate a holotype for *G. melitensis*; therefore, in accordance with the rules of the ICZN, Article 74, I suggest that the syntype tarsometatarsus BM(NH) 49358 should be designated its lectotype and that the individual characteristics of that bone as described here should form the basis of an emended diagnosis of this species. The tibiotarsus becomes the paralectotype. This procedure prevents *G. melitensis* from being placed in the synonymy of *G. grus* and preserves a long-standing name.

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TOOTH FORM, GROWTH, AND FUNCTION IN TRIASSIC RHYNCHOSAURS (REPTILIA, DIAPSIDA)

by MICHAEL J. BENTON

ABSTRACT. The rhynchosaurs (Reptilia, Diapsida) were important medium-sized herbivores in the middle to late Triassic (245–208 Ma). They had a remarkable multiple-row dentition with a powerful precision-shear bite. Their teeth had ankylotheodont implantation—that is, the deeply rooted teeth were fused to bone of attachment which could also invade the pulp chambers, but there was no socket. There was no typical reptilian tooth replacement from below. Detailed analyses of two typical rhynchosaurs, *Stenaulorhynchus* (middle Triassic) and *Hyperodapedon* (late Triassic), show that the teeth on each jaw are organized into clear longitudinal Zahnreihen. In each of these Zahnreihen, an ontogenetic series of teeth may be seen clearly from the back to the front of the jaw, ranging from newly ankylosed teeth to fully worn and largely resorbed teeth. The cycle of tooth growth and resorption is controlled by normal jaw growth in which the occlusal area moves back constantly: teeth appear to ‘swing’ into occlusion at the back and out of occlusion at the front of this area of wear. The multiple-row rhynchosaur dentition effectively ‘freezes’ ontogeny and it offers important information on vertebrate tooth replacement, especially in view of the fact that the fossil material offers excellent histological detail.

RHYNCHOSAURS, a group of small- to medium-sized reptiles of the Triassic Period (245–208 Ma), have aroused considerable interest recently because of their problematic relationships, their debated ecological role, and the remarkable anatomy of their skulls and teeth. Rhynchosaurs have classically been grouped with the living tuatara *Sphenodon* in the Order Rhynchocephalia of the Class Lepidosauria (e.g. Romer 1966; Kuhn 1969), whereas anatomical evidence strongly suggests a position close to the archosaurs (Hughes 1968; Cruickshank 1972; Benton 1983*b*, 1984). Rhynchosaurs were dominant in several faunas of the middle and late Triassic, and they became extinct just before the radiation of the dinosaurs at the end of the Triassic. It has been suggested that rhynchosaurs ate plants (Huene 1939; Romer 1963; Sill 1971*a, b*; Benton 1983*a, b*) or molluscs (Burckhardt 1900; Chatterjee 1969, 1974, 1980).

The teeth of rhynchosaurs are not acrodont, as has been stated (e.g. Romer 1956, p. 450; Edmund 1969, p. 153), but deeply rooted and firmly fixed with bone of attachment (ankylotheodont: Chatterjee 1974). The most remarkable feature of the teeth is that they were not replaced in a typical reptilian way, but continued to grow throughout their functional life.

The aims of this paper are to describe the morphology, histology, and growth of the teeth in two rhynchosaurs, *Hyperodapedon* from the late Triassic of Elgin, north-east Scotland, and *Stenaulorhynchus* from the middle Triassic of the Songea district, southern Tanzania; to discuss the functions and adaptations of the peculiar rhynchosaur dentition; and to consider the evolution of such a dentition.

Repository abbreviations used are: BM(NH), British Museum (Natural History); CUMZ, Cambridge University Museum of Zoology; NUGD, Newcastle University, Geology Department. Additional figures showing tracings of the serial sections have been deposited with the British Library, Boston Spa, Yorkshire, U.K., as Supplementary Publication No. SUP 14023 (7 pages).

MATERIALS AND METHODS

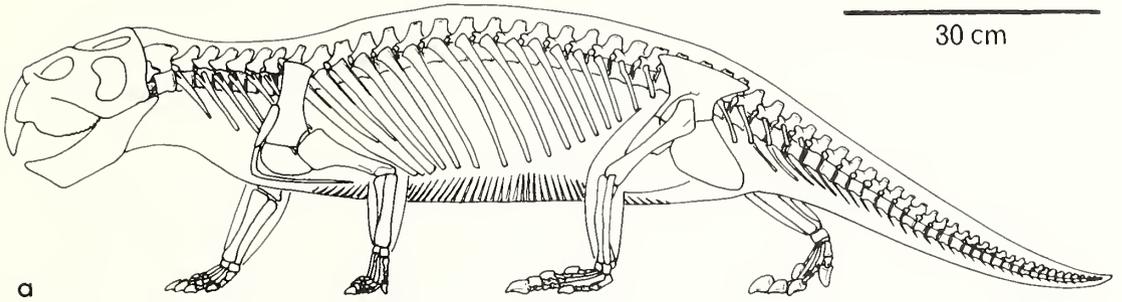
Rhynchosaur teeth and jaws

Tooth-bearing elements are the most commonly found remains of rhynchosaurs in many locations, and several accounts of the general morphology of the dentition have been given (e.g. Huxley 1869; Lydekker 1885; Huene 1938; Sill 1971*b*; Chatterjee 1974). The last two authors gave some histological information also. The anatomy of the maxilla and dentary suggests that true rhynchosaurs fall into two natural groups: those of the middle Triassic (*Stenaulorhynchus* from Tanzania, *Mesodapedon* from India, and *Rhynchosaurus* from England), and those of the late Triassic (*Hyperodapedon gordonii* from Scotland, *H. huxleyi* ('*Paradapedon*') from India, *Scaphonyx fischeri* from Brazil, *S. sanjuanensis* from Argentina, '*Supradapedon*' from Tanzania, as well as some unnamed forms from Nova Scotia and Texas). In the present study, tooth-bearing elements of *H. gordonii* and *Stenaulorhynchus* were sectioned in several ways in order to provide further information on the late Triassic forms and new information on one of the earliest known rhynchosaurs. A selection of sectioning techniques was necessary because of the complexity of the arrangement of the teeth—normal methods of preparation by the removal of matrix and outer bone layers would have yielded little information.

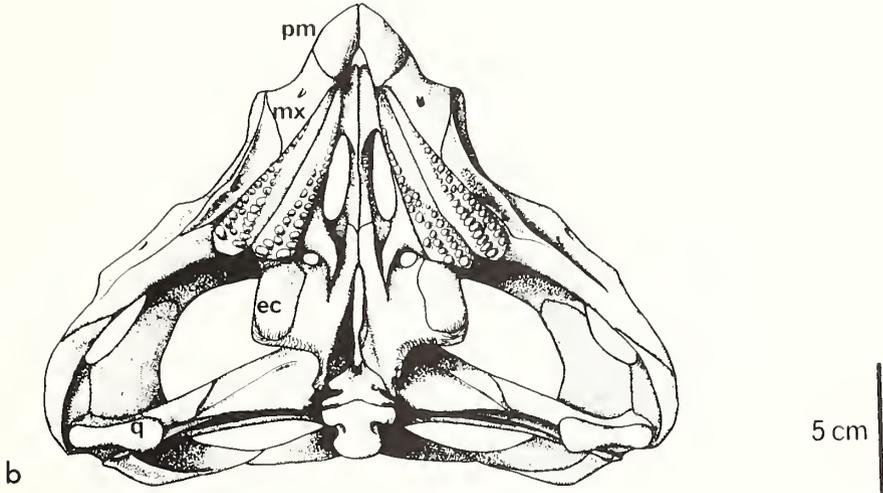
H. gordonii is represented by about thirty-five individuals from the Lossiemouth Sandstone Formation (early Norian?) of Lossiemouth East and West Quarries (Nat. Grid Ref. NJ 236707, NJ 231704) and Spynie Quarries (NJ 219656, NJ 223657). The remains include most portions of the skeleton and skull, and detailed restorations have been possible (Benton 1983*b*). *Hyperodapedon* was a squat, 1.3 m long quadruped with powerful hindlimbs that could have been used for scratch-digging (text-fig. 1*a*). The skull was specialized, with a broad posterior portion to accommodate powerful jaw adductor muscles (text-fig. 1*b*). The upper dentition is borne on two maxillary tooth-plates, each of which has several rows of teeth and is bisected by a deep longitudinal groove. The lower jaw fits snugly into this groove when the jaws are shut, and this can be likened to the blade of a penknife fitting into its handle (Huxley 1869). There are toothless beak-like premaxillae at the front of the skull, and the lower jaws curve up on either side to a high pointed rostrum (text-fig. 1*c*). The quadrate-articular jaw articulation permitted no antero-posterior sliding, and patterns of tooth wear confirm that *Hyperodapedon* had a powerful precision-shear bite (Benton 1983*b*) rather than a cutting-sawing movement as suggested in *Scaphonyx* by Sill (1971*b*). There are two series of teeth in the lower jaw (text-fig. 1*d*, *e*). Along the dorsal margin of the dentary is a palisade of tightly packed buccal teeth with no intervening bone and lower down, on the medial surface of the dentary, is a series of broader lingual teeth.

Stenaulorhynchus stockleyi Haughton 1932 is represented by remains of fifty to fifty-five individuals (Huene 1938, A. R. I. Cruickshank, pers. comm.) from the Manda Formation (early Anisian?) of the Songea district, southern Tanzania. Specific localities include the region of the Litumba to Songea road, west of Njalila and west of Mkongoleko (Attridge/Charig/Cox field notes, BM(NH); Parrington field notes, CUMZ). *Stenaulorhynchus* was about 1.6 m long, and very like *Hyperodapedon* in general appearance. However, the skull shows less of the advanced rhynchosaur characters (Huene 1938, pl. 1, 2). It is lower and less broad at the back, and the eye faces more

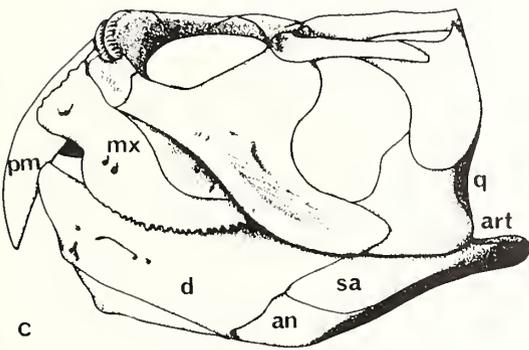
TEXT-FIG. 1 (*opposite*). The rhynchosaur *Hyperodapedon gordonii* from the Lossiemouth Sandstone Formation of Elgin, north-east Scotland: *a*, lateral view of the skeleton in walking pose; *b*, ventral view of the skull, showing the maxillary tooth-plates; *c*, lateral view of the skull with the lower jaw in place; *d*, medial view of the lower jaw showing the two distinct tooth rows on the dentary; *e*, diagrammatic cross-section through the lower jaw and maxilla to show occlusal relationships of the teeth. Abbreviations: an, angular; art, articular; bt, buccal teeth; d, dentary; ec, ectopterygoid; lt, lingual teeth; mx, maxilla; pm, premaxilla; pra, prearticular; q, quadrate; sa, surangular; sp, splenial.



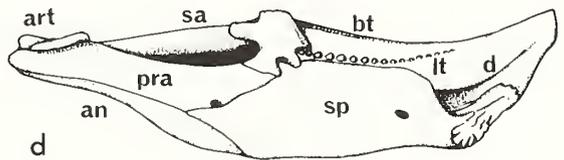
a



b



c



d



e

sideways, and the braincase is placed further forward. The arrangement of the dentition of the maxillary tooth-plate and of the dentary is rather different from that of *Hyperodapedon*. The maxilla bears one large longitudinal row of teeth laterally and two or more further rows of smaller teeth in the middle and medial portions of the tooth-plate, on the occlusal and lingual surfaces. The dentary is rather flat-topped and bears several rows of teeth that pass from the occlusal to the lingual surface. In both cases, it is hard to distinguish which teeth should be termed buccal and which lingual.

Specimens examined

Hyperodapedon gordon Huxley 1859

- BM(NH) R3140. Partial skull; Lossiemouth (E).
- BM(NH) R4780. Left dentary; Lossiemouth (E).
- EM 1926. 6. Left maxilla; Lossiemouth (E)?
- NUGD A. Partial skull; Spynie.
- NUGD B. Skull; Spynie.

Stenaulorhynchus stockleyi Houghton 1932

- BM(NH) R9271. Partial right dentary; Songea district, southern Tanzania.
- BM(NH) R9272. Right maxilla.
- BM(NH) R9273. Left dentary.
- BM(NH) R9274. Right dentary.
- BM(NH) R9275. Left maxilla.
- BM(NH) R9276, R9277. Right maxilla (cut into two pieces).
- BM(NH) R9278. Maxilla.
- BM(NH) R9279. Juvenile left maxilla.
- BM(NH) R9280. Right maxilla.
- BM(NH) R9281. Right maxilla.
- BM(NH) R10007. Partial right dentary.
- BM(NH) R10008. Partial right maxilla.
- CUMZ T992. Right maxilla.
- CUMZ T993. Juvenile left maxilla.
- CUMZ T1112 (FRP 2). Right lower jaw, lacking splenial (on loan to the BM(NH)).
- CUMZ T1138. Right maxilla.

Serial grinding and thin sectioning

In the course of the present study, the morphology and arrangement of the maxillary and dentary teeth of all available material of *Hyperodapedon* was studied (Benton 1983*b*). Some general information on the teeth of *Stenaulorhynchus* has been presented (Huene 1938; Chatterjee 1980) and further details, based on an examination of the specimens preserved in the BM(NH) and CUMZ are given below. Two methods were employed in order to study the internal arrangement and histology of the teeth: serial grinding and peeling, and standard thin sectioning.

The serial grinding and peeling technique used was similar to that employed in studies of the internal structure of invertebrate fossils such as brachiopods and corals and in studies of calcareous sediments (e.g. Ager 1965; Allman and Lawrence, 1972). A piece of tooth-bearing bone was selected that appeared to be well preserved internally, and yet was broken, or otherwise damaged and of little use in studies of its external form. The procedure was as follows:

1. Mount the specimen in the desired orientation in a cold-setting compound (e.g. polyester resin, or other embedding resin) and attach this to the serial grinder base plate.
2. Grind first flat surface.
3. Remove specimen from grinder and polish flat surface with progressively finer grades of moistened carborundum powder, to grade 600 or 1000, on a glass plate.
4. Wash the polished surface and dry. Do not touch the cleaned surface.
5. Etch by holding polished surface of specimen in a tray of 5% hydrochloric acid for 20 seconds in order to heighten non-calcareous features.

6. Neutralize the acid and wash with distilled water.
7. Dry by slight heating or with acetone.
8. Mount specimen in a sand box or in plasticene, if necessary, so that etched surface faces up and is horizontal.
9. Cut a piece of acetate film to allow at least 1 cm all round the specimen.
10. Flood etched surface of specimen with acetone (not too much).
11. Hold acetate film in U-shape and apply carefully from the centre outwards in order to exclude gas bubbles. This must be done smoothly without touching the film or moving it around.
12. Allow five minutes or more for the acetate film to harden and remove by peeling back from one corner.
13. Trim the acetate film to the edge of the impression, and mount it immediately between two microscope slides. Tape these together on the long edges.
14. Return specimen to serial grinder in exactly the original orientation, advance by 0.1 or 0.5 mm, and repeat steps 2-14.

This technique produced good results for materials of both *Hyperodapedon* and *Stenaulorhynchus*. The bone of *Hyperodapedon* is normally preserved very poorly and is so soft that positive preparation is very difficult. The natural rock moulds were of high fidelity and casts of bones were made using flexible synthetic rubber compounds (Benton and Walker 1981). The bone is still in the form of apatite and occasionally it has been infiltrated with iron oxide minerals (e.g. goethite) which fill all vessel canals and cracks. A lower jaw of *Hyperodapedon* (NUGD B) was retrieved and sectioned in three planes: vertical transverse, vertical longitudinal, and horizontal. On ground surfaces and on peels, bone was white, dentine yellow, enamel translucent, and the infilled cavities steely blue (unweathered) or reddish brown (weathered). Unfortunately, no suitable maxilla of *Hyperodapedon* could be found for serial sectioning. In *Stenaulorhynchus* the bone is preserved as apatite with good detail of the original structures. It is usually hard, the cavities are infilled with iron oxide minerals, and the surface is often badly cracked. Isolated fragments of maxilla and dentary (BM(NH) R10007, R10008) were sectioned in the vertical longitudinal and vertical transverse planes respectively. In section, bone is white, dentine cream-coloured, enamel translucent, and the infilled cavities steely blue (unweathered) or reddish brown (weathered).

The peels were then used in two ways: (1) to reconstruct the jaw and teeth in three dimensions, and (2) to study microscopic detail.

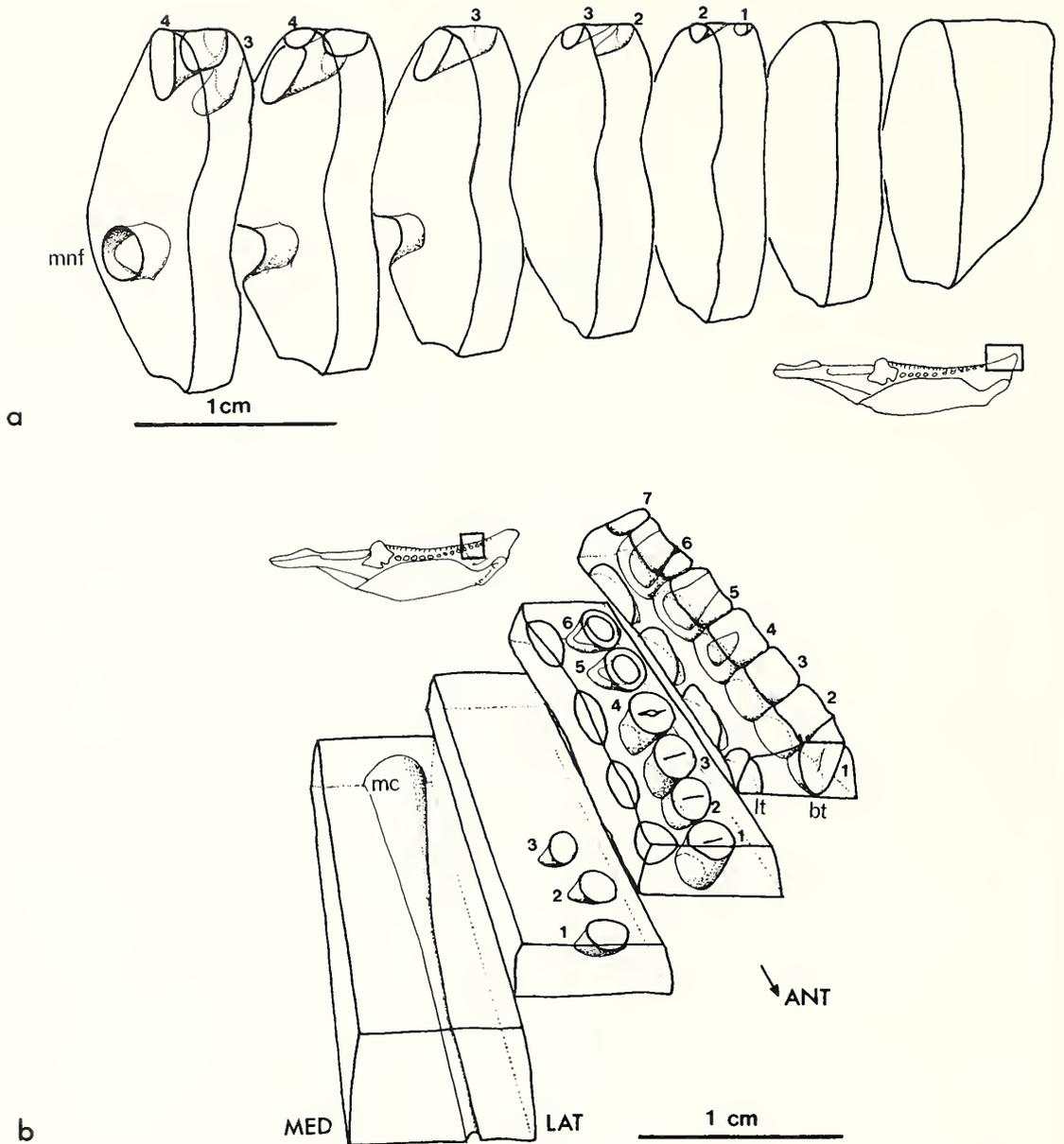
1. Three-dimensional reconstruction. A tracing was made of each peel using an ordinary photographic enlarger, and these were arranged in sequence. Copies were made on to glass plates with an indelible pen. The enlargement here was calculated so that it matched the scaling-up factor given by the ratio,

$$\frac{\text{thickness of glass plate}}{\text{original peel spacing.}}$$

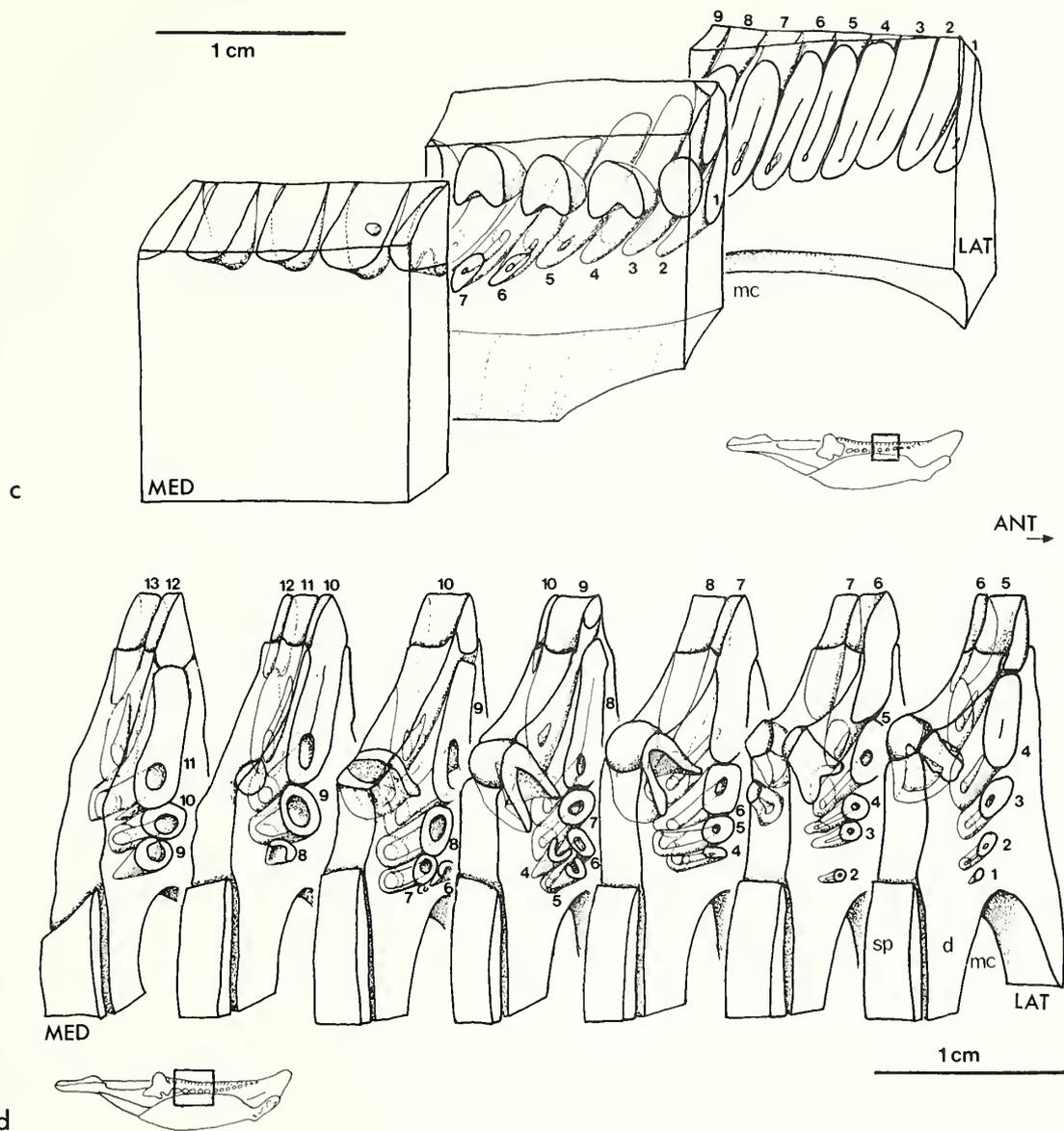
Bundles of five or so glass plates were bound together with clear tape so that the tracings on each were in register. These bundles were drawn as block diagrams to give a three-dimensional reconstruction of the arrangement of the teeth (text-figs. 2, 7, 8).

2. Microscopic detail. Individual peels were examined under an ordinary light microscope in order to elucidate histological details of the bone and teeth. Tracings were made using an ordinary photographic enlarger or a microscope with a drawing attachment. Photographs were also taken through a microscope.

Normal thin sections were made from some pieces of jaw, ground to a thickness of 30 μ , the standard for geological material. These preserved colours better than the peels, and they were used for higher magnification drawings and photographs, and for examination under cross-polarized light. Nevertheless, the peels also preserved fine detail and produced extremely good photographs (e.g. Pls. 67, 68).



TEXT-FIG. 2. Graphic reconstructions of the dentition of the left lower jaw of *Hyperodapedon gordonii* (NUGD B). Drawn from serial sections taken at 0.5 mm spacing, and traced on to glass plates at a magnification of $10\times$. The block diagrams are drawn in different orientations: *a*, anterior part of the dentary; *b*, anterior middle part of the dentary; *c*, middle part of the dentary; *d*, posterior part of the dentary. The location of each block diagram is indicated on an outline lower jaw. Teeth are numbered from front to rear in each view. Abbreviations: ANT, anterior; bt, buccal teeth; d, dentary; LAT, lateral; lt, lingual teeth; mc, Meckel's canal; MED, medial; mnf, mandibular foramen; sp, splenial.



THE DENTITION OF *HYPERODAPEDON*

Arrangement of teeth in the maxilla

The teeth on either side of the central groove in the maxillary tooth-plate are arranged in approximately longitudinal and diagonal rows (text-fig. 1*b*; Pl. 66, fig. 1). Most specimens show a medial field with three or four longitudinal rows that is wider than the lateral field with two or three rows. At the front of the tooth-plate, usually only one row of teeth is to be seen, which is partly because of wear by the dentary teeth and dentary bone. Further back, additional longitudinal rows of teeth appear at the sides of the groove. Very large old specimens of *Hyperodapedon gordonii* are not

known, but they may have added supplementary rows up to a total of six or seven at the back of the tooth-plate, as in *H. luxleyi* and *Scaphonyx fischeri* (Lydekker 1885; Huene 1942; Chatterjee 1974, 1980). Some longitudinal rows show regular packing of teeth while others are irregular, and occasional stray teeth may occur at the edge of the tooth-plate (Benton 1983*b*, fig. 15). The row on the lateral side of the groove is regular and consists of triangular pyramidal teeth, with the longest flat plane facing forwards (Pl. 66, fig. 1). The other rows consist of conical teeth which are less regular in shape. In vertical section, the teeth are directed at right angles to the surface of the curved maxillary tooth-plate.

Arrangement of teeth in the dentary

Three-dimensional reconstructions, made in different planes, from a sequence of vertical transverse sections through the top of the lower jaw show the patterns of teeth in different parts of the jaw (text-fig. 2).

Teeth are virtually absent, or very small, near the front of the dentary, and they increase in length backwards until the roots are just above the meckelian canal at the back. The buccal teeth are tightly packed with very little intervening bone dorsally, and the exposed portion is flattened medio-laterally by tooth wear. They are deeply rooted cylindrical teeth that curve gently up, forwards, and laterally. The great variability in the pulp cavity may be seen in all sections.

The lingual teeth are regular in arrangement and occur in a single spaced row, although occasional extra teeth appear beneath the row (text-fig. 2*d*; Pl. 66, fig. 2). The lingual teeth are pyramid-shaped, superficially rather like the maxillary teeth, but they are clearly more thimble-shaped when seen in section (text-fig. 2*d*). They are spaced differently from the buccal teeth (five lingual to nine buccal teeth longitudinally).

Jaw occlusion and tooth wear

Clear indications of tooth wear have been observed in *Hyperodapedon* (Benton 1983*b*). In summary, the middle portion of the tooth-bearing area of both maxilla and dentary is worn. The teeth and surrounding bone that come into contact are flattened.

The curvature of the maxillary tooth-plate is greater than that of the dentary (text-fig. 1*c*) so that when the jaws close only the middle portions come into contact. Arc-shaped areas are worn flat on the medial and lateral sides of the dentary, and these exactly match the areas of wear on the maxilla (text-fig. 1*b*). The buccal teeth of the dentary bite against the bone in the groove, but lingual dentary teeth occasionally directly meet maxillary teeth (text-fig. 1*e*). When lingual teeth bite against bone of the maxilla, shallow pits may be left, which strongly indicates that *Hyperodapedon* had a precision-shear bite (Benton 1983*b*), as seen in the lizard *Uromastix* (Robinson 1976), rather than the propalinal sawing type of *Sphenodon* which was suggested by Sill (1971*b*) for *Scaphonyx*.

The newest teeth at the back of the jaws are not in occlusion, and are thus unworn. The oldest teeth at the front of the jaws are generally heavily worn. This wear must have occurred in juvenile stages,

EXPLANATION OF PLATE 66

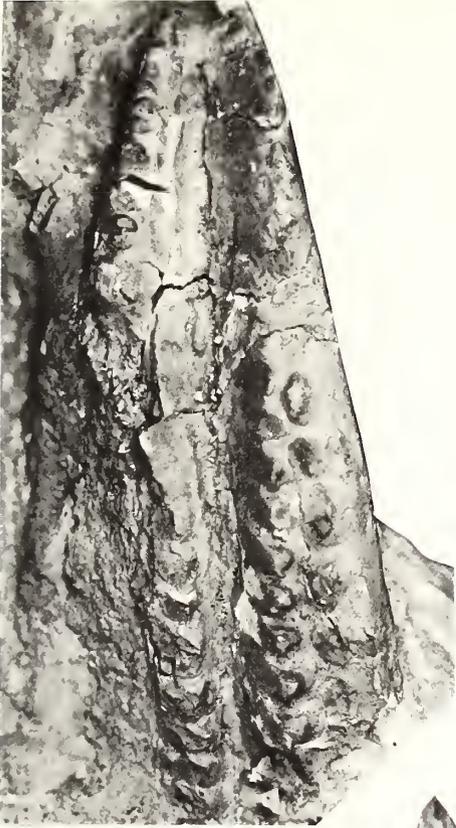
The dentition of *Hyperodapedon gordonii*.

Fig. 1. Occlusal view of a left maxillary tooth-plate, BM(NH) R3140; $\times 1.5$.

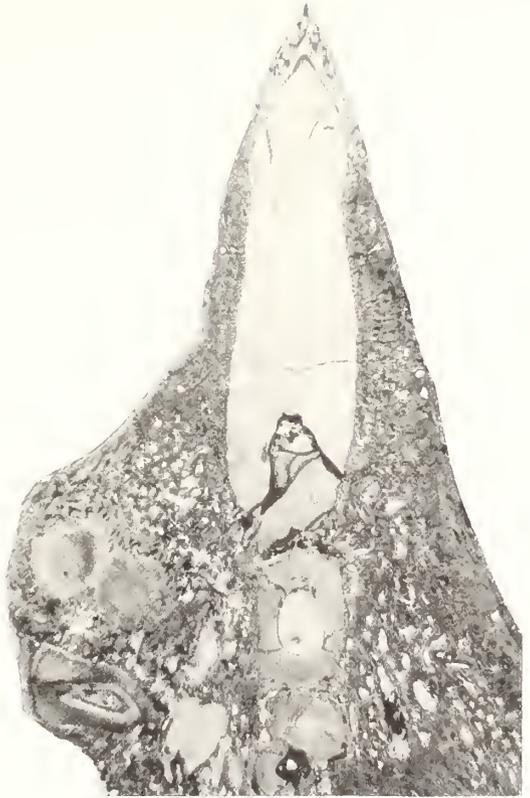
Fig. 2. Transverse vertical section through the top of the dentary, showing the 'waisted' shape of the buccal tooth just below the occlusal margin, the roots of adjacent buccal teeth in cross-section, and a supernumerary lingual tooth (left), $\times 8$.

Fig. 3. Transverse vertical section of a dentary buccal tooth, showing the typical wear shape; medial is to the left; this section is located in text-fig. 3*c*, $\times 15$.

Fig. 4. Transverse vertical section through the anterior part of the dentary, showing a heavily worn and resorbed tooth, and the 'track' of disturbed bone below it, $\times 5$.



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BENTON, rhynchosaur dentitions

since these teeth do not occlude in the adult. Relative growth causes the maxilla to curve upwards away from the dentary, and progressively more posterior portions of the tooth rows come into occlusion. It should be noted that the degree of tooth wear is not related to skull size, but probably depends on the individual's diet as in *Sphenodon* (Robinson 1976).

Tooth form

In general, the teeth of *Hyperodapedon* are deeply fixed in the bone of the jaw and they have open roots with pulp cavities of varying size. The bulk of the tooth is composed of dentine, and enamel may be seen capping the upper portion in some cases.

The maxillary teeth have short roots and shallow conical pulp cavities. They may be nearly circular in cross-section with a central root canal. In microscopic sections they show occasional longitudinal fluting on the surface, and radial dentinal tubules (Pl. 67, fig. 4). These features have been described in detail in *H. huxleyi* by Chatterjee (1974, pp. 228–229).

More information is available on the dentary teeth of *Hyperodapedon*. A series of vertical transverse sections (text-fig. 3) shows the form and emplacement of the teeth and variation in their pattern along the jaw. Anterior portions (text-fig. 3a) lack teeth, probably as a result of wear and migration of the teeth occlusally, or the teeth are small and the roots closed (text-fig. 3b; Pl. 66, fig. 4). Further back, a series of buccal teeth is seen in every section. This is not a succession of teeth or a Zahnreihe. The buccal teeth slope forwards, laterally, and upwards, so that most of them are cut obliquely in vertical sections. Each tooth is waisted at about the mid point which is shown by unworn crowns (text-fig. 3; Pl. 66, fig. 2). Wear on the inner surface produces a medial concavity and the outer surface retains its original convex profile (Pl. 66, fig. 3). At the base, most buccal teeth display an axial pulp cavity that may be relatively large or small in an apparently random way and it is not dependent on the level of the section (text-fig. 3c–e). Vertical longitudinal sections through the dentary show the curved shape of the buccal teeth (text-fig. 4b–d), and horizontal sections (text-fig. 5a–c) show that they are nearly circular in section, rather than compressed, as suggested by Chatterjee (1974, p. 230) for *H. huxleyi*, except when they are worn to a knife-like edge on the top of the jaw (text-fig. 5c).

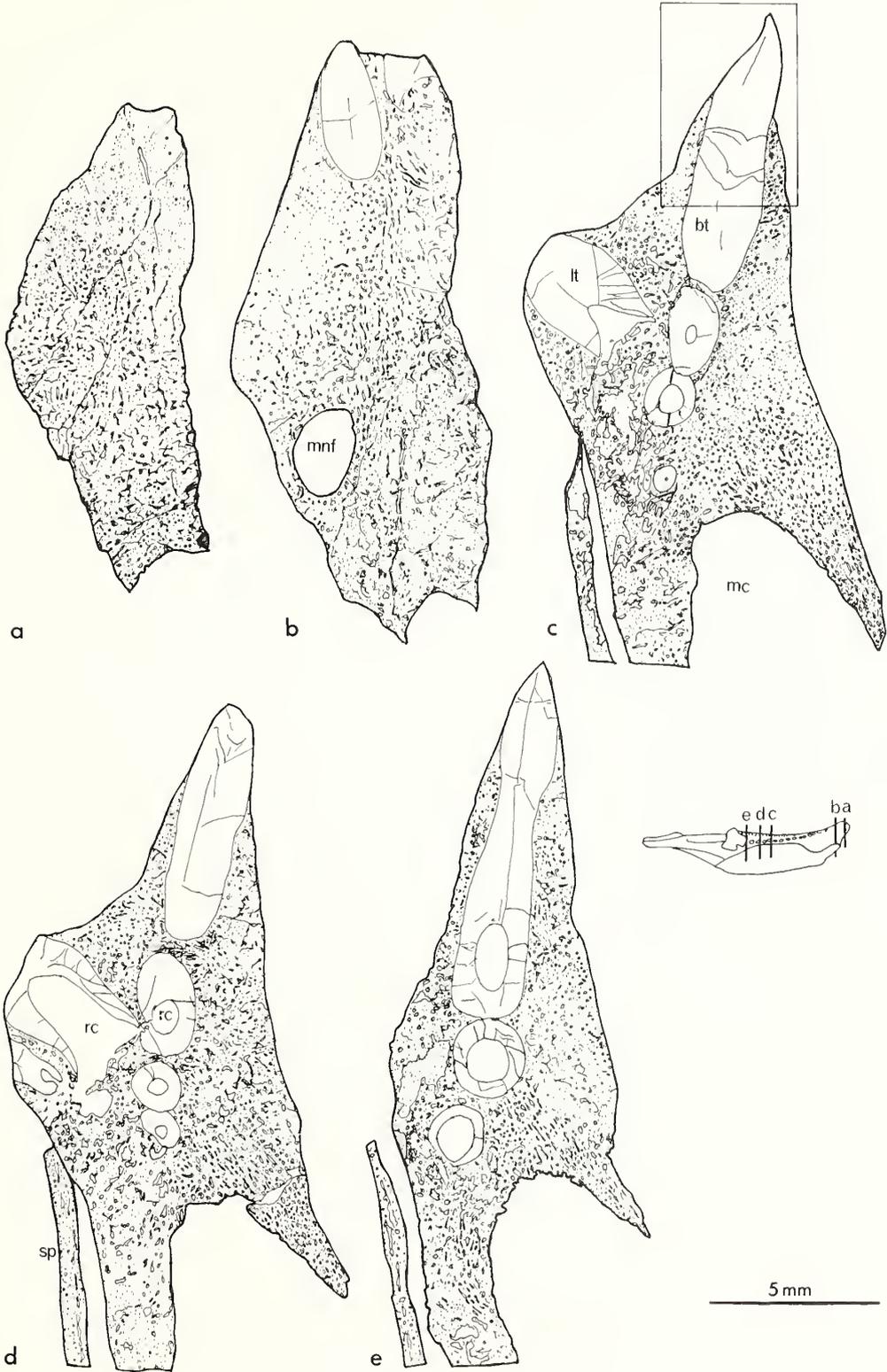
The lingual teeth are shorter and shaped like thick-walled thimbles. Because they are directed medio-dorsally, the standard sectioning planes do not cut them axially, but these teeth were clearly cylindrical with a deep and narrow conical pulp cavity (text-figs. 3c, d, 4a, b, 5b).

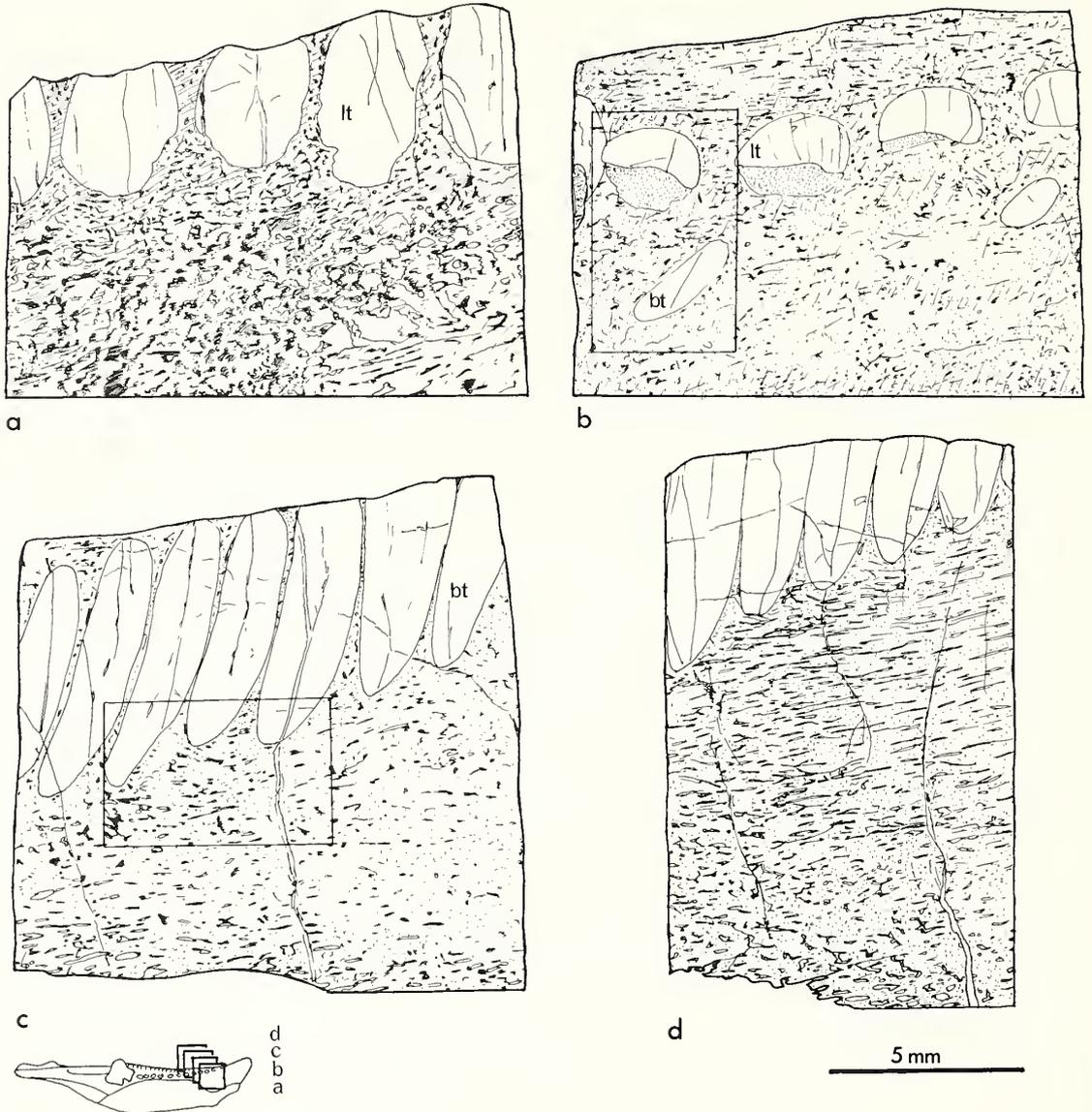
Bone and tooth histology

The serial peels and microscopic sections from the lower jaw of *Hyperodapedon* reveal a great deal of detail concerning the histology of the bone and teeth. The bone may be divided into three types:

1. Laminar fibrolamellar with parallel longitudinal primary osteons: in regions with teeth (Pl. 66, figs. 2–4; Pl. 67, figs. 1, 2, 4). The osteons are occluded to a greater extent towards the edge of the jaws

TEXT-FIG. 3 (*opposite*). Transverse vertical sections of the upper part of the mandible of *Hyperodapedon gordonii* (NUGD B) showing buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, anterior mandible; teeth are absent. *b*, anterior mandible, further back; heavily worn teeth with closed roots, and a large vessel canal. *c*, mid-jaw; a heavily worn lingual tooth and a series of buccal teeth sectioned at different positions along their length. The upper one shows a characteristic wear shape; the lower ones show open roots near the apex. These are not successional teeth, but sections at an angle through teeth that slope up and forwards, and all are functional. The area shown in Pl. 66, fig. 3 is outlined. *d*, further back; a rare abnormality where a small additional lingual tooth occurs, and erosion of a buccal tooth by the growth of a lingual tooth is also seen. *e*, posterior part of dentary, behind the lingual tooth row; a series of sections of buccal teeth with broad root canals and the characteristic 'waisted' appearance of the barely erupted dorsal tooth. Abbreviations: bt, buccal teeth; lt, lingual teeth; mc, Meckel's canal; mnf, mandibular foramen; sp, splenial.





TEXT-FIG. 4. Longitudinal vertical sections of the upper part of the mandible of *Hyperodapedon gordoni* (NUGD B), showing the buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, medially located section; lingual teeth only are seen. *b*, slightly more laterally; the lingual teeth are much reduced and the roots of the buccal teeth appear, indicating that they slope up, forwards, and laterally. The area shown in Pl. 67, fig. 3 is outlined. *c*, more laterally; the full shape of longitudinal sections through the closely packed buccal teeth is clear. The area shown in Pl. 67, fig. 4 is outlined. *d*, towards the lateral margin of the jaw; only partial oblique sections through buccal teeth appear, and show their very close packing. Abbreviations: bt, buccal teeth; lt, lingual teeth.

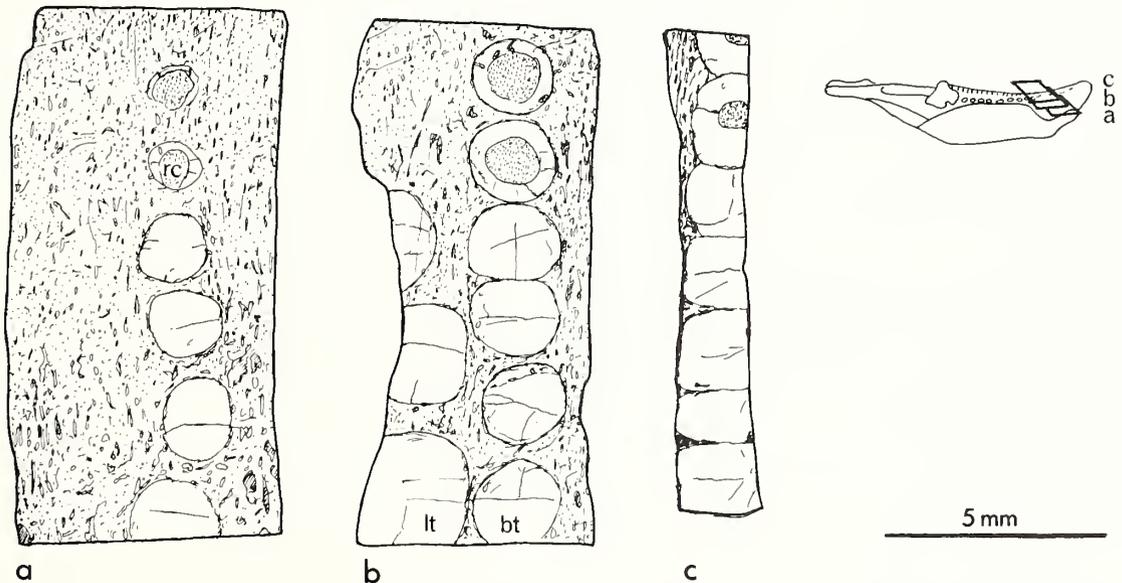
and on either side of the teeth where the bone itself may be subject to wear. This may be functionally equivalent in part to the highly calcified layer of bone observed on the sides of the jaw of *Sphenodon* by Harrison (1901, pp. 200–201). Further forwards in the jaw, where the teeth are older and they have closed root canals, the bone becomes almost wholly compact in the vicinity of the teeth (text-fig. 3*a, b*; Pl. 66, fig. 4).

2. Reticular (cancellous) fibrolamellar: in the centre of bones and away from the teeth (text-figs. 3, 4; Pl. 66, figs. 2, 4).

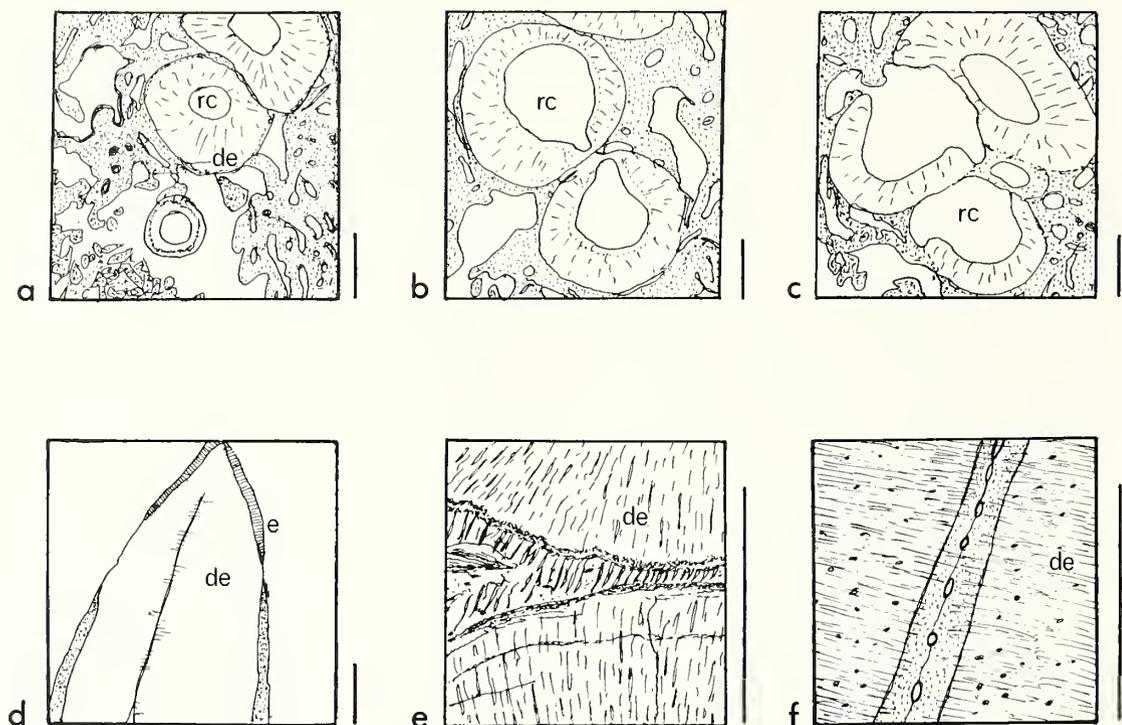
3. Bone of attachment: around the sides of the teeth, the bone is remodelled and takes on a regular appearance with tightly packed small osteons (Pl. 66, figs. 2, 3; Pl. 67, fig. 3). These may have a compressed appearance when they occur between two closely spaced teeth (Pl. 67, figs. 4, 6). At the base of the growing teeth the bone is highly vascular (e.g. text-fig. 6*a–c*; Pl. 66, fig. 2; Pl. 67, figs. 2, 3, 4), and this is particularly marked in posterior parts of the jaw. In the front of the jaw, a track of extensively remodelled bone may be seen at the base of certain teeth (Pl. 66, fig. 4)—this probably marks the passage of the tooth through the bone during jaw growth when the tooth was maintaining its position in occlusion. The remodelled bone may also indicate resorption of a tooth that is no longer in occlusion.

In micrographs of the *Hyperodapedon* jaw (e.g. Pl. 67, fig. 6), osteocyte lacunae are clearly visible in the bone matrix. In some cases there appear to be transverse fibres that run from one tooth to the next (text-fig. 6*e*). These may be traces of collagen fibre directions, or they may be preservational artefacts.

Enamel is not always present on the dentary teeth, but it may be represented by some white, radially prismatic, deposits (text-fig. 6*d*). Enamel is probably present initially on the tooth crowns and is later worn off, rather than being totally absent as suggested by Sill (1971*b*) for *Scaphonyx*. In



TEXT-FIG. 5. Horizontal sections of the upper part of the mandible of *Hyperodapedon gordonii* (NUGD B) showing the buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, ventrally placed section; only the roots of some buccal teeth are seen, some with open root canals. *b*, higher up; both lingual and buccal teeth appear, and the latter can be seen to be more closely packed than the former. *c*, section near the occlusal margin of the dentary; the worn, closely packed buccal teeth occupy nearly the whole width of the jaw. Abbreviations: bt, buccal teeth; lt, lingual teeth; rc, root canal.



TEXT-FIG. 6. Sections of dentary teeth of *Hyperodapedon gordoni* (NUGD B). Scale bars all measure 0.5 mm. *a-c*, transverse sections of buccal teeth near the root apices, showing open root canals and some erosion of tooth material by neighbouring teeth; *d*, transverse vertical section through the upper part of a buccal tooth, showing a thin enamel cap with perpendicular prismatic fabric; *e*, detail of the compact bone between two buccal teeth in horizontal section, showing the diffuse tooth margin and 'fibres' in the bone perpendicular to the tooth surface; *f*, detail of the bone between two buccal teeth in vertical section, showing the closely packed primary osteons and the dentinal tubules. Abbreviations: de, dentine; e, enamel; rc, root canal.

EXPLANATION OF PLATE 67

Histology of the bone and teeth of the dentary of *Hyperodapedon gordoni*. Sections from NUGD B.

- Fig. 1. Horizontal section taken above Meckel's canal, showing laminar fibrolamellar bone with largely occluded canals, $\times 30$.
- Fig. 2. Horizontal section taken at the root apex of a buccal tooth, showing compact laminar fibrolamellar bone, and some bone of attachment, $\times 30$.
- Fig. 3. Longitudinal vertical section taken towards the medial side of the dentary, showing part of a lingual tooth with open root canal and loose bone at the base (top), and the lower part of a buccal tooth; the shiny mineral that infills the cavities is goethite; this section is located in text-fig. 5*b*, $\times 13$.
- Fig. 4. Longitudinal vertical section through the bases of four buccal teeth showing the laminar fibrolamellar bone, and the diffuse tooth/bone of attachment margin; this section is located in text-fig. 4*c*, $\times 13$.
- Fig. 5. Transverse vertical section through the roots of some buccal teeth and a lingual tooth, showing erosion of the former by the latter; the erosion occurs along a typical arcuate front, $\times 12$.
- Fig. 6. Horizontal section through two buccal dentary teeth, showing the margins of two teeth with clear radial dentinal tubules, and the close-packed bone of attachment between the teeth, $\times 80$.



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BENTON, rhynchosaur dentitions

Hyperodapedon, the bulk of the tooth is composed of orange-yellow orthodentine which clearly shows radial dentinal tubules in microscopic section (Pl. 67, fig. 6), and these are picked out by the iron oxide infill of the pulp cavity on etched polished surfaces. The tubules run from the pulp cavity to a diffuse area at the junction of tooth and bone with no apparent cement layer.

In horizontal section, many buccal dentary teeth show possible growth rings in the dentine (Pl. 67, fig. 2). These mark the boundary between primary dentine, laid down initially around the circumference of the tooth, and secondary dentine. Secondary dentine seems to be laid down in most teeth of *Hyperodapedon*, occluding the pulp cavity, but there is no regular pattern. Adjacent teeth may have root canals occluded to completely different extents, and the canal may become completely closed in the middle portion of the mandible (text-figs. 3c-e, 5). The root canal generally appears to remain open in all but the most anterior teeth (text-fig. 3b). The apical foramen is also usually open which indicates continued deposition of secondary dentine. The apical foramen may be axial, but it is frequently lateral, in which case the root tip is crescentic in section (text-fig. 6a-c; Pl. 66, fig. 2).

These lower parts of the teeth also show resorption effects. The tips of the roots are often randomly arranged (text-fig. 6a-c) and the growth of one clearly causes resorption of another along an arcuate front. This also occurs higher up where lingual teeth are growing close to buccal teeth, and one tooth achieves its normal form to the detriment of the other (text-fig. 3d; Pl. 67, fig. 5).

THE DENTITION OF *STENAULORHYNCHUS*

Arrangement of teeth in the maxilla

Stenaulorhynchus has two grooves on the maxillary tooth-plate. In juveniles, these lie between three distinct rows of teeth which are raised on sharp ridges (text-fig. 7b, c). However, in adults (text-fig. 7e, g), the grooves become apparently less regular as the teeth and bone are worn down. The medial groove runs the length of the maxilla, but the lateral one is restricted to the posterior portion. The grooves become shallower and rounded, and the teeth are not wholly restricted to the ridges. These facts suggest that the grooves in *Stenaulorhynchus* are initiated in the bone between the juvenile tooth rows, but that their subsequent appearance depends on wear to a far greater extent than in *Hyperodapedon* and other late Triassic rhynchosaurs, where the groove is a regular inherent part of the maxillary tooth-plate (Chatterjee 1974; Benton 1983b).

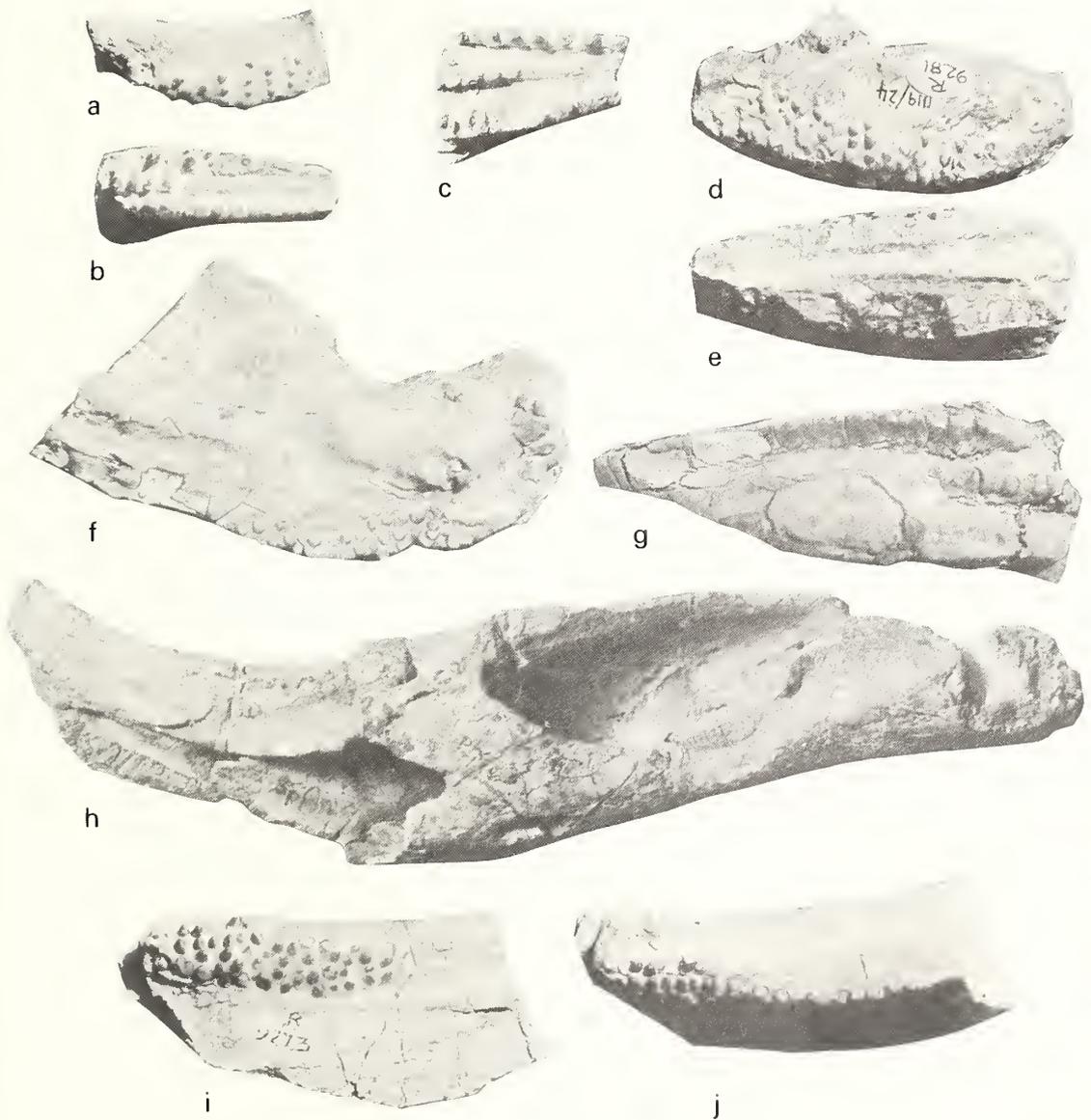
The teeth are arranged in longitudinal rows. In juvenile specimens (text-fig. 7b, c) there are three rows on the occlusal surface of the maxilla, the two outer ones running the length of the jaw, and the middle one only occupying the posterior third of the length. On the medial side of the maxilla (text-fig. 7a) a series of longitudinal rows of teeth may be seen running diagonally down and forwards to the crest of the jaw. Similar features may be seen in adult specimens (text-fig. 7d-g) where additional longitudinal rows are added to the occlusal surface from the medial diagonal rows. The pattern of tooth rows is generally regular, but a scattering of odd teeth that cannot easily be assigned to rows may occur in the medial groove (text-fig. 7g).

The tooth pattern of the maxilla of *Stenaulorhynchus* has been interpreted as consisting of distinguishable occlusal and lingual teeth (Huene 1938; Chatterjee 1974, 1980), but this is not an appropriate description. The 'lingual' diagonal rows all run to the jaw margin and continue without break on to the medial portion of the occlusal surface. It is not possible to distinguish between the 'occlusal' and the 'lingual' series of teeth in any specimen, and in terms of tooth growth the distinction is meaningless since 'lingual' teeth become 'occlusal' as the jaw is remodelled and worn (see below).

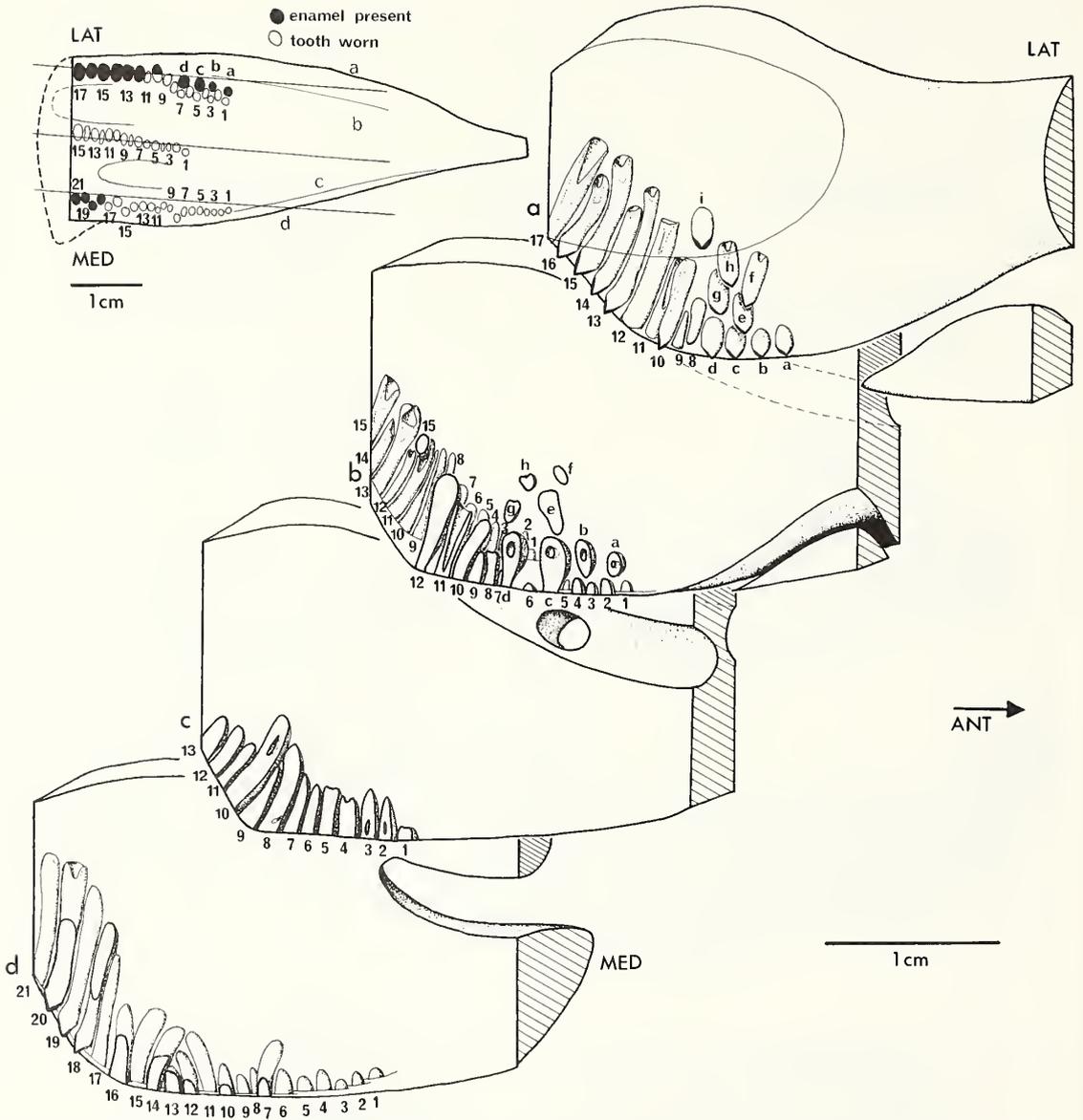
In order to check if any differences existed between longitudinal tooth rows, a series of longitudinal vertical sections through a complete maxillary tooth-plate was made. The three-dimensional reconstruction (text-fig. 8) shows the pattern of teeth in several longitudinal rows through the maxilla. Unfortunately, the most posterior portion of the tooth-plate was missing, and the youngest teeth cannot be shown.

The tooth arrangement is clearly rather irregular within individual longitudinal rows. Even the lateral row is not quite as simple as it appears in occlusal view (text-fig. 7g). In the example sectioned,

two series of teeth of rather different shape are involved, and they are cut at an angle by the plane of section (text-fig. 8). The anterior set consists of nine short teeth (*a-i*) with closed roots and enamel caps. None of these anterior teeth is particularly worn—they barely reach the occlusal margin in the side of the lateral groove—and the posterior one (*i*) does not erupt at all. The posterior set consists of seventeen long-rooted teeth (1-17), all of which have erupted. The anterior nine teeth (1-9)



TEXT-FIG. 7. Tooth-bearing bones of *Stenaulorhynchus stockleyi*: maxillae (*a-g*) and dentaries (*i, j*) (cf. text-fig. 14). *a, b*, juvenile left maxilla (BM(NH) R9279) in medial and occlusal views. *c*, juvenile left maxilla (CUMZ T993) in occlusal view. *d, e*, right maxilla (BM(NH)R9281) in medial and occlusal views. *f, g*, right maxilla (CUMZ T1138) in medial and occlusal views. *h*, right lower jaw (CUMZ T1112), lacking the splenial, in medial view (cf. text-fig. 9c). *i, j*, left dentary (BM(NH) R9273) in medial and occlusal views. All $\times 1$, except *h*, $\times 0.71$.



TEXT-FIG. 8. Graphic reconstruction of the dentition of the right maxilla of *Stenaulorhynchus* (BM(NH) R10008). Drawn from serial sections taken at 0.5 mm spacing, and traced on to glass plates at a magnification of 2x. The four block diagrams (a-d) are drawn as if the bone is transparent, and individual teeth are numbered or lettered in sequence from oldest to youngest in each row (see the text). The lines of section that separate the blocks are indicated on the occlusal view of the tooth-plate. The medialmost rows of teeth are missing owing to damage of the specimen. Abbreviations: ANT, anterior; LAT, lateral; MED, medial.

are heavily worn and rather mixed up with the anterior set just described. Of the posterior eight teeth, six (10, 13–17) still have their points and enamel caps, but the other two (11, 12) are worn. Two teeth (11, 17) have widely open roots—which indicates active deposition of dentine—and it could be that the posterior tooth series (1–17) splits into two longitudinal series (1–11, 12–17) where teeth 11 and 17 were initiated latest of all. In this case, it would be difficult to assign tooth 10 to either series.

The middle longitudinal series of fifteen teeth is easier to interpret. The teeth occur in one sequence, with the anterior group heavily worn, and the posterior group just coming into occlusion. The teeth in the latter group (11–15) have open roots. There is a considerable space between the middle row and the rows of the lingual (medial) side of the tooth-plate. The anterior teeth of the lingual rows are most heavily worn, and the posterior ones have open roots and unworn crowns. The twenty-one teeth are divided tentatively into three series (1–8, 9–15, 16–21), where the youngest teeth of each group are 6, 15, and 21. However, the sectioned maxilla does not show a well-developed battery of 'lingual' teeth, as in other jaws of similar size (e.g. text-fig. 7*f, g*), possibly as a result of damage, and this makes a full reconstruction difficult.

In summary, the teeth in the maxilla of *Stenaulorhynchus* are arranged in several longitudinal rows. There are three tooth-bearing areas in the tooth-plate: lateral, median, and medial. In the medial area, several diagonal rows of teeth pass into occlusion in sequence (text-fig. 8*b*), and there is no clear distinction between 'lingual' and 'occlusal' teeth.

Arrangement of teeth in the dentary

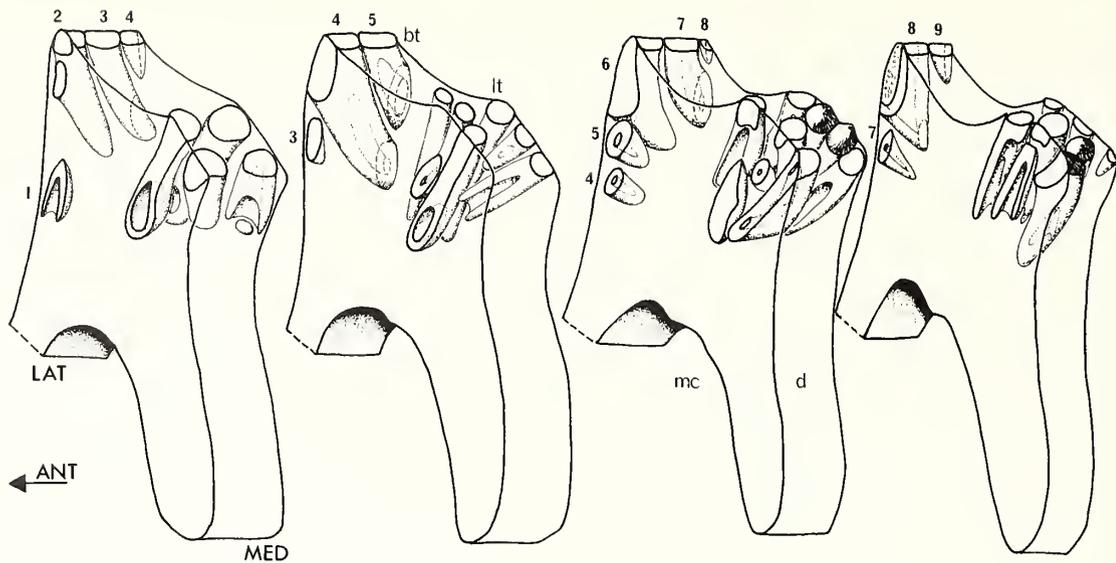
The lower jaw of *Stenaulorhynchus* (text-fig. 7*h*) is longer and lower than that of *Hyperodapedon* (c.f. text-fig. 1*c, d*) and the tooth-bearing portion is concentrated further forward. Well-preserved dentaries (text-fig. 7*i, j*) show that there is a raised longitudinal row of buccal teeth (lateral) and several diagonal rows of lingual teeth (medial) that run up into occlusion on top of the jaw. The lowest lingual teeth are small and occasional (?) replacement pits are seen (text-fig. 7*i*). The teeth are separated by a broad, shallow groove which changes in shape along its length. At the very back of the tooth row the posterior ten or twelve buccal teeth, which are not in occlusion, are raised on a high ridge and separated from the coronoid by a clear groove (text-fig. 9*c*).

A three-dimensional reconstruction of the *Stenaulorhynchus* dentary (text-fig. 9*a*) shows how the buccal teeth are deep-rooted and slope up and forwards, as in *Hyperodapedon*. The lingual teeth also slope up and forwards, but they also slope medially when low on the inside of the jaw. The most lateral tooth of the lingual series at any point is generally the largest and nearly all have open roots. The lingual teeth remain distinct from the buccal teeth, but there is little difference in shape or size between the two kinds, as seen in *Hyperodapedon*.

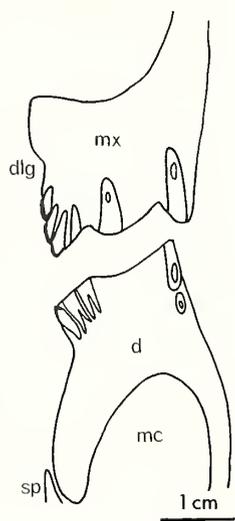
Jaw occlusion and tooth wear

Tooth and bone wear is clearly shown on the occlusal surfaces of the maxilla and dentary of *Stenaulorhynchus*. The relative curvature of the two tooth-bearing elements is not as great as in *Hyperodapedon*, and larger areas are in contact. Juvenile specimens show little wear (text-fig. 7*a–c*), but adult maxillae and dentaries (e.g. text-fig. 7*g, j*) are worn smooth except at the very back. The small enamel cap of each tooth is stained dark brown or black in some specimens, and this highlights the degree of wear (text-fig. 7*j*). As in *Hyperodapedon*, teeth generally bite against bone, although some medial teeth occlude (text-fig. 9*b*). Buccal teeth may be heavily worn on the lateral side of the dentary as well as on the occlusal surface (text-fig. 9*b, c*). Tooth and bone seem to wear at the same rate, and distinct pits or striations are not seen.

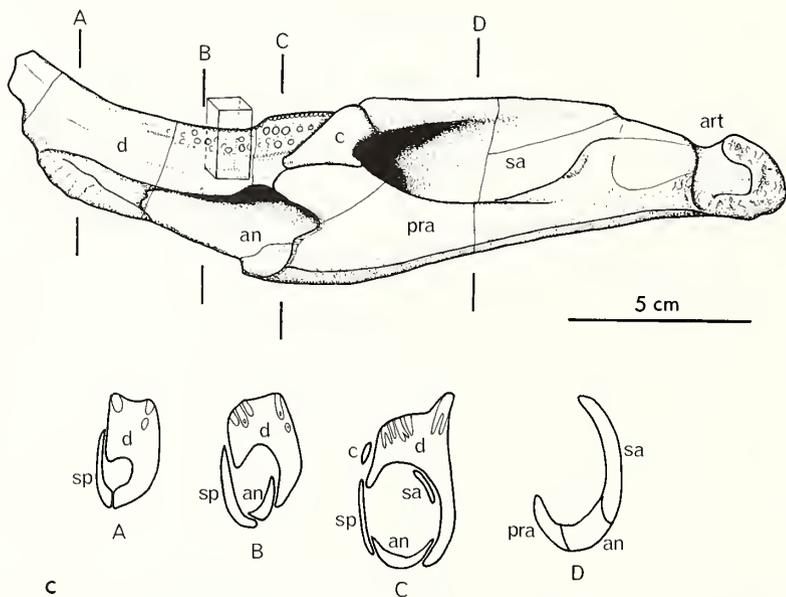
Stenaulorhynchus probably had a precision-shear bite, as in *Hyperodapedon*. The quadrate-articular joint appears to be rather tight (Huene 1938), and the strong symphysis would prevent rotation of the lower jaws—a necessary feature if they are to move back and forwards in such a broad skull. These points, and the apparent precise fit of dentary and maxilla, would prevent any marked fore and aft sawing of the jaws.



a



b



c

TEXT-FIG. 9. The right dentary of *Stenaulorhynchus* (BM(NH) R10007). *a*, graphic reconstruction of the dentition, drawn from serial sections taken at 0.5 mm spacing, and traced on to glass plates at a magnification of $2\times$. The single row of buccal teeth is numbered in sequence from the front backwards. The lingual teeth occur in several longitudinal rows, but these are rather confused by bone remodelling and relative tooth movement. *b*, transverse vertical section through the dentary and maxilla with the jaws slightly apart, to show the nature of the occlusion. A tooth may bite against another tooth, or against bone. *c*, medial view of a right lower jaw (CUMZ T1112, Songea district; cf. text-fig. 7*h*) which lacks the splenial (cf. *Hyperodapedon gordonii*, text-fig. 1*d*). The boxed region of the dentary is equivalent to that shown in the graphic reconstruction. Four cross-sections of the lower jaw at different positions along its length (A, B, C, D) are also given. Abbreviations: an, angular; ANT, anterior; art, articular; bt, buccal teeth; c, coronoid; d, dentary; dlg, dental lamina groove; LAT, lateral; lt, lingual teeth; mc, Meckel's canal; MED, medial; mx, maxilla; pra, prearticular; sa, surangular; sp, splenial.

Tooth form and histology

The teeth of *Stenaulorhynchus* are generally long-rooted and deeply fused in the bone of the jaw. The shapes are less regular than in *Hyperodapedon*, and the root canal is open in less teeth. The bulk of the tooth is composed of dentine, and unerupted or unworn teeth may display a small cap of enamel.

Tooth shape and size vary slightly across the maxilla. In juveniles, most teeth are unworn and their round conical pointed shape may be seen (text-fig. 7a–c). It is not possible to distinguish ‘lingual’ from ‘buccal’ teeth as in *Hyperodapedon*. In older specimens, most of the occlusal teeth are worn flush with the surrounding bone (text-figs. 7d–g, 10a, b). Teeth of the lateral row are nearly always larger than the others (2–3 mm in diameter, compared with 1–2 mm or less). They are rather compressed, or oval, in shape, with the long axis directed transversely—this may be a result of their tight packing with only a thin wall of intervening bone. Other maxillary teeth are more circular in cross-section. The teeth on the lingual surface are small and unworn. They are pointed and conical and still retain their enamel caps (text-figs. 7a, d, f, 11b).

Teeth are generally absent from the most anterior portion of the maxilla—they have presumably been completely worn away. Tooth size increases backwards from the short heavily worn teeth at the front to the middle of the area currently in occlusion, where the teeth have the longest roots (text-figs. 7g, 10). They then diminish to the back of the jaw, where the most posterior, youngest, teeth have not yet come into occlusion.

Some anterior teeth in the lateral series are short and rounded (text-figs. 10a, 12c). Other teeth are long and compressed, or resorbed in an irregular way under the influence of neighbouring teeth. A selection of tooth shapes may be seen in text-figs. 10 and 12a–d. Newly formed teeth have open apical foramina and wide root canals surrounded by a thin tube of dentine (text-fig. 12a), while older teeth show signs of irregular resorption and irregular closure of the root canal (text-fig. 12b). The root canal becomes occluded (text-fig. 12c), and finally, heavily worn teeth may be resorbed at the base by the surrounding bone (text-fig. 12d). The teeth are circular to oval (long axis transverse to axis of jaw) in cross-section.

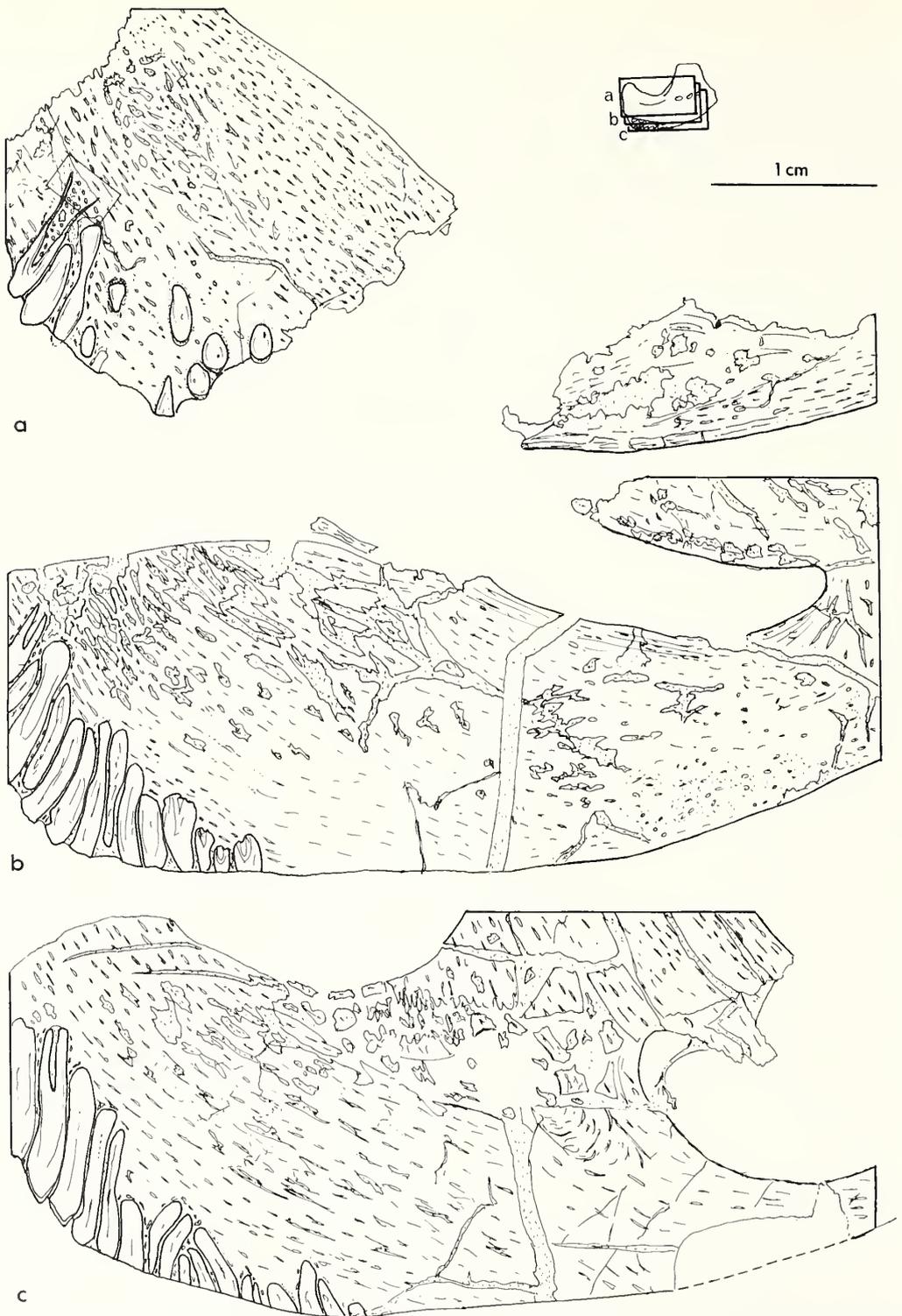
A transverse section of a *Stenaulorhynchus* maxilla (text-fig. 11b) shows how successive longitudinal rows of ‘lingual’ teeth grow down into the teeth below. Each tooth bears an enamel cap that extends further medially where it erupts on the inside of the jaw, and the teeth in occlusion are worn flush with the surface of the bone.

Teeth are present in middle and posterior portions of the occlusal edge of the dentary. Teeth are absent from the very front of the jaw (text-fig. 11c), but they may be seen in the buccal row a short distance back (text-fig. 11d). Here, the lower portion of the next tooth has an open root canal. Further back, the buccal teeth are deeply rooted, and they slope up and forwards (text-fig. 11e, f). The lingual teeth slope up, forwards, and medially. They often have open root canals, and the enamel caps may be seen when the teeth are not in occlusion (text-fig. 11f). The teeth are cylindrical, but the shape may be disturbed by irregular resorption as a result of close-packed neighbouring teeth. Tooth shape is just as variable in the maxilla. Newly formed teeth have large root canals (text-fig. 12e), which become partly closed off (text-fig. 12b) and occluded, often in an irregular way (text-fig. 12g). The relationships between neighbouring lingual teeth may be complex (text-fig. 12h). Resorption of teeth at the base is not seen in the dentary as much as in the maxilla.

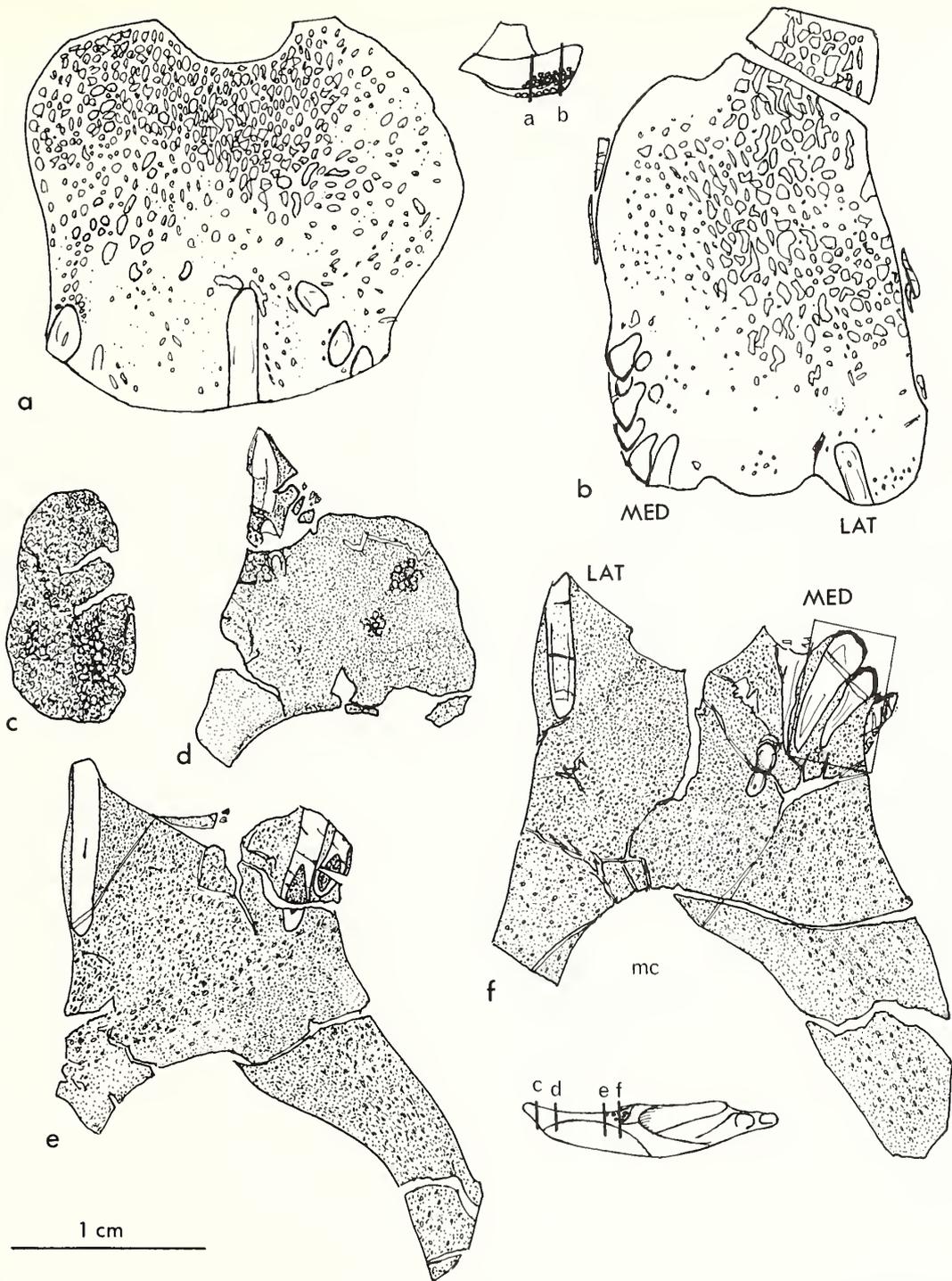
Bone and tooth histology

As with *Hyperodapedon*, the serial peels and microscopic sections of *Stenaulorhynchus* jaws have shown a great deal of histological detail. The bone of the jaws includes four types:

1. Avascular lamellar-zonal periosteal bone in the anterior occlusal edge of the maxilla (text-fig. 10a) and around blood vessel canals (Pl. 68, fig. 1) where the ‘track’ of the vessel as the bone grows may be seen.
2. Laminal fibrolamellar bone with parallel longitudinal primary osteons in regions with teeth (text-figs. 10, 11; Pl. 68, fig. 5).



TEXT-FIG. 10. Longitudinal vertical sections of the maxilla of *Stenaulorhynchus* (BM(NH) R10008) showing teeth. The locations of the sections are indicated on an outline maxilla. *a*, lateral tooth row; several largely unworn teeth are shown, one with a wide open root canal. This shows teeth numbered as *a-d*, 10, 13-17 (text-fig. 8). The boxed area is shown at higher magnification in Pl. 68, fig. 2. *b*, middle tooth row; the youngest (left-hand) tooth has an open root, while the oldest (right-hand) teeth show resorption of the base. This shows teeth numbered as 2-15 (text-fig. 7). *c*, medial tooth row(s); anterior teeth are heavily worn and resorbed. This shows teeth numbered as 5-21 (text-fig. 9).



TEXT-FIG. 11. Transverse vertical sections of the right maxilla (*a, b*) and right dentary (*c-f*) of *Stenaulorhynchus*. The locations of the sections are indicated on an outline maxilla and lower jaw. *a, b*, cross-sections of the maxilla, traced from polished end sections (BM(NH) R9276, R9277), and showing the arrangement of teeth in the lateral, middle, and medial rows. Lingual teeth of young (high) Zahnreihen can be seen to have caused erosion of older teeth in *b*. The dentary: *c*, anterior portion where the bone is compact and the teeth have been worn away and resorbed; *d*, further back, worn buccal teeth may be seen on the lateral side; *e*, in the occlusal area, large buccal and lingual teeth are present, with open root canals; *f*, at the back, some teeth are in occlusion, and others with unworn enamel caps have just been implanted. The boxed area is shown at higher magnification in Pl. 68, fig. 6. Abbreviations: LAT, lateral; mc, Meckel's canal; MED, medial.

3. Reticular (cancellous) fibrolamellar bone in the centre of bones and away from the teeth (text-figs. 10, 11).

4. Bone of attachment: secondary reticular fibrolamellar bone surrounding teeth and cross-cutting laminar fibrolamellar bone. The sheath of reticular bone surrounds each tooth and accompanies it through the jaw (text-figs. 10, 11; Pl. 68, figs. 3, 4, 6). Between close-packed teeth, the osteons of the bone of attachment may be distorted and flattened (Pl. 68, figs. 4, 6). The bone is especially cancellous at the base of teeth, and spongy reticular bone may fill the wide open root canals of newly formed teeth (Pl. 68, fig. 2).

Micrographs of the bone of *Stenaulorhynchus* maxillae and dentaries show osteocyte lacunae, and the centripetal arrangement of finely lamellated bone in primary osteons around vascular canals is clear (e.g. Pl. 68, figs. 5, 7).

Enamel is present in a cap on most unerupted or unworn maxillary and dentary teeth (Pl. 68, figs. 3, 6), but the crystal structure is not seen. The enamel cap is very small and covers only the tip of the tooth and the exposed sides of those that erupt first on the lingual side of the maxilla or dentary. The enamel is soon worn away when teeth come into occlusion (text-fig. 7j). The dentine clearly shows radial dentinal tubules (Pl. 68, figs. 7, 8), as in *Hyperodapedon*.

Growth lines (contour lines of Owen) in the dentine are very clear (text-fig. 12; Pl. 68, figs. 3, 4, 6-8) and these are marked by bends in the dentinal tubules. They clearly show the sequential centripetal filling of the pulp cavity, with periods of slow and fast deposition of secondary dentine. Adjacent teeth show matching sequences of dark and light, and broad and narrow bands (Pl. 68, fig. 4), and these catalogue periods of growth (food availability/seasonality?).

The effects of resorption of tooth material may be seen in several ways. Adjacent teeth may cause extensive resorption along an arcuate front where they contact their neighbours and give rise to irregular constrictions and bends (e.g. text-figs. 10, 11), and, in some cases, teeth are excluded from the jaw margin by others (text-fig. 10b). The resorption cuts through the incremental lines in the

EXPLANATION OF PLATE 68

The dentition and bone of the maxilla (figs. 1-4) and dentary (figs. 5-8) of *Stenaulorhynchus*. Sections from BM(NH) R10008 (figs. 1-4) and BM(NH) R10007 (figs. 5-8).

Fig. 1. Longitudinal vertical section through the anterior portion of the maxilla, showing the laminar fibrolamellar bone with the canals running up and backwards, and two small blood-vessels and their 'tracks' of remodelled bone also running up and backwards, $\times 4.5$.

Fig. 2. Longitudinal vertical section through the root apex of a posterior tooth, showing the widely open root canal filled with spongy bone and the bone of attachment, set in the normal laminar fibrolamellar bone of the jaw; this section is located in text-fig. 13a, $\times 17$.

Fig. 3. Longitudinal vertical section through some unerupted anterior teeth of the lateral series, showing the bone of attachment, the circumferential growth lines in the dentine and erosion of an older (lower) tooth in the bottom right-hand corner, by a younger (higher) tooth, $\times 12$.

Fig. 4. Longitudinal vertical section through some anterior heavily worn teeth (occlusal margin at foot of picture), showing dentine growth lines, fully closed root canals, irregular resorption of the base of the teeth, and associated irregular bone, $\times 12$.

Fig. 5. Transverse vertical section, showing typical primary osteons of the laminar fibrolamellar bone, $\times 30$.

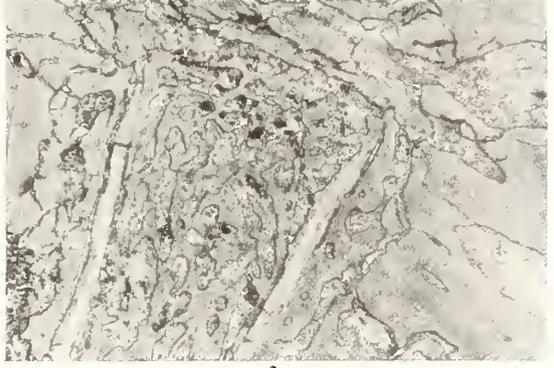
Fig. 6. Transverse vertical section through two lingual teeth, showing the unworn enamel caps, growth rings in the dentine, and erosion of the side of the older (left-hand) tooth by the younger (right-hand) tooth; this section is localized in text-fig. 11f, $\times 12$.

Fig. 7. Transverse vertical section through part of a lingual tooth showing the bone of attachment, the root canal, secondary dentine with growth rings, and radial dentinal tubules, $\times 25$.

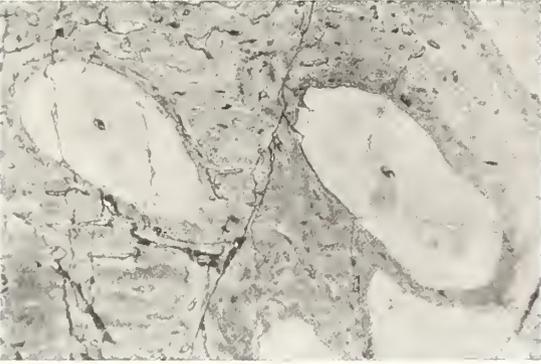
Fig. 8. A similar transverse vertical section through parts of two lingual teeth with occluded root canals, showing the relationship between the growth lines in the secondary dentine and the radial dentinal tubules, $\times 45$.



1



2



3



4



5



6

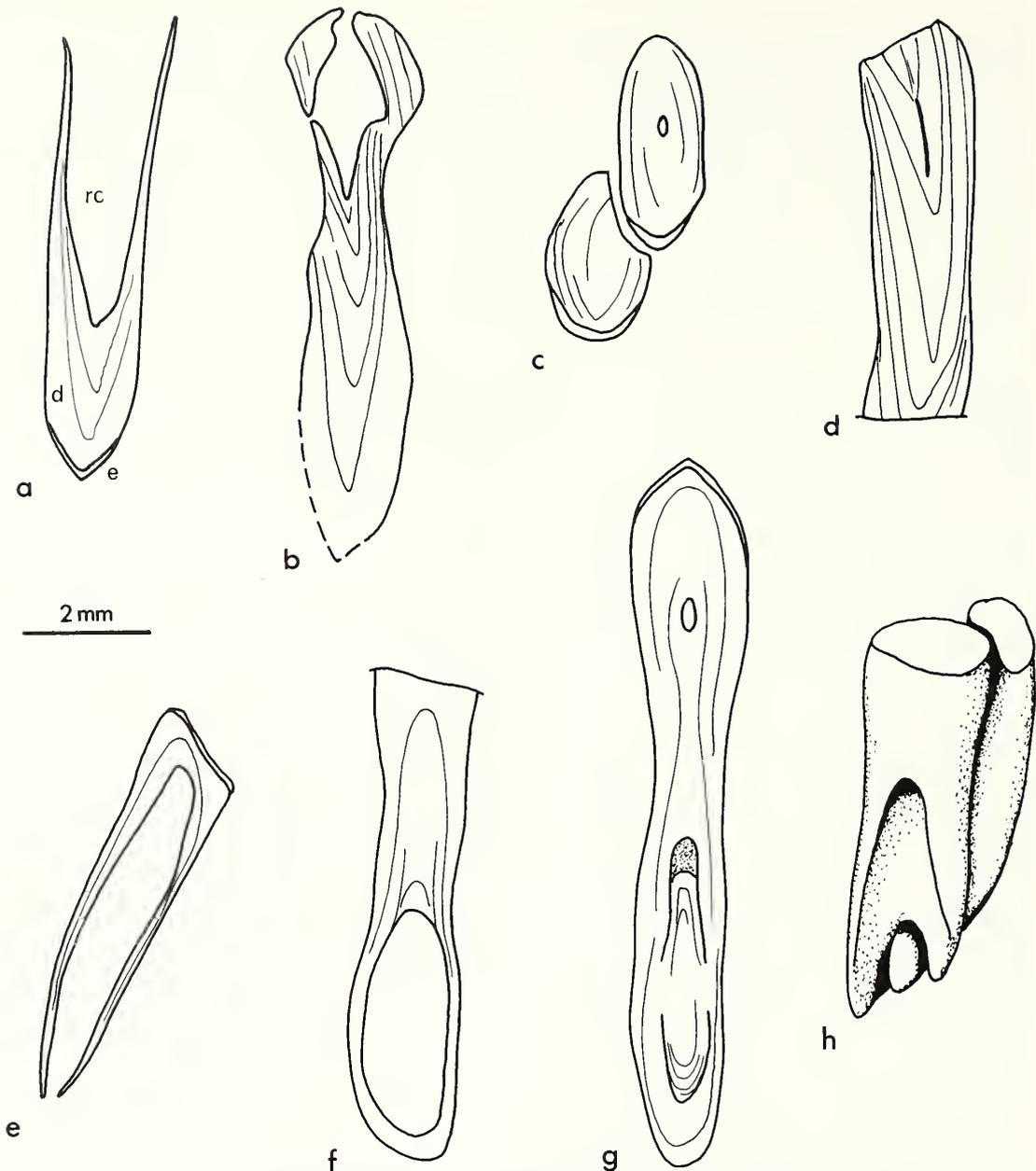


7



8

BENTON, rhynchosaur dentitions



TEXT-FIG. 12. Sketches of individual teeth of *Stenaulorhynchus*: *a-d*, from the maxilla with the crown facing downwards; *e-h*, from the dentary, with the crown facing upwards. *a*, newly implanted tooth with open root canal, some secondary dentine deposition and an unworn enamel cap; *b*, slightly older tooth, partly worn, with more deposition of secondary dentine, and irregular closure of the root canal owing to extensive erosion by neighbouring teeth; *c*, two small unerupted teeth with complete enamel caps, and 'interference' in which the younger (upper) one causes erosion of the older (lower) one; *d*, an old heavily worn tooth in which the root canal has been completely occluded, and resorption of the base has begun; *e*, a newly implanted lingual dentary tooth in which little secondary dentine has been deposited; *f*, an older lingual tooth in which the crown is worn, but the root canal is still open; *g*, a large lingual tooth with unworn enamel cap and extensive occlusion of the root canal by secondary dentine; *h*, graphic reconstruction of two lingual teeth which have been implanted so close together that each has interfered with the normal development of the other. Abbreviations: d, dentine; e, enamel; rc, root canal.

dentine, and may open up the root canal (text-fig. 12*b*). In other cases, the crown of a growing tooth may pass through the root of a tooth in occlusion and cause loss of dentine in the latter (text-fig. 12*c*; Pl. 68, fig. 3). This pattern of extensive resorption is more common in *Stenaulorhynchus* than in *Hyperodapedon*, as is resorption of the base of old worn teeth by the surrounding bone (text-figs. 10*b*, 12*d*). This resorption occurs especially in the maxilla where the bone of attachment can be seen to invade the dentine, often along particular growth lines, leaving the root of the tooth ragged and incomplete (Pl. 68, fig. 4).

TOOTH IMPLANTATION IN RHYNCHOSAURS

Rhynchosaurs have deeply rooted teeth fused to bone of attachment. They show a combination of features of both the thecodont and acrodont systems, and Chatterjee (1974) has termed this mode of attachment 'ankylotheodont'. A characteristic feature is the secondary bone of attachment which has also been identified in *Scaphonyx fischeri* (Sill 1971*b*, pl. 4*c*) and *H. huxleyi* (Chatterjee 1974, p. 230). The latter author described this bone of attachment as 'spongy in appearance resembling a foam of very small bubbles', and it is clearly demarcated from the surrounding bone. *H. gordonii* does not show the 'bony layered structure . . . at the base of some teeth, invading the pulp cavity' observed by Chatterjee (1974) in *H. huxleyi*, but reticulate bone has been noted above in the pulp chamber of *Stenaulorhynchus*.

Most early reptiles (e.g. pelycosaurs, captorhinomorphs, early diapsids) had subthecodont (= protothecodont) tooth implantation (Edmund 1969). In *Captorhinus* the subthecodont teeth have relatively shallow roots and they are ankylosed into a socket by bone of attachment with 'no space . . . for a periodontal ligament or other soft tissues between the socket and the base of the tooth' (Bolt and DeMar 1975). Most early diapsids have also been stated to have subthecodont teeth, and that is probably the primitive character for the group (Benton 1983*b*), although there is much confusion about the terminology here, and detailed histological information is needed. Some diapsids evolved thecodont teeth in the Triassic (thecodontians, dinosaurs, crocodiles), while others evolved acrodont teeth (sphenodontids) or 'subpleurodont' teeth (early squamates). The rhynchosaurs evolved a fourth system—ankylotheodont teeth (deeply rooted teeth surrounded by bone of attachment which may also invade the pulp chamber; no 'socket' with soft tissues around the teeth; no typical reptilian tooth replacement).

The acrodont agamid lizard *Uromastix* may also show a bony core in the pulp chamber of posterior teeth, but its function is uncertain (Throckmorton 1979). An analogous condition also occurs in adult *Sphenodon*. Secondary bone grows round the bases of the teeth and encloses many of them in shallow alveoli. The teeth are still firmly fused with the base and sides of the alveoli and are thus not thecodont. Howes and Swinnerton (1901) and Harrison (1901) describe this condition in *Sphenodon* as 'hyperacrodont'.

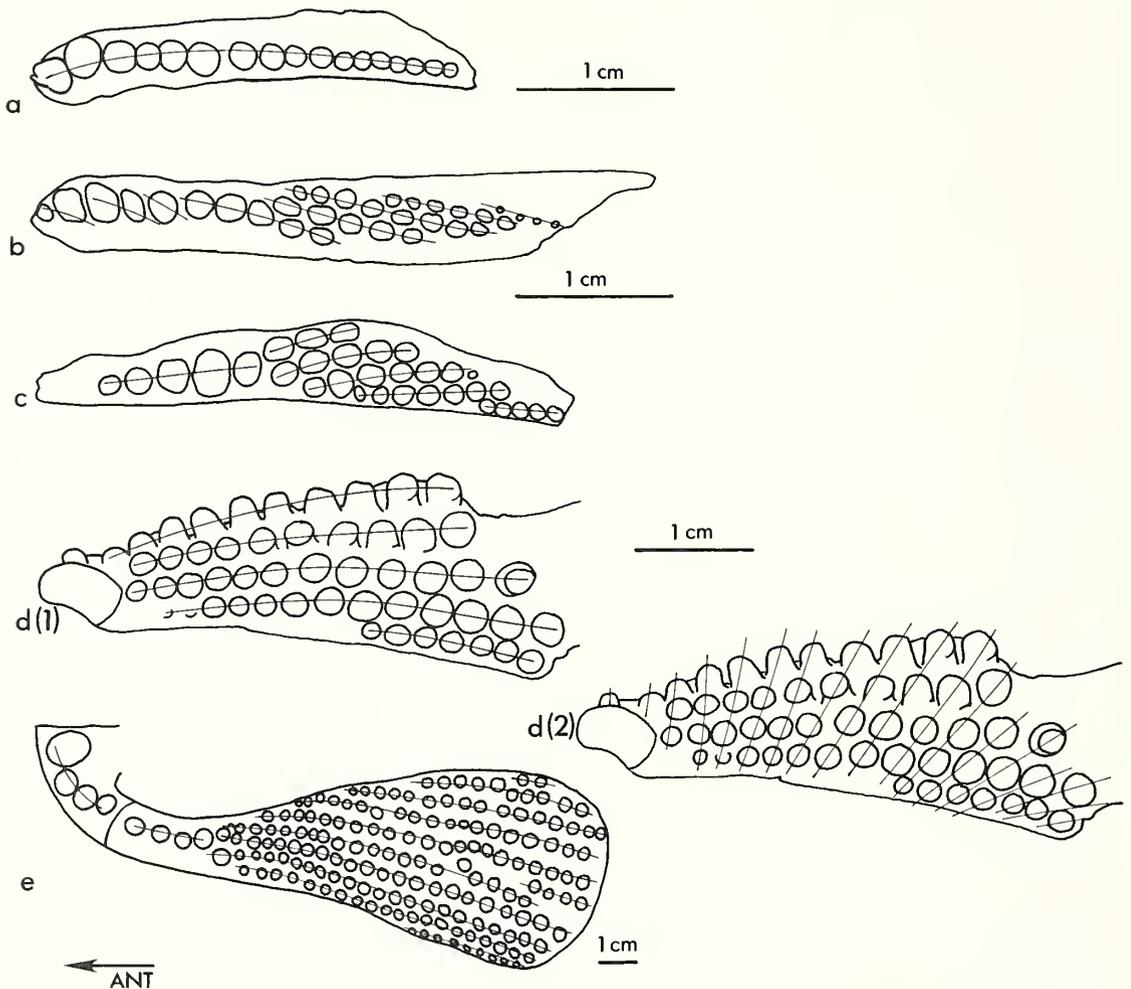
TOOTH ADDITION IN RHYNCHOSAURS

The multiple row dentition of the rhynchosaur maxilla and dentary has been interpreted as the retention in the adult of an embryonic type of dentition, with the diagonal tooth rows equivalent to the Zahnreihen of Woerdemann (1921) (Edmund 1960, p. 59; 1969, p. 153; Chatterjee 1974, p. 234). The captorhinomorphs *Captorhinus*, *Labidosaurikos*, and *Moradisaurus* also retain apparently similar diagonal rows of functional teeth in the adult, and a brief consideration of these early reptiles may throw light on the development of the rhynchosaur dentition.

Multiple tooth rows in captorhinomorphs

Early captorhinomorphs, such as *Eocaptorhinus laticeps* from the lower Permian of Texas and Oklahoma, had a single-row dentition of subthecodont teeth in premaxilla-maxilla and dentary (text-fig. 13*a*). There is evidence of tooth replacement from below (replacement gaps, replacement scars), and the tooth rows have been divided tentatively into Zahnreihen (Heaton 1979).

The slightly later *C. aguti* (lower Permian, Texas, New Mexico, Oklahoma) normally has three or four clear subparallel postero-medially directed rows (total range, one to eight rows) of subtheodont teeth on premaxilla-maxilla and dentary (text-fig. 13*b, c*). Bolt and DeMar (1975) and Ricqlès and Bolt (1983) have demonstrated that all teeth were continuously replaced and that the number of teeth and of rows did not depend on the size of the animal. Each diagonal row is interpreted as a Zahnreihe, and tooth replacement proceeded in such a way that matching diagonal rows of lower and upper teeth were maintained for an efficient shearing jaw action. Teeth were replaced from a lingually situated dental lamina at the posterior end of each Zahnreihe, and teeth were lost anteriorly/labially. There was a limit to this addition, and at times whole Zahnreihen would be lost anteriorly.



TEXT-FIG. 13. Occlusal views of the jaws of captorhinomorphs, showing the teeth in outline: *a*, right dentary of *Eocaptorhinus*; *b*, right dentary of *Captorhinus*; *c*, right maxilla of *Captorhinus*; *d*, right maxilla of *Labidosaurikos*; *e*, right maxilla of *Moradisaurus*. Zahnreihen are indicated with thin lines; two alternative interpretations are given for *Labidosaurikos*, in terms of Zahnreihen (*d* (1)) and tooth families (*d* (2)). (*a*, after Heaton 1979; *b, c*, after Ricqlès and Bolt 1983; *d* (1), after Edmund 1960; *d* (2) after Osborn 1977; *e*, after Ricqlès and Taquet 1982).

Several captorhinomorphs had yet more highly developed multiple tooth rows: *Labidosaurikos* from the lower Permian of Oklahoma and Texas had four or five long diagonal rows of teeth in each jaw (text-fig. 13d). Edmund (1960, pp. 31–32) compared tooth replacement in the maxilla of *L. bakeri* with *C. aguti*. His view was that *C. aguti* did not have tooth replacement and that Zahnreihen were added lingually throughout life. Edmund assumed that the posterior rows of small teeth were present in the juvenile and that teeth were added only anteriorly and lingually. He did not make it clear how this model applies to *Labidosaurikos*, but the available figures and descriptions (Stovall 1950; Olson 1954; Seltin 1959; Edmund 1960, p. 31) clearly do not support his view of anterior tooth addition. Heaton (1979, p. 22) noted that a simple model of replacement waves of teeth erupting lingually and displacing existing tooth generations labially could give rise to the pattern seen in *Labidosaurikos*. However, the specimens must be restudied in order to determine whether replacement from below occurred, whether teeth were added to the postero-lingual ends of Zahnreihen, and whether the Zahnreihen migrated labially.

The upper Permian captorhinomorph *Moradisaurus* from the Niger (Taquet 1969; Ricqlès 1980; Ricqlès and Taquet 1982) had eleven to twelve longitudinal rows of teeth in the maxilla (text-fig. 13e). *Moradisaurus* had a very large skull (c. 40 cm long) which was broad posteriorly, as in rhynchosaurs. However, it did not have the groove in the maxillary tooth-plates typical of most rhynchosaurs.

Osborn (1977) has recently reinterpreted the multiple-row captorhinomorph dentition in terms of tooth families and inhibitory control of tooth alternation (cf. text-figs. 13d (1) and 13d (2)). The Zahnreihe and inhibitory models, as applied to more typical polyphyodont reptiles, must be compared as explanations of multiple tooth rows in captorhinomorphs and rhynchosaurs.

Development of patterns in reptile dentitions

In most reptiles, teeth are replaced continuously throughout life. New teeth are initiated deep within the jaw and as they grow they pass towards the jaw margin where they erupt and function for a few months before being replaced from below. The teeth are replaced in regular waves which sweep through alternate tooth positions generally from the back to the front of the jaw. Diagonal rows of developing teeth are termed Zahnreihen and vertical lines of teeth initiated at specific positions are called tooth families. The problem is to determine whether either of these pattern lines has a biological significance.

Edmund (1960) suggested that Zahnreihen are the key to reptile tooth replacement. A stimulus passes from the front to the back of the jaw and initiates the development of a new tooth at each tooth position. New stimuli are regularly initiated and several Zahnreihen are being developed at any time.

Osborn (1970, 1972) argued that Zahnreihen have no biological meaning. He proposed (Osborn 1971, 1974, 1977) that teeth may be initiated anywhere along the dental lamina, and that the spacing and rate of growth are controlled by the production of a fixed area of inhibition around a tooth germ, which reduces as the tooth grows. According to this model, descriptive units such as Zahnreihen, tooth families, and replacement waves have no developmental significance since they are subjectively selected by the observer (Osborn 1977). They are the result of the ontogeny of the teeth.

A problem arises here in that the 'Zahnreihen theory' of Edmund (1960) and the 'inhibition theory' of Osborn (1971, 1977) are not opposites that can be tested against each other. The former has not been fully developed as a theory of causation (DeMar and Bolt 1981) and experiments have not been designed to test the inhibition theory (Osborn 1974, 1977). Osborn (1971) found that tooth families were better units to use than Zahnreihen in interpreting the dentition of the lizard *Lacerta vivipara*. He later (Osborn 1977) interpreted the dentition of *Captorhinus* and *Labidosaurikos* in terms of the inhibition model and tooth families (text-fig. 13d (2)). On the other hand, Bolt and DeMar (1975) and Ricqlès and Bolt (1983) concluded that Zahnreihen provided the simplest explanation of the dentition of *Captorhinus*, and an examination of the multiple tooth rows of other captorhinomorphs confirms this descriptive interpretation of the pattern. The longitudinal diagonal rows are far more obvious as independent units than any other lines selected. The Zahnreihen terminology will also be used here for rhynchosaurs on the grounds of simplicity of description.

Interpretation of the rhynchosaur dentition

The functioning dentition of rhynchosaurs consists of several longitudinal or longitudinal/diagonal Zahnreihen. Teeth were not replaced from below but their root canals remained open while they were in occlusion. Teeth were formed on a dental lamina which lay lingual and posterior (*Stenaulorhynchus*) or posterior (*Hyperodapedon*) to the tooth-bearing bones. Teeth became ankylosed to the jaw adjacent to the dental lamina and out of the zone of occlusion. With growth of the upper and lower jaws, the area of wear expanded backwards and lingually. New teeth came into occlusion at the back and lingual side of the jaw and worn teeth at the front ceased to be used and became partly resorbed. Thus, teeth were added simultaneously to the posterior ends of several Zahnreihen which were losing teeth anteriorly, by remodelling and growth of the jaw. There was no extensive 'drift' or migration of teeth through the bone of the jaw, as has also been shown in *Captorhinus* (Ricqlès and Bolt 1983). In addition, Zahnreihen were initiated posteriorly and lingually as the dentigerous bones increased in size.

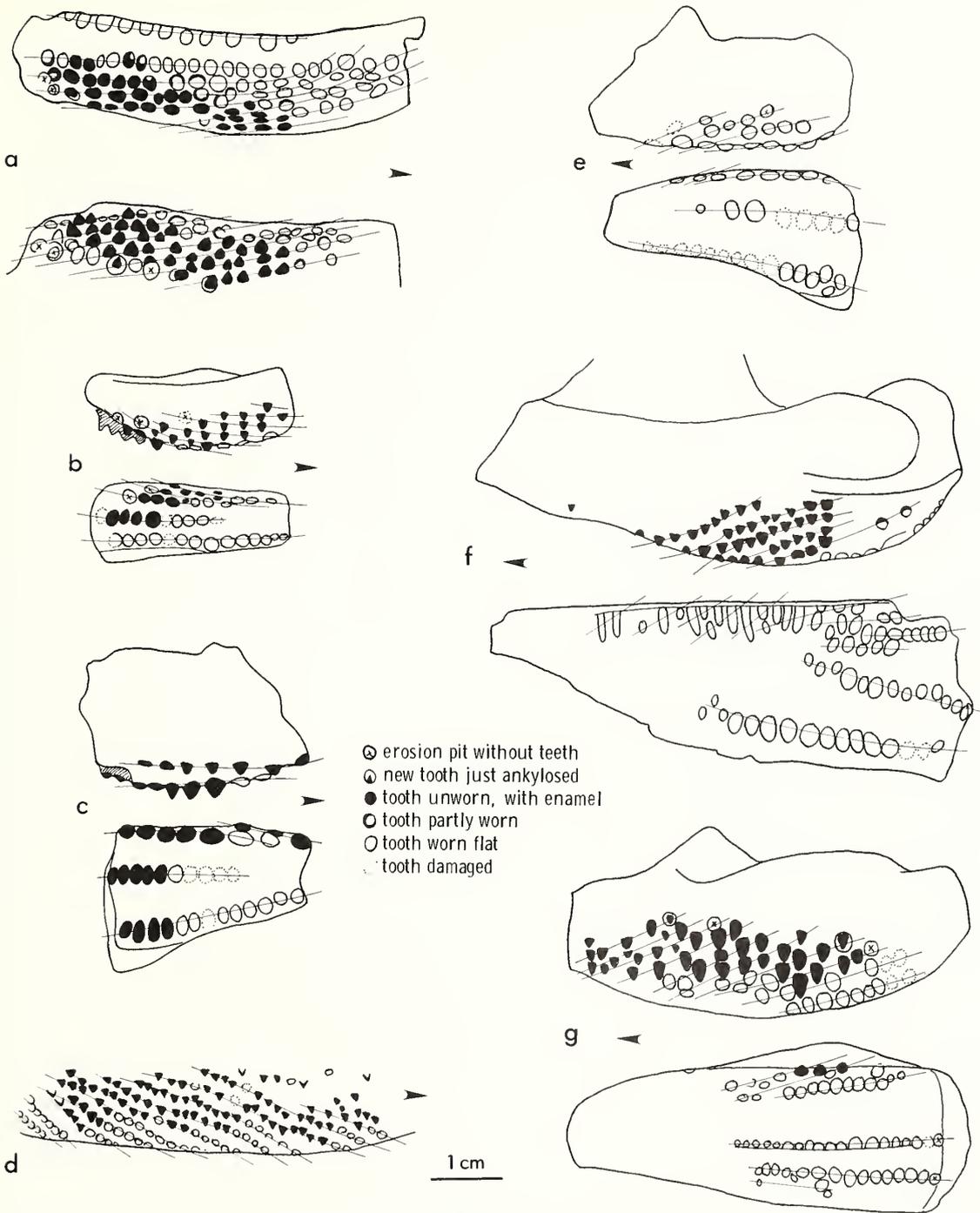
The assignment of teeth to Zahnreihen is relatively easy in *Stenaulorhynchus* (text-fig. 14). The rows may overlap slightly, but teeth are not exchanged between Zahnreihen. However, in *Hyperodapedon* (text-fig. 15) and other late Triassic rhynchosaurs the assignment is more difficult. Chatterjee (1974, pp. 230, 234) showed two ways of distinguishing tooth rows in maxillae of *H. huxleyi*: longitudinal rows and transverse rows. Longitudinal rows were easier to establish in young specimens, whereas transverse rows were more obvious near the posterior margin in large specimens. Chatterjee interpreted the transverse rows as Zahnreihen, and envisaged the regular addition of new rows posteriorly as soon as the jaw grew sufficiently. However, this is a misinterpretation of the meaning of Zahnreihen (Edmund 1960; DeMar 1974; Bolt and DeMar 1975), which may be regarded simply as rows of teeth in which relative age increases progressively from back to front. The last ankylosed tooth and the dental lamina are in the posteriormost position. Edmund (1960, p. 59) and Malan (1963) have also interpreted the longitudinal tooth rows in *Howesia*, a primitive rhynchosaur from the early Triassic of South Africa, as Zahnreihen.

The pattern of teeth that is seen on the occlusal surface of the rhynchosaur jaw is clearly much modified by jaw growth and remodelling and by 'interference' between individual teeth. The more anterior the position of a tooth, the older it is, and the more it will have been affected by events subsequent to budding and ankylosis.

Posterior addition of teeth

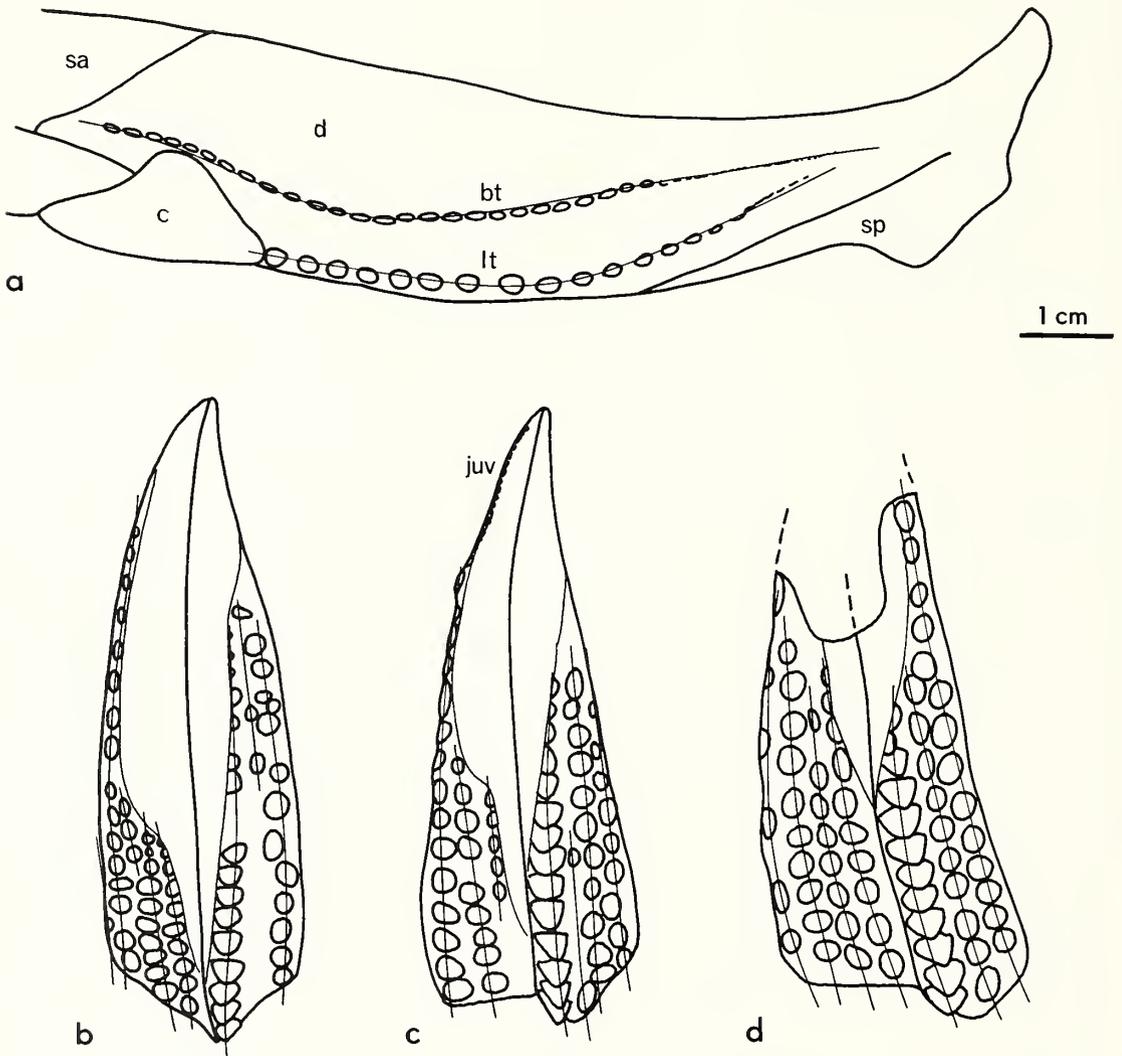
Evidence that rhynchosaurs added teeth posteriorly includes variation in tooth size, wear patterns, state of the pulp chamber, and growth of the tooth plate. The anterior teeth, when preserved, are tiny. One specimen of *Hyperodapedon gordoni* (NUGD B) shows ten to fifteen small teeth (diameter < 1 mm) on the medial edge which are sharply set off from those following behind (diameter 2–3 mm) (text-fig. 15c). These are probably equivalent to the remnant hatchling dentition of *Sphenodon* (Robinson 1976). Teeth initiated subsequently are of roughly equal size throughout life. The wear patterns clearly show the parts of the jaws that were in occlusion at death, and posterior teeth are unworn, which suggests that they had erupted last. The most posterior tooth in a longitudinal row may be very small, and probably barely erupted. In some specimens of *Stenaulorhynchus*, the most posterior tooth in certain Zahnreihen is missing, presumably since it failed to become ankylosed before the animal died (text-figs. 7j, 14a, b, g). Chatterjee (1974, p. 234) noted the same feature in *H. huxleyi*. Posterior teeth have open apical foramina and the occlusion of the root canal by deposition of secondary dentine may be followed in an irregular sequence along a Zahnreihe from the back of the jaw forwards (e.g. text-figs. 2, 10).

The maxillary tooth-plate at least grew by the addition of bone in successive layers. In *H. huxleyi*, the bone layers may be seen running diagonally upwards and forwards in a side view of the tooth-plate, and each layer is associated with a transverse row of teeth (Chatterjee 1974, pp. 232–233). This has the effect of lengthening and thickening the tooth-plate, and of making the front portion curve more and more upwards. Ricqlès and Bolt (1983, p. 11) noted 'strand lines' in the dentary of *Captorhinus* which they interpreted as indicating successive bursts of growth by posterior addition of



TEXT-FIG. 14. Patterns of teeth in the jaws of *Stenaulorhynchus*: dentary (a) and maxilla (b–g). The arrows indicate the anterior ends of each specimen. Zahnreihen are suggested and tooth form is coded. a, left dentary (BM(NH) R9273) in dorsal and medial views (cf. text-fig. 7i, j); b, left maxilla (BM(NH) R9279) in medial and ventral views (cf. text-fig. 7a, b); c, left maxilla (CUMZ T993) in medial and ventral views (cf. text-fig. 7c); d, left maxilla (BM(NH) R9275) in medial view; e, right maxilla (CUMZ T992) in medial and ventral views; f, right maxilla (CUMZ T1138) in medial and ventral views (cf. text-fig. 7f, g); g, right maxilla (BM(NH) R9281) in medial and ventral views (cf. text-fig. 7d, e).

bone. Similar indications of appositional growth may be seen in maxillae of *Stenaulorhynchus*, and the extensive 'migration' of blood-vessels through the bone confirms this (Pl. 68, fig. 1). The vessels all migrate up and backwards in order to maintain their correct relative positions as bone is added behind, below, and above. Further evidence for the growth directions of the jaws is seen in the clear orientation of vascular canals in the bone. In section, these run up and backwards in the dentary of *Hyperodapedon* (text-fig. 4d) and in the maxilla of *Stenaulorhynchus* (text-fig. 10), which indicates backwards and dorsal growth.



TEXT-FIG. 15. Patterns of teeth in the jaws of *Hyperodapedon gordonii*: dentary (a) and maxilla (b-d) in occlusal views. Zahnreihen are tentatively indicated: a, left dentary (NUGD B); b, left maxilla (NUGD A); c, left maxilla (NUGD B); d, left maxilla (EM 1926.6). In the maxillae, the areas of wear on either side of the groove are left blank and outlined. 'Juvenile' teeth (< 1 mm diameter) may be seen at the front of the maxilla of NUGD B (c). Abbreviations: bt, buccal teeth; c, coronoid; d, dentary; juv, juvenile teeth; lt, lingual teeth; sa, surangular; sp, splenial.

Dental lamina

The dental lamina in the dentary of *Stenaulorhynchus* probably lay in the marked U-shaped groove between the back of the tooth-bearing area and the coronoid (text-figs. 7*h*, 9*c*). The dental lamina probably continued forward in a shallow depression which runs forward from here on the medial surface of the dentary below the lingual tooth rows. There is a similar clear groove between the coronoid and dentary in *Hyperodapedon* for the dental lamina, but no sign of an anterior continuation, which was not necessary (text-fig. 1*d*). The dental lamina in the maxilla of *Stenaulorhynchus* also appears to have been situated partly posteriorly in the sharp groove between maxilla and ectopterygoid, and partly medially. There is a clear notch and anteriorly running depression on the side of the maxilla, just above the lingual teeth (text-fig. 7*f*, *g*). In *Hyperodapedon*, again, the dental lamina probably lay only posteriorly in the V-shaped notch between maxilla and ectopterygoid (text-fig. 1*b*). Chatterjee (1974, pp. 234, 236) noted just the same features in *H. huxleyi*.

Erosion, resorption and anterior loss of teeth

Individual teeth commonly cause resorption in others, although there is no evidence in rhynchosaurs of tooth replacement from below with the associated resorption of old teeth. The patterns seem to be associated with the small movements of the ankylosed teeth relative to each other as a result of continuous growth and remodelling of the bone of the jaws. A similar effect of tooth 'crowding' and consequent erosion has been noted in *Captorhinus* (Bolt and DeMar 1975; Ricqlès and Bolt 1983).

The patterns of erosion appear to indicate the relative ages of the teeth involved. Younger, more recently implanted teeth generally cause erosion in older ones. In the dentary of *Hyperodapedon*, the lingual teeth appear to cause damage to the buccal teeth when they come into proximity (e.g. text-fig. 3*d*; Pl. 67, fig. 5). The active open root apices of buccal teeth may cause mutual erosion when they meet (text-fig. 6*a-c*). In the maxilla of *Stenaulorhynchus*, young open-rooted teeth 'squeeze' their older anterior neighbours (text-figs. 10, 12*b*). Similarly, young teeth belonging to high Zahnreihen grow down into, and erode, older teeth that belong to other Zahnreihen (text-figs. 11*a, b*, 12*c*; Pl. 68, fig. 3). Exactly the same effects are seen in the dentary of *Stenaulorhynchus* (text-figs. 9*a*, 11*f*, 12*h*, 14*a*). In general then, in becoming ankylosed, a tooth may excavate a space for itself in the jaw-bone and this may damage teeth of different Zahnreihen that are already implanted.

It has already been noted that anterior teeth in *Stenaulorhynchus* and *Hyperodapedon* are generally heavily worn and often reduced further by resorption. Large amounts of tooth material may be removed leaving the root apex ragged (e.g. Pl. 66, fig. 2; Pl. 68, fig. 4). Teeth are 'lost' anteriorly by a combination of wear of the crown in occlusion and resorption of the root. This 'drift' of teeth from the posterior/lingual portion of the jaw to the anterior/labial portion, where they are lost, is a result of bone growth and remodelling. When worn teeth 'swing' out of occlusion their roots are resorbed. This is very similar to the mechanism postulated by Ricqlès and Bolt (1983) in *Captorhinus*.

Model of tooth replacement in rhynchosaurs

Rhynchosaurs have several longitudinal rows of teeth (Zahnreihen) in each tooth-bearing jaw element (maxilla and dentary). Teeth are not replaced from below. During normal jaw growth, teeth are added posteriorly or anteriorly and lingually to each Zahnreihe. If the tooth-bearing bone becomes wide enough, additional Zahnreihen may be initiated. The addition of teeth appears to depend on the available area of dentigerous bone in the proximity of the dental lamina. Newly implanted teeth have widely open pulp chambers and small enamel caps. They swing into occlusion as the jaw-bones rotate relative to each other. This 'rotation' is slight and occurs to maintain an adequate occlusal surface between dentary and maxilla as the animal increases in size. In occlusion, the enamel tooth cap is soon lost and the tooth becomes flattened, and then dentine and bone are worn at the same rate. Secondary dentine gradually fills the pulp chamber. As the occlusal area moves back with further growth, the heavily worn anterior teeth swing out of occlusion. Their roots are largely resorbed and they are reduced in size. They are finally lost anteriorly or antero-labially. Throughout its life, a tooth may seem to move forwards through the jaw, as if on a conveyor belt, but

this effect is produced by relative growth of the jaw and remodelling rather than by 'drift' of teeth through the bone of the jaw.

The reality of the Zahnreihen is indicated by the simple observations of the relative ages of teeth in one longitudinal row: oldest at the front and youngest at the back. Further, the youngest Zahnreihe is located medially of the older ones. This is shown in a cross-section by the stages of development of individual teeth that belong to different Zahnreihen, and their mutual erosion effects: medially placed teeth cause erosion of their laterally placed neighbours. The former were clearly implanted after the latter.

FUNCTION OF THE RHYNCHOSAUR DENTITION

Many of the anatomical and histological features of the ankylotheodont rhynchosaur teeth may be understood by a comparison with living acrodont reptiles in which teeth are also not replaced from below, but are added posteriorly. Amongst living reptiles, acrodont teeth are seen in *Sphenodon* (Robinson 1976), and in two families of lizards, the Agamidae and the Chameleontidae. Such teeth must have a longer functional life than those of a typical polyphyodont reptile. The large agamid *Uromastix* displays various mechanisms that contribute to this (Throckmorton 1979): enamel and dentine layers are thickened; secondary dentine grows to fill the pulp chamber; a bony core in the pulp chamber facilitates its eventual obliteration; the jaw-bone is able to perform a shearing function once the teeth are completely worn away; the cancellous bone supporting posteriormost teeth changes to completely compact bone supporting anterior teeth; the teeth may move through the jaw-bones to remain in good occlusion.

Stenaulorhynchus and *Hyperodapedon* display a thick dentine layer and the slow obliteration of the pulp chamber by the growth of secondary dentine. However, the enamel layer is not well developed—it is little more than a cap on the crown and it is rapidly worn away. A bony core in the pulp chamber was not seen in *H. gordonii*, although Chatterjee (1974, p. 230) reported this feature in *H. huxleyi*. The loose bone noted above in the pulp chambers of some *Stenaulorhynchus* teeth may be an homologous structure. The bone of dentary and maxilla clearly performs the same function as the teeth and, in fact, most occlusion is between tooth and bone. Because of this, precise tooth-tooth occlusion and extensive remodelling of the bone was probably not necessary. The bone at the roots of the teeth of *Stenaulorhynchus* and *Hyperodapedon* is cancellous around the posterior 'active' teeth, and compact around the anterior teeth that have moved out of occlusion.

It has been suggested that rhynchosaur ate plant material (Huene 1939; Romer 1963; Sill 1971*a, b*) or molluscs (Burckhardt 1900; Chatterjee 1969, 1974, 1980). In support of the latter view, Chatterjee (1974, 1980) has noted wear facets on teeth of *H. huxleyi* not caused by the opposing teeth, and the presence of molluscs in association with the Indian rhynchosaur.

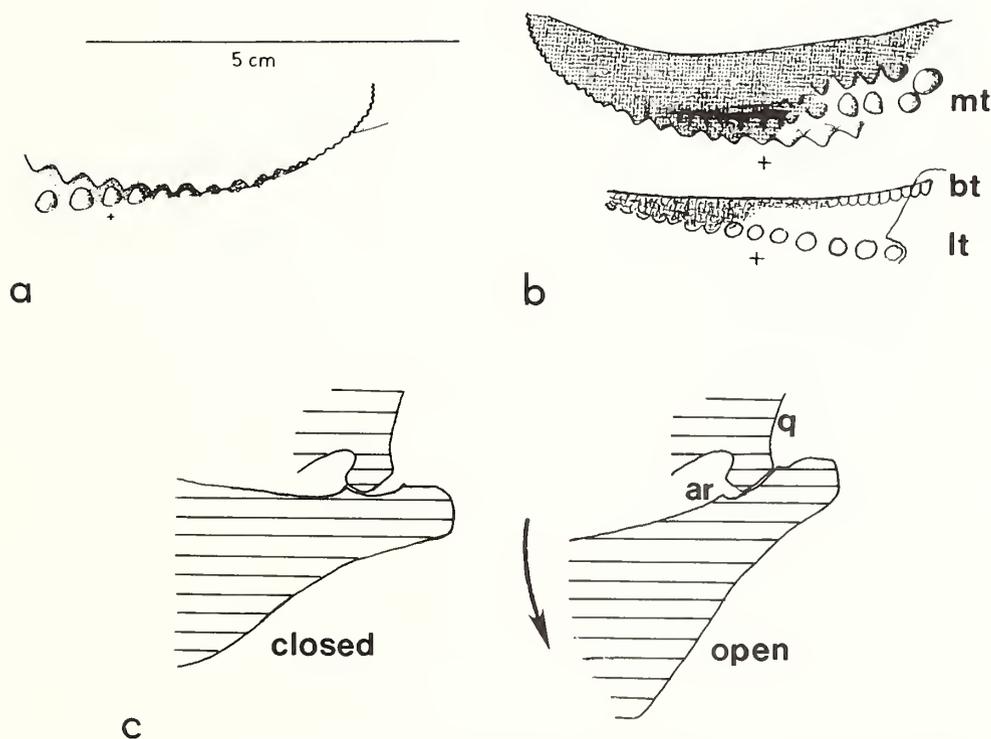
A detailed study of the teeth and jaws of *Hyperodapedon* and *Stenaulorhynchus* gives no evidence for mollusc-eating. The teeth are not polished and hard like those of chimaeras, stingrays, dipnoans, the extinct placodonts, and other animals that crush shells (Hildebrand 1974, p. 683). In fact, enamel is present only as a thin layer (Sill 1971*b*; Chatterjee 1974; Benton 1983*b*), and is usually worn from the exposed portions of occluding teeth. The tooth shape and arrangement are also different from those of living mulluscivores. Rhynchosaur teeth were sharp and conical rather than broad and flattened. The deep groove in the maxilla and the blade-like dentary are also quite different from the usual flattened pavement-like pounding-board dentition of a shell-crusher.

Wear patterns on the teeth and the jaw articulation of *Hyperodapedon* indicate a precision-shear biting action—that is, an accurate scissor-like cutting stroke with no back-and-forwards movement. Wear is clearly indicated in smooth arc-shaped areas and flattened tooth crowns in the middle and anterior parts of the maxilla and dentary (text-fig. 16*a*). There are several clear pits on the medial side of the maxillary tooth-plate groove for the lingual teeth of the dentary (text-fig. 16*b*), and these show that no longitudinal sliding of the jaws could have occurred. Posterior teeth do not come into contact and they often have very sharp points. The jaw articulation is between a heavy quadrate condyle and a cup-like glenoid facet on the articular of the lower jaw. Each facet is divided into two portions set at

a slight angle to each other. When models of the elements are placed together, it can be shown that the contact rocks back and forwards on the facets without sliding (text-fig. 16c). An anterior and posterior lip on the articular further prevent any back-and-forwards motion of the lower jaw, contrary to the findings of Sill (1971b) in *Scaphonyx*. The jaw mechanics of *Hyperodapedon* have been described in more detail elsewhere (Benton 1983b).

All of these features of the jaws and teeth of rhynchosaurs again suggest an appropriate modern functional analogue in the agamid lizard *Uromastix* (Robinson 1976; Throckmorton 1976, 1979). *Uromastix* is herbivorous and it efficiently crops leaves, flowers, shoots, and fruit of a wide variety of plants, but does not masticate the food. Unlike insectivorous and carnivorous agamids, the teeth of *Uromastix* are expanded back and forwards to form a nearly continuous cutting edge, the jaw action is scissor-like and both tooth and jaw-bone can perform the cutting function.

Further evidence in favour of an herbivorous diet for *Hyperodapedon* and other 'typical' rhynchosaurs is the barrel-shaped body (to accommodate a large gut for the slow digestion of vegetable material), the large numbers of these animals present in their respective faunas, and the



TEXT-FIG. 16. Tooth wear and jaw action in *Hyperodapedon gordonii*. *a*, close-up view of the jaws closed in medial view, with maxillary teeth (above) overhanging the lower jaw buccal teeth and most of the lingual teeth (cf. text-fig. 1). *b*, lateral view of the medial half of the maxillary tooth plate (above) and medial view of part of the dentary (reversed) so that corresponding teeth and wear cavities may be matched: the lingual tooth marked '+' fits into the pit marked '+' on the maxilla; areas of wear are patterned; posterior teeth of all series are unworn. *c*, jaw opening movement at the articulation in diagrammatic longitudinal section; there are two articulating fields on both articular and quadrate, and the contact changes to the posterior fields when the jaw opens. Abbreviations: ar, articular; bt, buccal teeth; lt, lingual teeth; mt, maxillary teeth; q, quadrate.

general rarity of associated fossil mollusc shells. Several rhynchosaurs have been found associated with fragmentary plants, and the diet probably consisted of leaves, stems, fruit, and seeds of seed-ferns, conifers, ginkgos, equisetaleans, and ferns. Rhynchosaurs could not grind up plant food, but they may have been able to 'ruminant'. Food could be gathered by the use of the beak-like premaxillae, manipulated with the large tongue, and efficiently cropped and sliced by the powerful jaws. The hindlimb was strong and apparently adapted for scratch-digging (Benton 1983*b*), so that *Hyperodapedon* could dig up edible tubers and roots.

EVOLUTION OF THE RHYNCHOSAUR DENTITION

The origin of the rhynchosaurs (early-late Triassic) is uncertain. They clearly belong within the Subclass Diapsida and within an archosauromorph assemblage, which also includes prolacertiforms (early-late Triassic) and archosaurs (latest Permian-present day) (Benton 1983*b*, 1984). They are not closely related to *Sphenodon*, as has been assumed hitherto by most authors. Romer (1956) suggested that rhynchosaurs were derived from a generalized 'eosuchian' ancestor such as *Youngina* from the late Permian of South Africa. However, *Youngina* is a lepidosauromorph diapsid on the basis of its specialized intervertebral articulations, single-headed dorsal ribs, and probable fused bony sternum, and it has no particular relationship to rhynchosaurs. Carroll (1976) redescribed *Noteosuchus* from the earliest Triassic *Lystrosaurus* Assemblage Zone of South Africa as the oldest-known rhynchosaur on the basis of numerous characters shared with the slightly later rhynchosaurs *Mesosuchus* and *Howesia*. However, these are shared also with prolacertiforms and early thecodontians, and *Noteosuchus* must be classified as 'Archosauromorpha *incertae sedis*' at present (Benton, 1983*b*). Diagnostic portions such as the forelimb and the skull have not been found.

The remaining rhynchosaurs have been classified as follows (text-fig. 17) on the basis of shared derived characters of the skull and skeleton (Benton 1984):

Order Rhynchosauria Osborn 1903 (Gervais 1859)

Suborder Mesosuchidia Haughton 1924

Family Mesosuchidae Haughton 1924

Mesosuchus (*Kannemeyeria* Assemblage Zone (*Cynognathus* Zone), South Africa; lower Triassic)

Suborder Rhynchosauroida Nopcsa 1928

Family Howesiidae Watson 1917

Howesia (*Kannemeyeria* Assemblage Zone (*Cynognathus* Zone), South Africa; lower Triassic)

Family Rhynchosauridae Huxley 1887

Subfamily Rhynchosaurinae Nopcsa 1923

Rhynchosaurus (Helsby Sandstone Formation, Tarporley Siltstone Formation, Bromsgrove Sandstone Formation, Otter Sandstone Formation, England; middle Triassic)

Mesodapedon (Yerrapalli Formation, India; middle Triassic)

Stenaulorhynchus (Manda Formation, Tanzania; middle Triassic)

Subfamily Hyperodapedontinae Chatterjee 1969

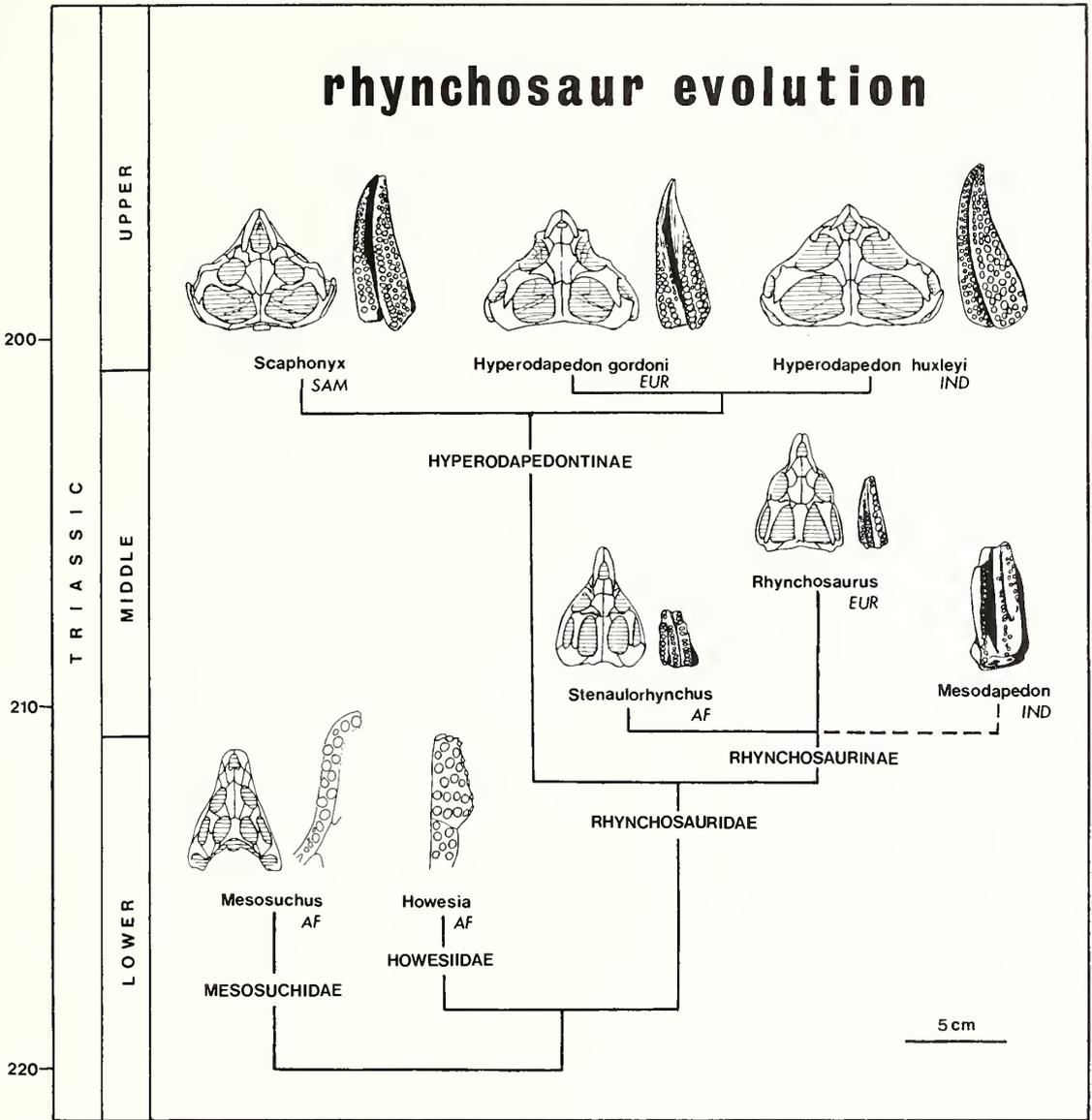
Hyperodapedon (Lossiemouth Sandstone Formation, Scotland and Maleri Formation, India; upper Triassic)

Scaphonyx (Santa Maria Formation, Brazil and Ischigualasto Formation, Argentina; upper Triassic)

'*Supradapedon*' (Tanzania; ?upper Triassic)

Undescribed genera (Wolfville Sandstone, Nova Scotia and Dockum Group, Texas; upper Triassic)

Mesosuchus has rhynchosaur-like features of the skull and skeleton, but the dentition is rather different. The teeth on maxilla and dentary appear to have a zigzag arrangement (Malan 1963). *Howesia* has multiple rows of ankylotheodont teeth with lingual and posterior addition, but



TEXT-FIG. 17. Evolution of the rhynchosaur. A dorsal view of each skull is given, when known (all drawn to a standard length), and a left maxillary tooth-plate (see 5 cm scale) is shown for each genus. The relationships are based on a detailed phenetic and cladistic study of all genera (Benton 1983b). The occurrence in time and space (AF, Africa; EUR, Europe; IND, India; SAM, South America) is indicated for each genus. The early Triassic *Noteosuchus* is omitted since its skull is not known and its relationships are uncertain. '*Supradapedon*' (a large maxillary tooth-plate from the ?late Triassic of Tanzania; Chatterjee 1980) and the undescribed North American rhynchosaur are also omitted. Sketches after Woodward (1907), Huene (1938), Malan (1963), Romer (1966), Chatterjee (1974, 1980), and Benton (1983b).

apparently no 'groove and blade' mechanism of the jaws. In many respects, its dentition resembles that of advanced captorhinomorphs (c.f. text-fig. 13).

The middle Triassic rhynchosaur form a distinct group. Their maxillae show two grooves and one or more tooth rows between the grooves. There are teeth on the lingual face of the maxillae in all three forms, but these run over the jaw edge on to the occlusal surface. The dentary has tooth rows elevated on two ridges that fit into the maxillary grooves. In both dentigerous elements, the teeth are organized into longitudinal Zahnreihen, clearly analogous with those of *Howesia* and captorhinomorphs.

The late Triassic rhynchosaur forms are all very similar in characters of the skull and skeleton, and they form another natural group. The maxilla has one groove and the dentary has a single sharp ridge that fits neatly into the groove. Maxillary teeth are organized into longitudinal rows on the occlusal surface with none on the lingual side. The teeth on the dentary form two clearly separate rows—one on the apex (the buccal teeth) and one lower down on the medial face (the lingual teeth). The latter row engages with teeth on the medial portion of the occlusal surface of the maxilla. The South American form *Scaphonyx* generally lacks lingual teeth on the dentary, although Contreras (1982) has recently described a rhynchosaur from the lower Ischigualasto Formation of Argentina which has well-developed lingual teeth.

The dentition of the late Triassic group of rhynchosaur can be regarded as a modification and simplification of that of the middle Triassic group (text-fig. 17): there is a single groove in the maxilla, and the tooth rows of the maxilla are all on the occlusal surface (and the dental lamina is probably entirely posterior in position), and the number of tooth rows on the dentary reduces.

Chatterjee (1980) has recently proposed a classification of rhynchosaur which differs from that given above in which he associates the European and African forms (*Stenaulorhynchus*, *Rhynchosaurus*, *Hyperodapedon gordonii*, '*Supradapedon*') in one subfamily, and the American and Indian forms (*Mesodapedon*, *Scaphonyx*, *H. huxleyi*, North American forms) in another. This classification was based on a single character of the arrangement of the teeth on the maxillary tooth-plate. I believe that this character is not consistently present and the classification is therefore unworkable. The weight of evidence is very much against Chatterjee's (1980) classification (see Benton (1983*b*) for fuller details).

CONCLUSIONS

1. The dentition of rhynchosaur is of great taxonomic importance since it has been used as evidence that rhynchosaur are closely related to *Sphenodon*. However, the dentitions are quite different: rhynchosaur do *not* have acrodont teeth, the groove is on the maxilla only (not between maxilla and palatine, as in *Sphenodon*), and the jaw action is quite different (no propalinal movement, as is seen in *Sphenodon*).

2. The dentition of rhynchosaur is highly unusual in terms of anatomy and development. Many parallels have been discovered with the acrodont teeth of some living lizards and with the dentition of fossil captorhinomorphs. In all of these groups, teeth are not replaced from below, as is the case in typical polyphyodont reptiles. There is clear evidence here for the reality of Zahnreihen as a feature of the pattern of the dentition, and in all cases the history of a Zahnreihe may be followed from newly ankylosed, unworn teeth at the back, through actively remodelling areas which are in occlusion, to old heavily worn and largely resorbed teeth at the front. The bone of the jaws grew mainly at the back of the tooth rows, and teeth appeared posteriorly as the area of dentigerous bone increased. There is no evidence for subsequent 'drift' of the teeth through the bone, other than minor movements produced by normal remodelling of the jaws while in occlusion.

3. Problems for further study include a detailed examination of the teeth of the early rhynchosaur *Mesosuchus* and *Howesia* in the hope that this might shed some light on the origin of the typical multiple-rowed dentitions of later forms. It must be assumed that the ancestors had a single-row dentition, but nothing is known of that. The specific adaptations of the rhynchosaur feeding mechanism are also a matter for further work. Rhynchosaur were very important animals in the Triassic, and yet their ecological role is still a matter of debate (Benton 1983*a, b*). Further study

should also be devoted to the problems of tooth maintenance and replacement in non-polyphyodont reptiles and the question of the evolutionary advantages or disadvantages of such a system. Finally, multiple-row reptile dentitions, which effectively 'freeze' a considerable time span of tooth pattern development, should shed further light on the problem of the reality, or non-reality, of Zahnreihen as descriptive units, if not as developmental indicators.

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Note added in press. The two skulls of *Hyperodapedon* referred to as NUGDA and B have now been catalogued as RSM. GY. 1984. 20. 1, 2 respectively in the Royal Scottish Museum, Edinburgh.

A NEW POLYSEPTATE THECIDACEAN BRACHIOPOD FROM THE MIDDLE JURASSIC OF THE COTSWOLDS, ENGLAND

by P. G. BAKER *and* D. G. ELSTON

ABSTRACT. Study of material from a new locality reveals the presence of an Aalenian thecideacean which, in its morphology and shell microstructure, is similar to certain upper Jurassic and lower Cretaceous species. The new Aalenian specimens are assigned to *Mimikonstantia sculpta* gen. et sp. nov. because of the doubtful validity of the upper Jurassic genus *Konstantia* Pajaud 1970. Although impunctate, the shell microstructure, with its suppressed secondary fibrous mosaic, closely resembles that of the lower Cretaceous *Thecidiopsis tetragona* (Roemer) and *T. lata* Smirnova. It is therefore considered that *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* are phylogenetically linked. The evidence obtained from the study of *M. sculpta* enables the onset of the neotenus suppression of the secondary fibrous shell layer to be placed much earlier in the history of the Thecideidina than has previously been suspected.

DURING investigation of the shell microstructure of thecideidine brachiopods of Aalenian age from a number of localities in the Cotswolds, collections were obtained from Salterley Grange Quarry (grid ref. SO 946 177) and Crickley Hill (grid ref. SO 928 163) near Cheltenham, in which the majority of the specimens could be assigned to previously described species of *Moorellina* Elliott 1953. However, a small number of brachial valves were noticed which showed a septal arrangement previously unrecognized in lower Inferior Oolite species. Lack of material, however, prevented their systematic study until collections were subsequently obtained from a locality in a small overgrown quarry (grid ref. SO 832 036) on Selsley Common near Stroud.

At the localities mentioned, specimens were collected from the upper part of the Pea Grit (upper Aalenian), lithologically a medium to coarse grained shelly pisolite (pisomicrite of Morris 1980) with occasional coralliferous horizons and hardgrounds overlain by more loosely consolidated marly horizons. It was from these marly horizons that the collections were obtained. Thecideidines were found to be a particularly common element of the Selsley fauna and a collection of 1,332 brachial valves was obtained of which 15% (200) belonged to a form resembling the upper Jurassic genus, *Konstantia* Pajaud 1970. A detailed study of the specimens revealed the presence of a new genus, necessarily described by reference mainly to the characters of separated brachial valves, due to the usual problems involved in the accurate identification of complete thecideidine shells and pedicle valves (Baker and Laurie 1978, p. 557).

Registration of material. The holotype, paratypes, and topotypes, together with sectioned material are housed in the British Museum (Natural History) under numbers BB 84690–BB 84701

Preparation of material. Bulk samples of pisolitic marl were initially washed to remove clay-grade sediment. The residue was dried and passed through a nest of 2.4 mm, 1.68 mm, 850 μm , 500 μm , and 350 μm sieves. The thecideidines were then hand-picked from the sieved residues under a binocular microscope. The majority of specimens were obtained from the 850 μm and 500 μm sizes. The *Konstantia*-like specimens were then carefully cleaned under water, using tweezers, a surgical needle, and a very fine brush. Owing to the risk of damaging the thin and often already cracked shells sonication was not attempted. Specimens selected for sectioning were gold-coated, photographed using a scanning electron microscope for the purpose of obtaining a photographic record, and mounted in cold setting resin. Figured material was also gold-coated prior to photomicrography. The characters depicted in text-figs. 1–3 were traced from actual specimens with the aid of a 'Wild' stereomicroscope fitted with a drawing tube.

SYSTEMATIC PALAEOLOGY

Order UNCERTAIN

Suborder THECIDEIDINA Elliott, 1958

Superfamily THECIDEACEA (Gray, 1840) H. and G. Termier, 1949

Family THECIDEIDAE Gray, 1840

Subfamily THECIDEINAE (Gray, 1840) Dall, 1870

Genus MIMIKONSTANTIA gen. nov.

Diagnosis. Impunctate, polyseptate thecideinin having brachial cavities devoid of brachial lobes and the pedicle valve with a characteristic marginal rim with tuberculate inner and smooth outer zones.

Description. Small, wider than long, ventribiconvex, the pedicle valve with a relatively large attachment scar and well-developed free ventral wall; ventral interarea relatively small, pseudodeltidium ill-defined; anterior commissure straight; growth lines obscure; impunctate. Pedicle valve interior with strong teeth and dental ridges united with raised hemispondylium; marginal rim with tuberculate inner and smooth outer zones. Brachial valve interior with small, weakly bilobate cardinal process; bridge abutments sharply angled but with no positive evidence of a brachial bridge; brachial cavities without brachial lobes, the brachial apparatus consisting of four or five approximately radially disposed septa in contact with the anterior and antero-lateral border of the valve.

Age. Middle Jurassic, Aalenian

Etymology. From the Greek *mimikos* (mimic) after the development of the polyseptate anterior without any trace of brachial lobes in the brachial cavities.

Type species. *Mimikonstantia sculpta* sp. nov.

Mimikonstantia sculpta sp. nov.

Plates 69, 70, and 71; text-figs. 1–4, 5A

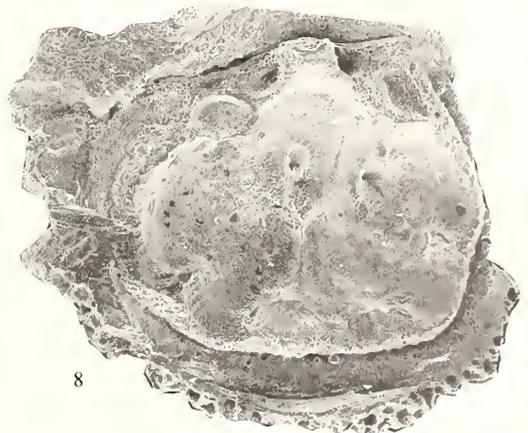
Diagnosis. *Mimikonstantia* up to about 2.5 mm in length, 3.5 mm in width, and 1.5 mm in thickness. Outline transversely elliptical, typically with the width approaching one and a half times the length. Anterior commissure straight, or with a very slight invagination.

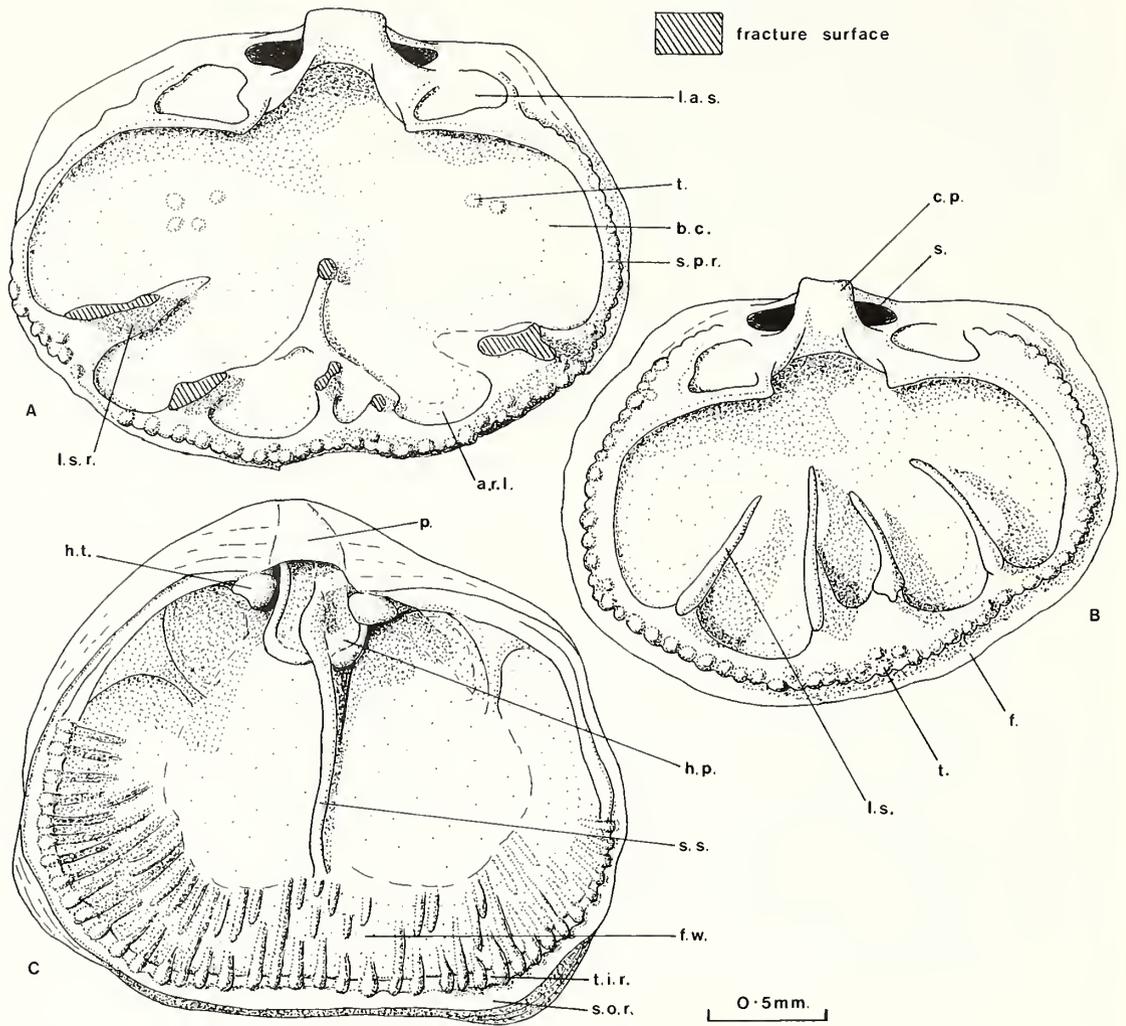
Dimensions of holotype. Length 1.8 mm, width 2.6 mm, thickness 0.5 mm.

Distribution. Geographic distribution unknown but probably local in its occurrence. Stratigraphically the species occurs near the top of the Pea Grit (Aalenian, *murchisonae* Zone, *murchisonae* Subzone) at Salterley Grange Quarry (grid ref. SO 946 177), and Crickley Hill (grid ref. SO 928 163) near Cheltenham, also at Selsley Common (grid ref. SO 832 036) near Stroud.

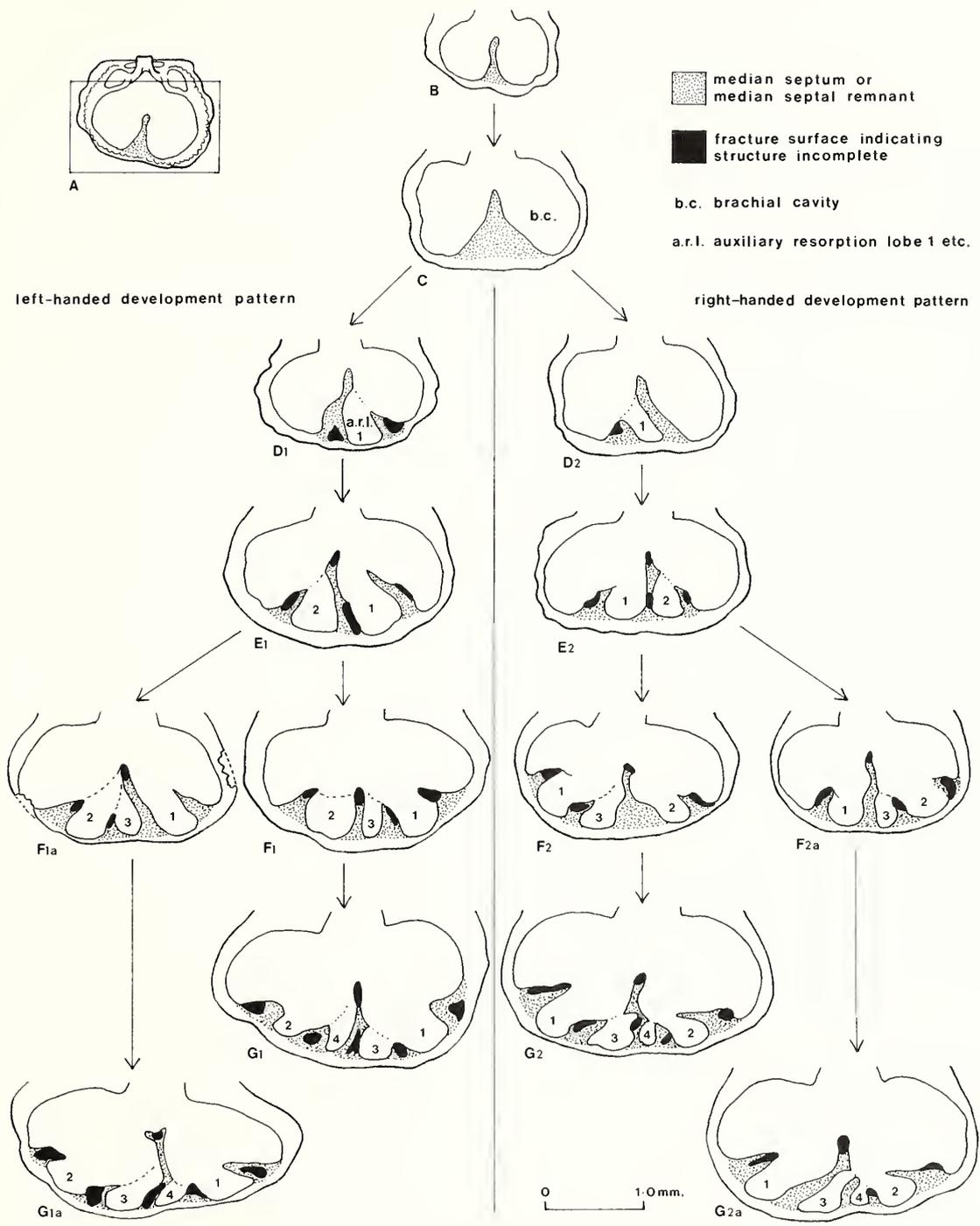
EXPLANATION OF PLATE 69

Figs. 1–8. Stereoscan photomicrographs of specimens of *Mimikonstantia sculpta* gen. et sp. nov. from the Pea Grit, Selsley Hill, near Stroud. All figures are of specimens coated with evaporated gold before photography. 1–3, brachial, lateral, and anterior views of the holotype BB 84690, $\times 25$. 4, enlarged portion of the margin of pedicle valve BB 84693, showing the ornamented internal surface of the free ventral wall and the tuberculate inner and smooth outer zones of the marginal rim; ornament and tubercles slightly abraded in this specimen, $\times 160$. 5, interior view showing the morphology of the pedicle valve of paratype BB 84693, $\times 25$. 6, brachial view of a matrix-filled brachial valve, paratype BB 84691, showing the blade-like extensions of the septa. The left (as viewed) lateral septum (arrowed) has been fractured and compressed sideways during diagenesis of the sediment, $\times 30$. 7, brachial view of a complete specimen, paratype BB 84694, showing the relationship between the fragile flange round the brachial border, left antero-lateral sector, and the way in which breakage results in the exposure of the characteristic marginal rim, right antero-lateral sector, of the pedicle valve, $\times 25$. 8, brachial view of a bryozoan-encrusted brachial valve, paratype BB 84692, showing a mould of the complete brachial flange. The apparent pores are really rhomb-shaped diagenetic structures (see Pl. 71, fig. 1), $\times 20$.





TEXT-FIG. 1A. 'Wild' stereomicroscope trace of the holotype of *Mimikonstantia sculpta* gen. et sp. nov. (BB 84690) to show the lateral septal remnants, typical of the adult brachial valve in its separated state. B, reconstruction of the adult brachial valve based on specimens BB 84690–BB 84692 and sectioned specimen BB 84698 to show the form of the lateral septa and the delicate peripheral flange. C, reconstruction to show the typical internal morphology of the pedicle valve, based on a stereomicroscope trace of paratype BB 84693. Tuberculate rim enhancement incorporated from specimen BB 84694. a.r.l. = auxiliary resorption lobe, b.c. = brachial cavity, c.p. = cardinal process, f. = flange, f.w. = free ventral wall, h.p. = hemispondylium plate, h.t. = hinge tooth, l.a.s. = lateral adductor muscle scar, l.s. = lateral septum, l.s.r. = lateral septal remnant, p. = pseudodeltidium, s. = dental socket, s.o.r. = smooth outer rim, s.p.r. = sub-peripheral rim, s.s. = hemispondylium supporting septum, t. = tubercle, t.i.r. = tuberculate inner rim.



TEXT-FIG. 2. Series of drawings to show the development of the brachial supports in *Mimikonstantia sculpta*. A, locational diagram. B, C, early juveniles showing the development of the initial median septum. D, juveniles showing the thickened median septum invaded by an auxiliary resorption lobe (a.r.l. 1) extending from the left, D₁ and right, D₂, brachial cavities. E-G, left- and right-handed sequences showing the repeated division of the median septal remnant by progressive invasion by a succession (a.r.l. 2-4) of auxiliary resorption lobes as growth proceeds. Left-handed and right-handed defined anatomically, not as viewed.

Derivation of name. From the sculpturing of the polyseptate anterior of the brachial valve through the repeated invasion of an initially thickened median septum by a succession of resorption fronts.

Type specimens. Holotype BB 84690 and paratypes BB 84691–BB 84694

Description. A small ventribiconvex thecideinin with a moderately large attachment scar and well-developed free ventral wall giving rise to a depressed triangular lateral profile. The ventral interarea is reduced and indistinct with an ill-defined flat to slightly convex pseudodeltidium. There is no trace of an interarea in the brachial valve and the growth lines are usually indistinct.

MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE

Characters of pedicle valve

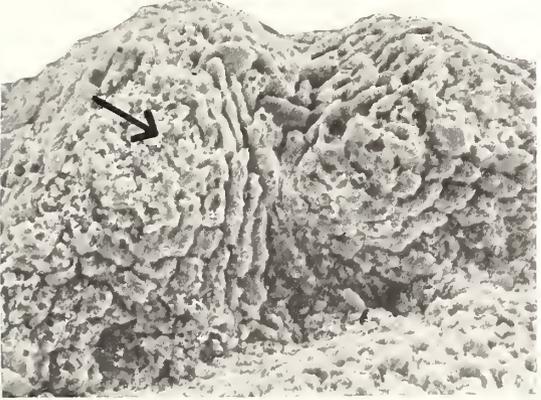
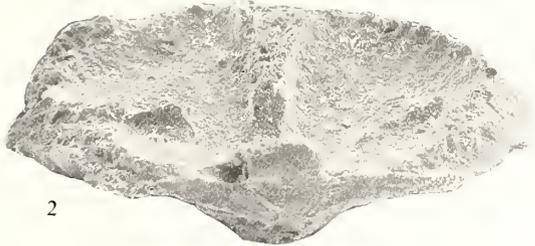
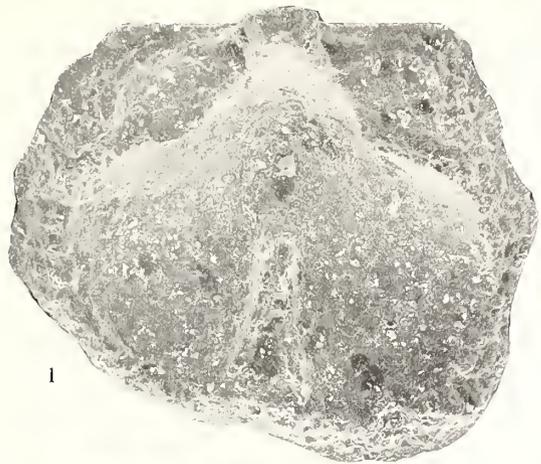
A raised hemispondylium is normally present with clearly defined dental ridges, hemispondylial plate, and a supporting septum (Pl. 69, fig. 5; text-fig. 1C) which extends anteriorly almost to the base of the free ventral wall. The teeth are typically thecideidine (Jaanusson 1971) and not widely separated. The internal surface of the free ventral wall is ornamented with ridges and grooves. The ridges, which are often slightly beaded, terminate near the commissure in a zone of tubercles which forms the inner part of a double marginal rim (Pl. 69, fig. 4). The outer part of the rim consists of a smooth flange which corresponds with a similar flange developed round the border of the brachial valve (text-fig. 1B). The floor of the valve, corresponding approximately with the area of attachment externally, is smooth with well-defined lateral adductor muscle scars on each side of the hemispondylium. The shell substance is impunctate.

Characters of brachial valve (Pl. 69, figs. 1–3; text-fig. 1A, B).

The brachial valve is transversely elliptical with a maximum width in the order of 3.5 mm. The posterior cardinal border is approximately two-thirds of the valve width. The cardinal process is small, weakly bilobate, and bounded by typically thecideidine dental sockets with its dorsal surface aligned almost perpendicular to the plane of the commissure (Pl. 70, figs. 2, 4). The lateral adductor muscle scars are oval and quite deeply impressed. The bridge abutments are quite sharply angled on well-preserved valves but no positive evidence of a bridge has been found, even in sectioned complete shells. The brachial cavities are shallow and, in the sense that the brachial supports do not arise from their floor, are without brachial lobes. The brachial apparatus consists of a maximum of five approximately radially disposed septa which are almost invariably broken in separated valves. Sectioned complete shells and occasional matrix-filled brachial valves (Pl. 69, fig. 6; text-fig. 1B), however, show that the majority of the septa, continuous with the sub-peripheral rim anteriorly,

EXPLANATION OF PLATE 70

Figs. 1–9. Stereoscan photomicrographs of specimens of *Mimikonstantia sculpta*. gen. et sp. nov. All figures are of specimens coated with evaporated gold before photography. Figs. 1, 3, and 5 illuminated from lower right. 1, 2, brachial and posterior views of an early juvenile brachial valve BB 84695 showing the essentially moorellinid character of the initial median septum, $\times 60$. 3, 4, brachial and posterior views of a juvenile brachial valve BB 84696 showing the greatly thickened anterior of the median septum, $\times 40$. 5, brachial view of an adolescent brachial valve BB 84697 at the two auxiliary resorption lobe phase of development, $\times 35$. 6, posterior view of the same specimen to show the nature of the newly formed embayments, $\times 35$. 7, posterior view of the holotype showing how enlargement of the auxiliary resorption lobes results in the gradual elimination of the earlier characters. Last-formed embayments are ‘stepped’ relative to earlier lobes, $\times 25$. 8, angled brachial view (backward rotation 30°) of a complete shell BB 84698 from which the brachial border flange has been removed to reveal the tubercles projecting round the inner surface of the free ventral wall, $\times 25$. 9, enlargement of a pedicle valve tubercle showing the granular tubercle core (arrowed) ensheathed in secondary fibres, $\times 500$.



possess on their ventral edge a posteriorly directed blade-like extension which curves backwards and downwards almost to reach the margin of the body cavity. The brachial cavities are usually smooth but in a few individuals contain a few small, low tubercles situated in a postero-lateral position (Pl. 69, fig. 1). Most adult brachial valves retain a residual boss of unresorbed shell almost in the centre of the valve floor and this sometimes retains a connection with the most centrally placed septum. Shell resorption gives the broken septa a somewhat stubby appearance (Pl. 70, fig. 5). The sub-peripheral rim is not strongly developed and in anterior and antero-lateral regions is often almost breached as a result of resorptive activity (Pl. 69, fig. 3; text-fig. 1A). The outer margin of the sub-peripheral rim is variably ornamented with tubercles, usually most strongly developed in the postero-lateral regions. A fairly wide but very thin and fragile border is present. This is invariably incomplete in separated valves and is usually damaged in complete shells also. In the latter case this results in the exposure of the characteristic marginal rim of the pedicle valve (Pl. 69, fig. 7) which greatly facilitates identification.

Ontogeny. Juveniles have a sub-circular outline but as a result of the characteristic growth pattern of the brachial valve (described later), the length:width ratio decreases with increasing size. However, the main feature of the ontogeny of *Minikonstantia sculpta* is the mode of development of the brachial apparatus, a feature which immediately separates the species from *Moorellina granulosa* (Moore) and *M. dundriensis* (Rollier) with which it is associated. As previously noted there are no brachial lobes in the sense that the brachial supports did not originate from the floor of the brachial cavities. The brachial supports were essentially the product of a complex shell accretion/resorption regime acting on a modified median septum. In the earliest growth stages (Pl. 70, figs. 1, 2) the median septum, although well developed, was essentially moorellinid in that it formed a blade-like partition between the left and right brachial cavities. The resorption regime of the developing cavities proceeded normally (Baker 1970) up to a brachial valve width of about 1.5 mm. At that stage the anterior portion of the median septum began to widen rapidly so that a triangular area of greatly thickened shell was produced (Pl. 70, figs. 3, 4; text-fig. 2C). Soon after its formation, this triangular area was invaded by a succession of auxiliary resorption lobes which developed sequentially from the main resorption fronts responsible for the enlargement of the brachial cavities. The first resorption front to invade the median septum extended from either the left or

EXPLANATION OF PLATE 71

Figs. 1–8. Stereoscan photomicrographs of gold-coated cellulose acetate peels (except figs. 1 and 5) of sectioned specimens of *Minikonstantia sculpta* gen. et sp. nov. 1, enlargement of an apparent pore on the internal surface of specimen BB 84692 enabling it to be identified as a rhomb-shaped pit. The origin of these pits remains unknown but it is assumed that they are diagenetic, probably pressure-solution, phenomena, $\times 3,500$. 2, section through the sub-peripheral rim of specimen BB 84699, showing a granular tubercle core in cross-section, deflecting secondary fibres. Section orientation: parallel with the plane of the commissure. Section location: brachial valve, anterior sector; $\times 800$. 3, section passing obliquely through the shell adjacent to the sub-peripheral rim of the same specimen, showing the relatively very thin secondary fibrous layer with granular calcite above and below it. Section orientation: as fig. 2. Section location: lateral sector; $\times 600$. 4, section passing obliquely through the sub-peripheral rim and a lateral septum of specimen BB 84698 showing the primary layer (lower), the tubercle cores associated with the secondary fibrous layer, and the inner granular calcite layer continuous with the granular calcite of the lateral septum (upper centre). Section orientation: parallel with the plane of the antero-lateral surface of the pedicle valve, intercepting the commissural plane at approximately 60° . Section location: brachial valve, right antero-lateral sector; $\times 250$. 5, floor of an auxiliary resorption lobe of the holotype showing detail of the granular calcite of which the thickened median septum is composed, $\times 3,500$. 6, section showing a granular tubercle core of pedicle valve BB 84700 in cross-section. Section orientation: horizontal, perpendicular to the shell surface. Section location: free ventral wall, anterior sector; $\times 700$. 7, section showing the granular tubercle cores and ensheathing secondary fibres in longitudinal section. Section orientation: transverse, parallel with the axis of the tubercle cores at an angle of approximately 3° from the shell surface. Section location: free ventral wall, pedicle valve, anterior sector; $\times 500$. 8, section showing the relatively thick inner granular layer, left, in the lateral sector of the pedicle valve. Section orientation: horizontal, perpendicular to the surface of the free ventral wall; $\times 500$.



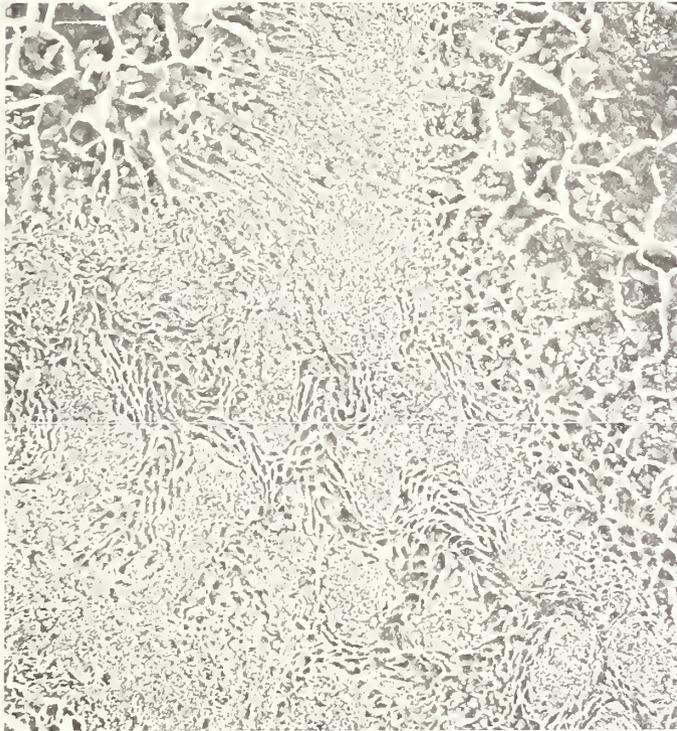
1



2



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4



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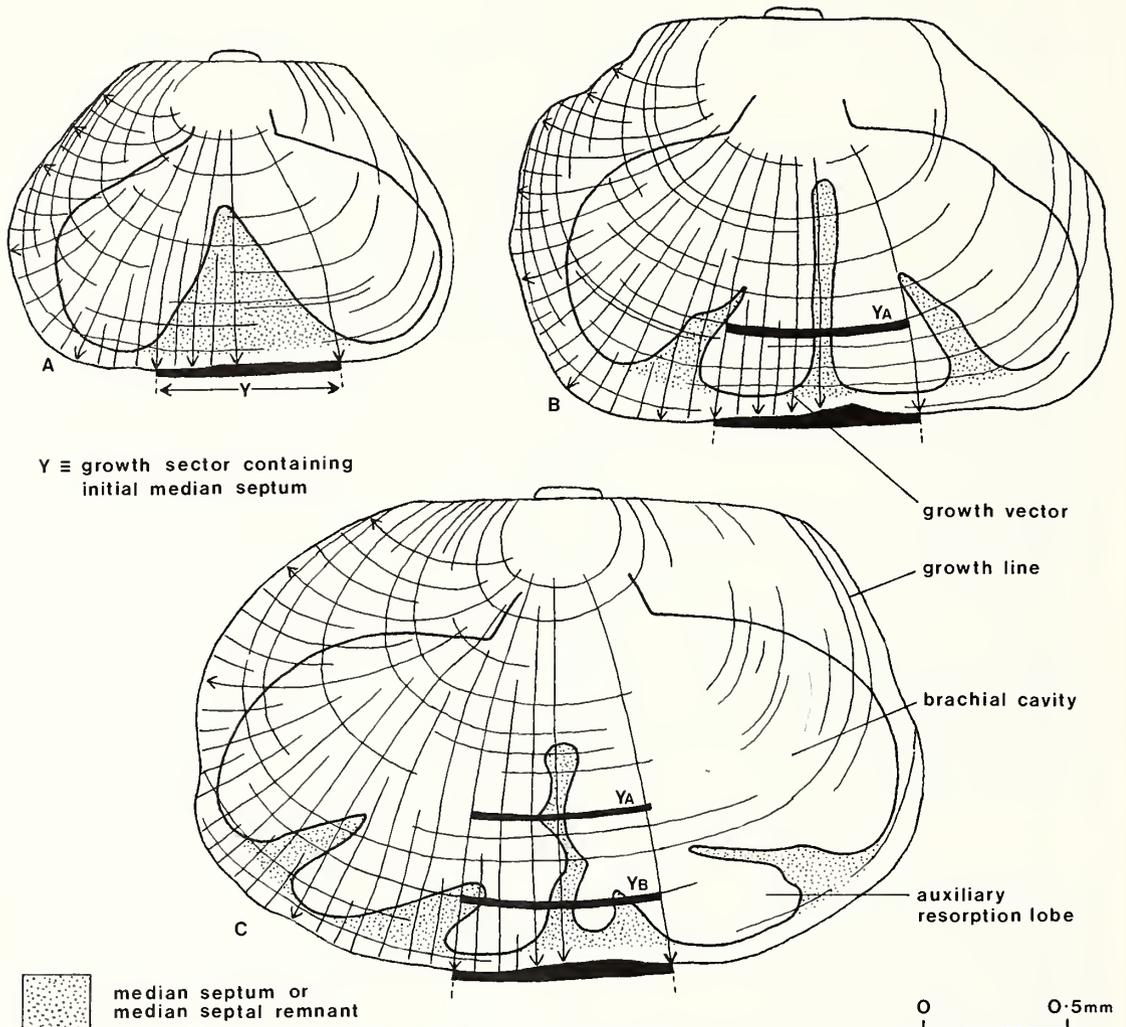


7



8

right brachial cavity and its effect was to isolate a strip of material (median septal remnant) from the original triangle (text-fig. 2D₁, D₂). As the shell continued to increase in size the residual portion of the triangle increased in size again and was subsequently invaded by a second auxiliary resorption front (Pl. 70, figs. 5, 6). Text-fig. 2 shows that the initiation of the respective auxiliary resorption fronts followed a definite pattern which may be termed left-handed or right-handed according to which brachial cavity the first lobe was extended from. Usually the initiation of the lobes followed an alternating sequence (text-fig. 2D₁-G₁, 2D₂-G₂) but partially consecutive sequences (text-fig. 2E₁-G_{1a}, 2E₂-G_{2a}) are also encountered. The order of development can be determined



TEXT-FIG. 3. Series of diagrams in which the growth lines and primary growth vectors of the right half of a brachial valve have been superimposed on to a trace of the interior of the same valve to show that the subsequent divergence of the septal elements in *Mimikonstantia sculpta* is not a function of simple growth, which remains essentially linear in the sector containing the initial median septum. A, early juvenile prior to the development of the first auxiliary resorption lobe. B, juvenile with two auxiliary resorption lobes in which lateral remnants of the median septum are beginning to migrate away from the critical growth sector as defined by YA. C, adult valve showing the continued antero-lateral migration of the septal remnants and the initiation of new auxiliary resorption lobes anteriorly. Solid black, YA, YB, locates the earlier position of the critical growth sector on subsequent growth stages.

because initially, the floor of each new embayment was at a higher level than that of the lobe from which it developed, thus a characteristic 'step' was formed (Pl. 70, fig. 7). As enlargement of the new auxiliary resorption lobe proceeded this step was gradually eliminated by the resorption of shell material. Most median septal remnants of detached brachial valves show a fracture surface (text-fig. 2). Sectioned material shows that accretion continued on their postero-ventral surfaces so that a blade-like lamina was formed (Pl. 69, fig. 6; text-fig. 1B).

Microstructure. In the presence of a granular primary layer and a fibrous secondary layer, in which the fibres are deflected by taleola-like tubercle cores, the shell microstructure is essentially similar (Baker 1970; Williams 1973) to that of other lower and middle Jurassic species. In strong contrast, however, there is a clear indication of the suppression of the secondary fibrous layer, as it is thinly developed and underlain by a further layer of granular calcite. Also the shell of *Mimikonstantia sculpta* is impunctate. Differences in organization of the fabric of brachial and pedicle valves are sufficient to warrant description of the two valves separately.

Brachial valve

Investigation shows that the tubercles of the brachial valve have short cylindrical cores of granular calcite which are continuous with, and disposed almost perpendicular to, the primary layer (Pl. 71, fig. 2; text-fig. 4B). The association of a thin sheet of secondary fibres with these tubercle cores is a characteristic and persistent feature of the shell (Pl. 71, fig. 4). The individual secondary fibres are normally fashioned *sensu* Williams (1968) and the secondary fibrous layer is particularly well developed in the inner socket ridges. The occurrence of secondary shell is restricted in *M. sculpta* compared with other lower middle Jurassic thecideidines and, in areas of the valve away from the sub-peripheral rim and inner socket ridges, may be reduced to a sheet no more than four or five fibres thick. It is underlain by a further layer of granular calcite indistinguishable from that of the primary layer (Pl. 71, figs. 3, 4, 8). Study of the microstructure of juvenile brachial valves indicates that development of this inner granular layer is initiated at about the time that the accelerated thickening of the median septum occurs during ontogeny. It is this thick triangular-shaped area of granular calcite (Pl. 70, fig. 3) which is sculpted by the resorption lobes to leave isolated patches standing out as septal lamellae (text-fig. 2D-G). Material continues to be accreted to these lamellae so that the brachial elements are composed entirely of granular shell material (Pl. 71, figs. 4, 5). The inner granular layer is not confined to these areas, however, as horizontal sections through adult valves show that it is developed all over the floor of the brachial and body cavities, especially between the inner socket ridges. Owing to the influence of resorptive activity during growth the brachial valve remains relatively thin. The resorption regime coupled with the very thin secondary fibrous layer probably imparts an inherent weakness to the valve, as indicated by the high proportion of cracked and broken valves encountered.

Pedicle valve

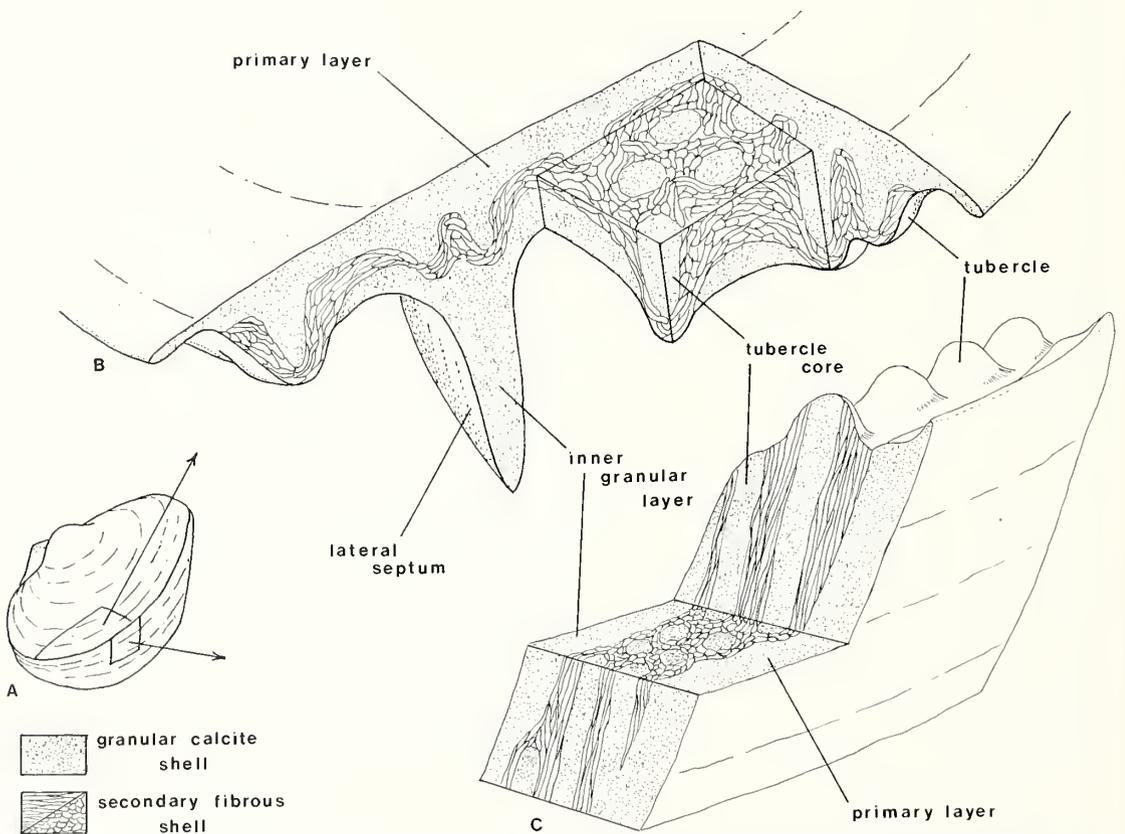
The tubercle cores of the pedicle valve are also composed of granular calcite. In contrast to those of the brachial valve, however, they form attenuated cylindrical structures (Pl. 71, figs. 6, 7; text-fig. 4C) continuous with and disposed at a low angle to (often almost parallel with) the primary layer. These granular cores, initiated in succession and ensheathed in secondary fibres, penetrate obliquely through the shell to form a row of tubercles round the inner rim of the edge of the valve (Pl. 70, figs. 8, 9). An inner granular layer is present but it does not appear to be as persistent as in the brachial valve. In anterior and antero-lateral sectors it is not sufficiently well developed to prevent the distal ends of previously formed tubercle cores from projecting through to form linear rows of ridges on the inner surface of the free ventral wall (Pl. 69, fig. 4). It is relatively much thicker in lateral sectors of the valve (Pl. 71, fig. 8) where it may attain a thickness of 65 μm .

DISCUSSION OF AFFINITY

Relationship with other genera

In general shape and characters, such as the small cardinal process and the polyseptate brachial valve, the new genus resembles an upper Jurassic form from the Volgian of the Podolian Plateau, USSR and

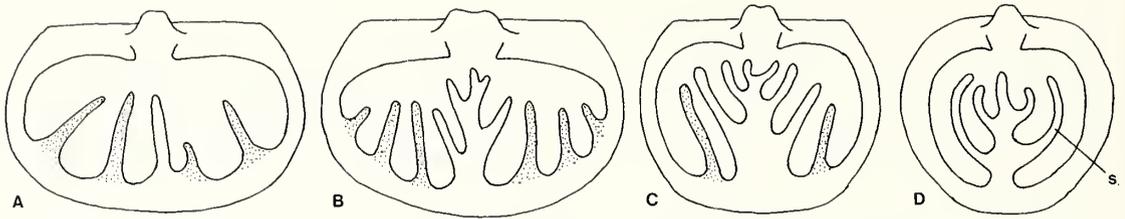
assigned to *Konstantia podolica* Pajaud 1970. Unfortunately, the validity of the original generic designation is questionable. Knowledge of the form is restricted to an account (around 1935) in an unpublished manuscript by K. Glazewski. Unhappily, the entire collection of 135 specimens referred to in the manuscript was subsequently destroyed or lost during the war. Description, text-figures, and photographs were later abstracted from the Glazewski manuscript and assigned to *Glazewskia* sp. (Glazewski and Pajaud 1964). Subsequently, Pajaud (1966) considered the species not to be a *Glazewskia* but was unable to do more than transfer it to genus X sp. A. Later, Pajaud (1970) assigned genus X to the new genus *Konstantia*, selecting *Glazewskia* sp. as the type species. At the same time he erected the species *K. podolica* (= genus X sp. A in Pajaud 1966) basing the holotype on a text-figure (graphotype) and a photograph (phototype) published in the 1964 paper. The genus and species were therefore erected on the basis of figures originating from an unpublished manuscript, a situation which led Pajaud himself to remark (1970, p. 189): 'Le binôme *Konstantia podolica* utilisé ici n'offre qu'un caractère utilitaire et ne peut être actuellement validé.' Nothing is known of the shell microstructure of *Konstantia* and the pores, presumably endopunctae, and brachial lobes identified in the Podolian specimens are not found in *Mimikonstantia*. In considering the systematic position of the new genus reference must be made to two other polyseptate genera, *Eudesella* Munier-Chalmas, 1880 and *Thecidiopsis* Munier-Chalmas, 1887.



TEXT-FIG. 4. Diagrammatic reconstruction of the shell microstructure of *Mimikonstantia sculpta*. A, locational diagram. B, block diagram showing the microstructure of the brachial valve. C, block diagram showing the microstructure of the pedicle valve.

Eudesella is first recorded from the Upper Lias, Toarcian, where it is represented by *E. mayensis* (Eudes-Deslongchamps). The species has well-developed brachial lobes and in consideration of the mode of development of the septa, Pajaud (1970, p. 184) observed that the last-formed septa were the most laterally placed, a condition which is the opposite of *Mimikonstantia*. Williams (1973) studied the shell microstructure of *E. mayensis* and concluded that the valves were lined with a continuous layer of secondary fibres. The evidence of these three characters alone is considered sufficient to separate *E. mayensis* from *M. sculpta*.

Thecidiopsis is first recorded from the Valanginian (lower Cretaceous), where it is represented by *T. cf. tetragona* Nekvasilová, 1966. The morphological resemblance between *Mimikonstantia* and *Thecidiopsis* is at first sight largely superficial because, in addition to the lateral septa, *Thecidiopsis* has a median septum divided into alternating septules. The embayments between the lateral septa are occupied by well-developed brachial lobes. Williams (1973, p. 469) studied the shell microstructure of an upper Cretaceous species *T. essenensis* (Roemer) and found the secondary fibrous layer almost completely (neotenuously) suppressed. He was only able to identify secondary fibres in the teeth and hemispondylium of the pedicle valve. A significant contribution by Smirnova (1979) provided information regarding the shell microstructure of two lower Cretaceous species, *T. tetragona* (Roemer) from the Hauterivian and *T. lata* Smirnova from the Barremian. In both species the secondary fibrous layer is almost completely suppressed in the brachial valve, being confined to the socket ridges. In the pedicle valve of *T. tetragona*, however, there is a clearly expressed secondary fibrous layer penetrated by rod-like bodies aligned almost parallel with the shell surface. In the vicinity of the muscle scars and hemispondylium the secondary layer is underlain by fine-grained acicular and granular calcite (third layer of Smirnova). In the pedicle valve of *T. lata* the secondary fibrous layer is very thin with the fine-grained inner layer better developed. The secretory regime of *Thecidiopsis* is therefore very similar to that of *Mimikonstantia* and, logically, may be regarded as further progress towards the ultimate suppression of the secondary fibrous shell layer. In addition, the polyseptate anterior of the two genera may not be as dissimilar as it appears. Study of the growth pattern of the brachial valve of *M. sculpta* (text-fig. 3) shows that as it increases in size the zones of maximum growth acceleration (Baker 1970, p. 78) associated with the initial brachial cavities (text-fig. 3A, B) become increasingly separated from the median septum. At about the four auxiliary resorption lobe phase (text-fig. 3C) the growth of the major portion of the anterior border has become essentially linear so that in order to make room for subsequent divisions, migration of the septal remnants must now be almost at right angles to the direction of growth of the shell. Thus it appears that although there seems to be no theoretical limit to the number of septal remnants which can be formed in *M. sculpta*, in practice the number is limited, through mechanical considerations, to a maximum of five. If a similar constraint operated in *Thecidiopsis*, the simplest mechanism for the formation of further septal elements would be the continuation of the resorption regime back along the sides of the median septum which would result in the development of a succession of embayments alternating on either side. As in *M. sculpta*, further accretion on the septal remnants would result in the characteristic *Thecidiopsis*-type septules (text-fig. 5B). Therefore, in terms of their mechanical requirements it is easy to reconcile the septal development pattern of *Mimikonstantia* with that of *Thecidiopsis* and also, by tachygenetic elimination of the lateral septa, with the development of the thecidiolophe of upper Cretaceous genera with sub-circular brachial valves such as *Backhausina* and *Thecidea* (text-fig. 5A-D). Thus, on the basis of morphology and ontogeny there appears to be a close relationship between *Mimikonstantia* and *Konstantia* and also, on the basis of morphology, ontogeny, and shell microstructure, between *Mimikonstantia* and *Thecidiopsis*. Pajaud (1970, p. 82, fig. 31) considered the possibility of the derivation of *Thecidiopsis* from *Konstantia*, but in the phylogeny proposed he actually derived *Thecidiopsis* from *Bosquetella*. This is thought to be an error since Pajaud states quite clearly (1970, p. 77) that *B. campichei* 'represents in no way a young stage of *T. tetragona*'. The error is all the more unfortunate since it is perpetuated in the phylogenetic chart of Williams (1973, p. 468, fig. 100). The link between *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* is substantiated by the present study. Pajaud tentatively derived *Konstantia* from *Rioulina* stock, a view no longer tenable owing to the fact that *Mimikonstantia* pre-dates *Rioulina*.



TEXT-FIG. 5. Diagrams to show the possible sequence (A-D) of events in the development of a thecidolophous form from a ptycholophous ancestor through the elimination of lateral septa (stippled) and the development of septules (s) on the median septum. A, *Mimikonstantia sculpta*, Aalenian. B, *Thecidiopsis tetragona* (Roemer), Valanginian. C, *Backhausina rugosa* (d'Orbigny), Cenomanian. D, *Thecidea papillata* (Schlotheim), Maastrichtian.

In addition, there is no trace of any structure even remotely resembling the characteristic rioultinid brachial lobes in the ontogeny of either *Mimikonstantia* or *Konstantia*. The absence of brachial lobes in *Mimikonstantia* would appear to eliminate *granulosa*-type moorellinids from an ancestral role. The clear development of the polyseptate condition from an early monoseptal phase does suggest origin from monoseptal stock and descent from a Liassic ancestor of *Moorellina bouchardi*-type remains a possibility.

In view of the uncertainty surrounding the validity of *Konstantia*, the complete lack of knowledge regarding its shell microstructure, its different stratigraphic and geographic distribution and, above all, the absence of any specimens for comparative study, it is considered inappropriate to assign the new species to that genus. However, in view of the morphological similarity in their brachial valves and particularly in the similarity of the septal development pattern, it is probable that there was a genetic link between the two forms. Indeed, it is possible that the early middle Jurassic representatives are very close to the ancestral stock from which the upper Jurassic forms were derived. In recognition of this, the genus *Mimikonstantia* is proposed to include the Aalenian species.

Relationship with other species

A supposed lower Cretaceous species, *K. inexpectata* Nekvasilová, 1976, is equally problematical because the figured specimens show the development of interbrachial lobes characteristic of a *Thecidiopsis*. Admittedly in *K. inexpectata* the septal arrangement lacks the median septum with septules of species such as *T. digitata* (Sowerby) but neither is that a feature characteristic of species such as *T. bohémica* Backhaus. In his account of the ontogeny of *K. podolica*, Pajaud (1970, p. 191) suggested that the original (median) septum divided to form two junior septa ('septes-fils') one of which migrated to a lateral position, the other assuming the role of a new median septum. The process was then repeated until, in all, four septa had been formed. Study of Pajaud's text-fig. 82 shows quite clearly that this could only have been accomplished by resorption and that the mode of development of the polyseptate condition must have been very similar to the mechanism postulated for *M. sculpta*. This can not be confirmed, however, owing to the unfortunate loss of the entire collection of *Konstantia* specimens.

Walter and Alméras (1981) have described a collection of Bajocian micromorphic brachiopods from Saint-Rome-de-Cernon, France. From their morphology, it seems highly probable that specimens figured (Walter and Alméras 1981, pl. 3, figs. 11, 17-20, 22, 24, 28) as *Moorellina granulosa* (Moore) would, if investigated more closely, need to be reassigned to a species closely allied to *Mimikonstantia sculpta*.

CONCLUSIONS

In *M. sculpta* the significance of the left-handed, as opposed to the right-handed, ontogenetic development pattern remains unknown. It seems unlikely that the feature is associated with sexual dimorphism. The variation in the order of initiation of the auxiliary resorption fronts clearly indicates, however, that *M. sculpta* represents a species in which the formation of the brachial supports had not yet stabilized into a standard development pattern and, in this respect, might represent a transitional form. The similarity in morphology, septal development and, as far as is known, the shell microstructure of *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* is considered to be sufficiently strong to be indicative of a genetic relationship and it is proposed that *Mimikonstantia* should be assigned to the Thecideinae, and that *Konstantia* should be reassigned to that subfamily also. The authors do not, at the present time, wish to attach any great taxonomic significance to the impunctate condition of the shell of *M. sculpta*, since the relationship between endopunctate and impunctate representatives of other taxa remains poorly understood.

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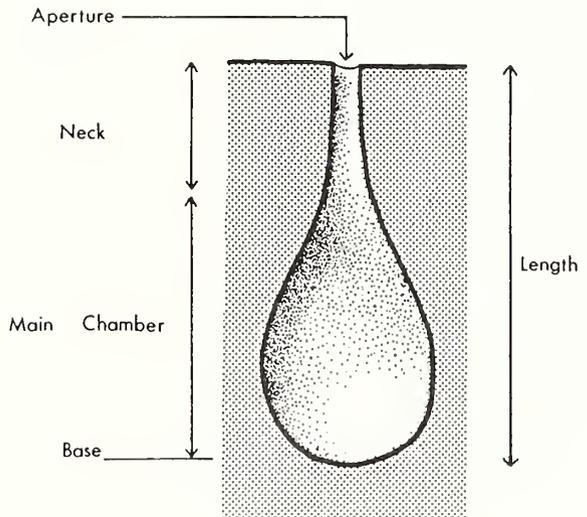
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ICHTHOLOGICAL NOMENCLATURE OF CLAVATE BORINGS

by SIMON R. A. KELLY *and* RICHARD G. BROMLEY

ABSTRACT. The use of ichnoterminology for flask-shaped borings is reviewed. The names *Gastrochaenolites* Leymerie and *Teredolites* Leymerie are recommended for use as ichnogenera for such borings in lithic and lignic substrates respectively. A range of morphology is recognized for each genus and the following new ichnospecies are described: *G. ampullatus*, *G. cluniformis*, *G. dijugus*, *G. lapidicus*, *G. orbicularis*, *G. ornatus*, *G. torpedo*, *G. turbinatus*, and *T. longissimus*. A key is given for rapid identification of the species, and stratigraphic distributions are given.

HITHERTO, there has been no nomenclatural stability in the naming of fossil flask-shaped and club-shaped borings which are common in hardgrounds and in fossil wood. These borings, which are here called clavate (Latin: *clava* = club), are those having usually a single narrow aperture, leading via a narrow neck to a wider chamber within the substrate (text-fig. 1). Such borings are immensely common both today and in the fossil record, and are principally, though not exclusively, the work of bivalves.



TEXT-FIG. 1. Terminology of a clavate boring.

A number of generic names have been used for the borings. The earliest names available are *Gastrochaenolites* and *Teredolites*, both introduced by Leymerie (1842), but they remained rarely used until the late 1960s. Bromley (1972) suggested synonymizing several boring ichnogenera under *Trypanites* but this suggestion did not gain popularity and is now regarded as excessive lumping. Bradshaw (1980) advocated the use of *Teredolites* for all club-shaped borings and redefined the name, but this use is felt here to be still too generalized. Kelly (1980) used *Gastrochaenolites* but later (in Balson 1980), considering that the name was invalid, used *Teredolites*. Other names in current usage may have no status for several reasons: they were not acceptably published, are subjective synonyms of earlier ichnotaxa, are misapplied names of different ichnotaxa, or they bear the names of supposed

zoological inhabitants. There are many excellent descriptions of clavate borings, e.g. Raynaud 1969; Evans 1970; Perkins 1971; Andersson 1979. Unfortunately in these cases no ichnotaxa were used.

In the present article the names in general use for clavate borings are examined for availability. The ichnogenera of Leymerie (1842) are found valid and are supplemented with new ichnospecies to name distinctive forms.

CLASSES OF SUBSTRATE

Leymerie (1842) introduced two names for clavate borings: *Gastrochaenolites* for those in lithic substrates, mollusc shell, coral, or limestone and *T. clavatus* for borings in wood. We believe this basic distinction between stony (lithic) and woody (lignic) substrates to be valid and useful. Trace fossils in unconsolidated sediments are named separately from those in hard substrates, e.g. the ichnogenera *Skolithos* and *Trypanites* s.s. and it seems natural to keep such forms separate from those in woody substrates. From the viewpoint of the borer, there are profound physical and ecological differences between stony and woody substrates, differences at least as significant as those between loose sediment and cemented sediment.

In the geological realm, lithic substrates include all indurated rock-types regardless of lithology, as well as hard skeletons such as coral, shell, and bone. In modern terms we must add brickwork, concrete, metal, and plastic. Woody substrates comprise driftwood, mangrove roots, submerged forests, and nut-shells, and today include pilings and ship hulls. Clavate borings occur in all these substrates. There will always be special cases such as how to name clavate borings made in the surface of a coal-seam apparently before it was coalified, but such cases will anyway deserve special description and interpretation, e.g. Bromley *et al.* (1984).

LIBERATED FILLS OF CLAVATE BORINGS

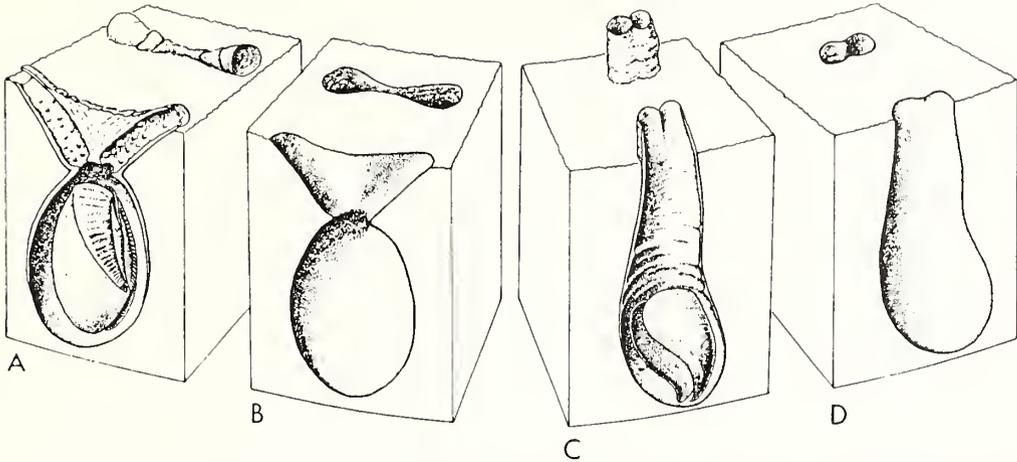
In some sediments, lithified clavate-boring fills occur as loose clasts, having been released by the destruction of their substrate (e.g. Radwanski 1977). This most often occurs in the case of woody substrates where the sediment filling the borings is cemented prior to breakdown of the wood. However, examples are also common where aragonite substrates have been destroyed at the sea floor. In such cases, the original nature of the substrate may not be immediately apparent. However, these borings commonly have a foreign sculptural ornament moulded on the surface which may characterize the vanished substrate, such as grain of wood (e.g. Vitalis 1961) or septal organization of coral (e.g. Damon 1860, p. 79, fig. 35). Also association with other borings that are still preserved in their substrate may provide such evidence. Foreign sculptural ornament can be described as xenoglyphic and should be contrasted with ornament due to direct boring activity such as that caused by the rotating rasping action of pholad bivalves—bioglyphic (terms introduced by Bromley *et al.* 1984).

In cases where there is no indication as to whether the original nature of the substrate was lithic or lignic, an ichnogenus cannot be applied. We anticipate, however, that such cases will be few and will merit individual discussion. They may simply be termed 'clavate-boring infills'.

CARBONATE LININGS IN CLAVATE BORINGS

Many of the organisms that produce clavate borings today, partly or completely line their borings with calcareous deposits. This is particularly the case among boring bivalves (e.g. Savazzi 1982). Some of these produce special linings around the siphonal region at the aperture and neck of the boring, and these deposits may extend as a chimney above the substrate surface (text-fig. 2). The walls of the main chamber may be more or less extensively coated with calcareous deposits, both in lithic and woody substrates. Such linings are commonly well preserved in fossil material.

The mere presence or absence of calcareous linings is of zoo-taxonomic significance; some species are incapable of secreting them, others do so. Among those that do, however, the extent,



TEXT-FIG. 2. A, longitudinal section of *Gastrochaenolites ampullatus* containing the body fossil: based on the boring of *Spengleria rostrata*. B, as A, but as preserved without the body fossil. C, longitudinal section of *G. dijugus* containing the body fossil: based on the boring of *Gastrochaena dubia*. D, as C, but without the body fossil.

morphology, and thickness of the lining is extremely variable from individual to individual. Degree and form of lining vary with ontogeny, substrate structure, crowding of individuals, etc. Furthermore, similar deposits are laid down in some bivalves upon the shells as well as the boring. For these reasons we prefer to regard the lining as part of the hard part of the shell, and to disregard it in ichnotaxonomy.

PREVIOUS NAMES

Gastrochaenolites Leymerie, 1842 and *Teredolites* Leymerie, 1842

In choosing these names, Leymerie was influenced, of course, by his opinion of the nature of the organism responsible for the boring. Thus he added the suffix *-ites*, as was then customary for fossilized material, to the biological taxa *Gastrochaena* and *Teredo*. However, it is clear from Leymerie's text and illustrations that it is the product of the activity of these animals rather than the animals themselves that bear the names, and these names are consequently ichnotaxa. This is a common form of confusion in the erection of early ichnotaxa, cf. *Clionites* Morris 1851, intended for fossil sponge borings (junior synonym of *Entobia* Bronn 1838). While the resulting names are unsatisfactory as ichnotaxa, in implying the work of a single biotaxon, it does not necessarily render the names unavailable, according to the rules of nomenclature. Thus, although *T. clavatus* does not closely resemble the work of *Teredo* spp., the ichnogenus, erected with the type species and well described and illustrated, must be considered available for clavate borings in wood. In contrast, *Gastrochaenolites* was erected without a nominal species, and was regarded by Keen (1968, p. N699) as a *nom. van.* and was placed as a synonym of the body fossil *Gastrochaena*. However, the original description is accompanied by a clear description and illustration and is therefore also valid (R. V. Melville, pers. comm.). Both names suffer from the suggestion of an implied original constructor but this does not affect availability of the names. Zittel (1881, p. 139) placed '*Teredolites* Deshayes' as a synonym of the body fossil *Teredo*. This was followed in the French translation by Barrois (Zittel 1887, p. 138). However, in the English translation by Eastman (Zittel 1900, p. 424, and subsequent edition, 1913, p. 501) it was ascribed correctly to Leymerie. Furthermore, in these translations the ichnotaxon was referred to as 'casts of borings of fossil Teredos'. Vokes (1980) placed *Gastrochaenolites* as *incertae sedis* within the bivalve subfamily *Gastrochaenacea*, and *Teredolites* as

'subfamily uncertain' within the family Teredinidae. But it must be stressed that *Gastrochaenolites* and *Teredolites* are not body fossils, they are traces of living activity, and cannot be accommodated within a strict zoological systematic nomenclature.

Teredolithus Bartsch, 1930

Bartsch intended this name only as an informal group name (therefore not italicized) for the linings of ship-worm borings of generically unknown status. It was never intended to have generic status and deliberately no type was designated. Turner (*in* Moore 1969: N740-741) used the name at generic level and placed it in 'subfamily uncertain' within the Pholadidae: it is probably only useful in the sense that Bartsch originally intended and, since we regard linings as related to the hard parts of fossils, we do not consider the name to be an available ichnogenus.

Trypanites Mägdefrau, 1932

The type ichnospecies, *T. weisei* Mägdefrau is a simple cylindrical boring having a single aperture. The apparent lack of a name for clavate borings led Bromley (1972) to suggest extending this ichnogenus to cover a wider range of single entrance borings, including clavate forms. However, this solution has not been generally accepted, and it would seem preferable to restrict *Trypanites* to cylindrical, commonly meandering, or convoluted borings.

Martesites Vitalis, 1961

This name refers to clavate borings in wood having a circular cross-section, and is a junior synonym of *Teredolites* Leymerie. Vokes (1980) regarded this as a body fossil placing it as a genus within the family Pholadidae Lamarck.

Paleolithophaga Chiplonkar and Ghare, 1967

This name was introduced as an ichnogenus with type species *P. andurensis* Chiplonkar and Ghare (1976, p. 162), to cover 'all the fossil borings of chemically-boring bivalves'. The diagnosis describes the borings as circular, having diameters from 0.7 to 1.0 cm and depths up to 2.0 cm. The only material is a single block of limestone containing many pits of varying morphology. No holotype was designated. It is a junior synonym of *Gastrochaenolites*.

Lithophaga, Teredo, etc.

In the absence of an ichnotaxon, a common procedure has been to apply the name of the *supposed* borer to the boring itself. Since, in the case of many borings, direct evidence of the nature of the borer is lacking, this is a most unsatisfactory solution to the problem (Bromley and Fürsich 1980; Bromley 1981).

SYSTEMATIC ICHNOLOGY

Key to identification of ichnospecies of *Gastrochaenolites* and *Teredolites*

- | | |
|---|-----------------------|
| 1. Substrate lithic | 2 |
| Substrate lignic | 10 |
| 2. Boring circular throughout length | 3 |
| Boring bilaterally symmetrical (apart from axial twists) | 6 |
| 3. Boring having near spherical main chamber | <i>G. orbicularis</i> |
| Boring having elongate main chamber | 4 |
| 4. Base of main chamber having concentrically/spirally grooved bioglyph | <i>G. ornatus</i> |
| Base of boring smooth | 5 |
| 5. Boring moderately elongate, widest at mid-length | <i>G. lapidicus</i> |
| Boring elongate, widest at base | <i>G. turbinatus</i> |

- | | |
|---|-----------------------|
| 6. Neck region of two tubes either connected or separate | 7 |
| Neck region a single tube, may be compressed | 8 |
| 7. Neck consisting of two separate diverging tubes or connecting slot | <i>G. ampullatus</i> |
| Neck with two parallel conjoined tubes | <i>G. dijugus</i> |
| 8. Base of boring bilobed | <i>G. cluniformis</i> |
| Base of boring smooth | 9 |
| 9. Base of boring bluntly parabolic | <i>G. lapidicus</i> |
| Base of boring acutely parabolic | <i>G. torpedo</i> |
| 10. Moderately elongate, substrate grain mainly perpendicular to axis of boring | <i>T. clavatus</i> |
| Very elongate, substrate grain mainly parallel to axis of boring | <i>T. longissimus</i> |

The systematic annotation of Richter (1948), described in English by Matthews (1973), is followed here.

Ichnogenus *Gastrochaenolites* Leymerie, 1842

- *. 1842 *Gastrochaenolites* Leymerie.
- p. 1972 *Trypanites* Mägdefrau; Bromley.
- . 1976 *Paleolithophaga* Chiplonkar and Ghare.
- . 1980 *Teredolites* Leymerie; Bradshaw.
- . 1980 *Gastrochaenolites* Leymerie; Kelly.
- . 1980 *Teredolites* Leymerie; Kelly (*in* Balson 1980).

Type species. *G. lapidicus* ichnosp. nov.

Diagnosis. Clavate borings in lithic substrates. The apertural region of the boring is narrower than the main chamber and may be circular, oval, or dumb-bell shaped. The aperture may be separated from the main chamber by a neck region which in some cases may be widely flared. The main chamber may vary from subspherical to elongate, having a parabolic to rounded truncated base and a circular to oval cross section, modified in some forms by a longitudinal ridge or grooves to produce an almond- or heart-shaped section. The general range in morphology of species of *Gastrochaenolites* is shown in text-fig. 3A-H.

Remarks. The axis of the boring may be straight, curved, or irregular. The widest part is usually between the mid-point and the base of the boring. The surface of the boring may be smooth, or bear sculptural ornament. The ornament may derive from the physical boring process, in which case, among bivalves, it may reflect the sculpture of the shells of the constructor (i.e. bioglyph); or it may derive from structural heterogeneity of the substrate (i.e. xenoglyph). The xenoglyph has no ichnotaxonomic significance at species level. Typical *Gastrochaenolites* range in size of diameter from 2 to 45 mm, and in length from 3 to 100 mm.

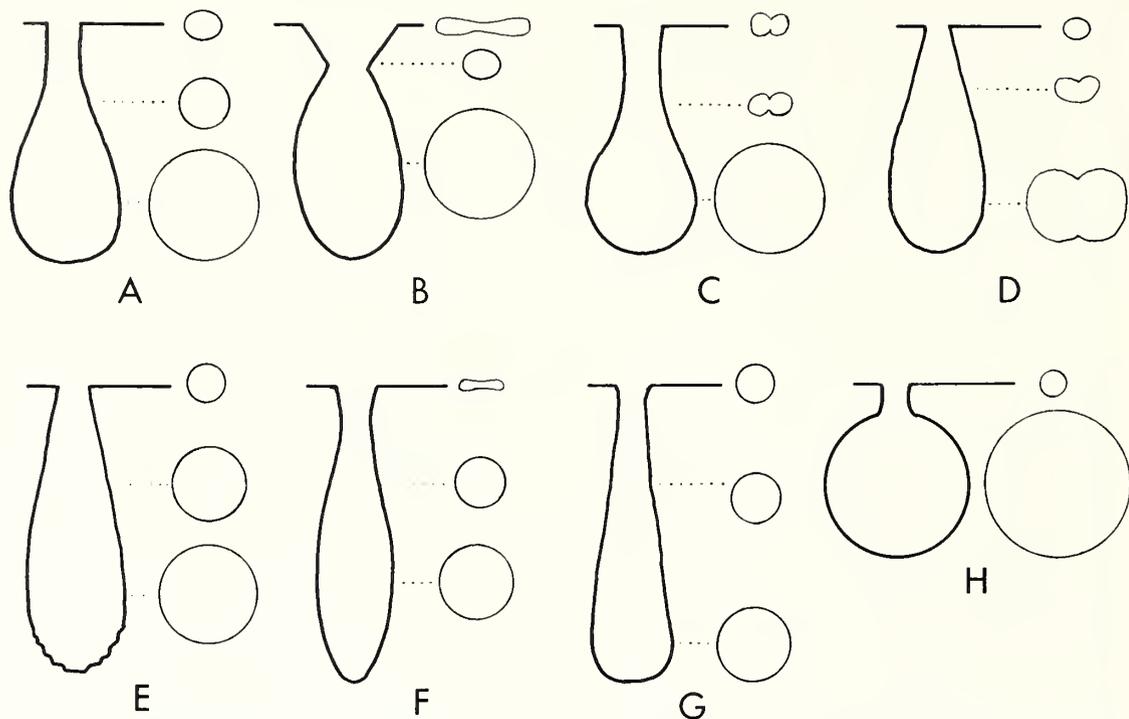
The constriction in the apertural/neck region immediately distinguishes it from *Trypanites* Mägdefrau. *Rogerella* Saint-Seine 1951, *Zapfella* Saint-Seine 1956, *Brachyzapfes* Codez and Saint-Seine 1958, and *Simonizapfes* Codez and Saint-Seine 1958 are all small oblique sac-like borings having a tendency towards a narrow tear-shaped slit aperture. They are attributed to acrothoracic barnacles. Borings of the polychaete *Polydora* have twin tube apertures, but there is no distinct chamber, the boring being a modified 'U' tube shape. The U-borings of the ichnogenus *Caulostrepsis* are morphologically distinct, lacking a main chamber (Bromley and D'Alessandro 1983).

Range. Jurassic to Recent.

Gastrochaenolites lapidicus ichnosp. nov.

Text-figs. 3A, 4A-B

- . 1842 *Gastrochaenolites* Leymerie, p. 2, pl. 3, fig. 1a-c.
- v. 1980 *Gastrochaenolites* Leymerie; Kelly, p. 771, text-figs. 2A-G, 3A-D, pl. 96, figs. 17-20, 22-24.
- v. 1980 *Teredolites* Leymerie; Kelly *in* Balson, p. 726.



TEXT-FIG. 3. Sketches of range in morphology of species of *Gastrochaenolites*, showing cross-sectional shape at various levels within the borings. A, *G. lapidicus*; B, *G. ampullatus*; C, *G. dijugus*; D, *G. cluniformis*; E, *G. ornatus*; F, *G. torpedo*; G, *G. turbinatus*; H, *G. orbicularis*.

In addition numerous references have been made to the boring with varying degrees of anonymity, e.g. Andersson (1979, type 3, p. 6, fig. 6c).

Holotype. British Geological Survey, Kelly Collection, Zu2230, from the Basal Spilsby Nodule Bed, Spilsby Sandstone, Middle Volgian; Nettleton, Lincolnshire, England. Figured originally by Kelly (1980, 771, fig. 2b).

Derivatio nominis. Latin, *lapidicus* = stonecutter.

Diagnosis. Smooth, clavate boring; elongate ovate; circular cross-section throughout length including the neck region except for the immediate area of the aperture where the section is usually oval, but may be circular; base bluntly paraboloid in longitudinal section; widest diameter located approximately central within the main chamber.

Remarks. There is a clear neck region which is a distinguishing feature separating it from *G. turbinatus*. Borings of this type are produced by several species of *Lithophaga* and *Hiatella* today, the former commonly lined but the lining never extending significantly beyond the aperture.

Range. Jurassic to Recent (pre-Jurassic *Lithophaga* probably had a nestling habit and are not yet known to have bored).

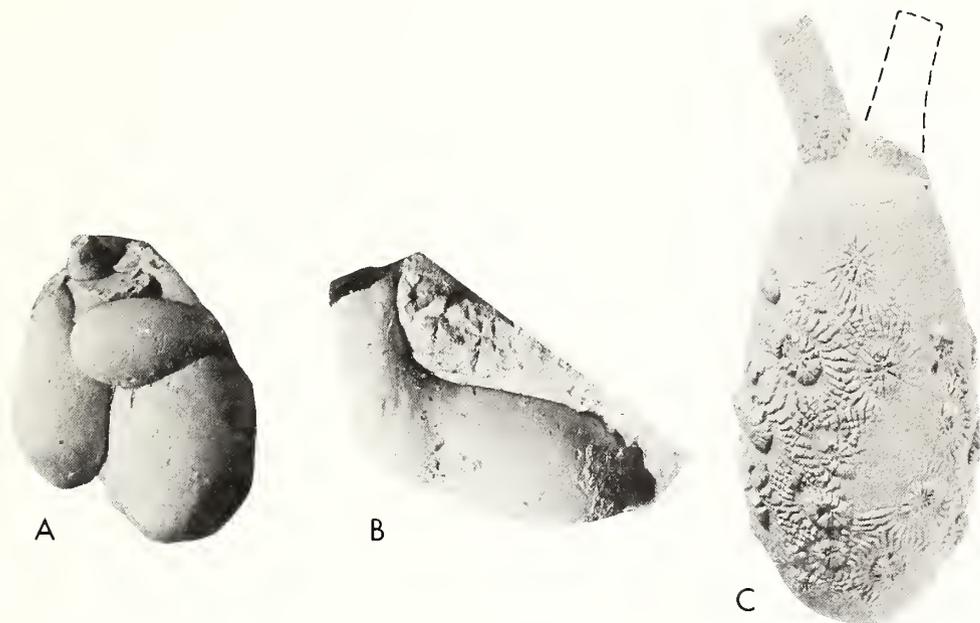
Gastrochaenolites ampullatus ichnosp. nov.

Text-figs. 2A-B, 3B, 4C

Holotype. BM(NH) 15174, Last Collection, Tertiary (Neogene) 40 ft from surface; Mbwani, Zanzibar (one apertural tube damaged).

Derivatio nominis. Latin, *ampulla* = small globular flask or bottle with two handles.

Diagnosis. Smooth borings with outline of main chamber spherical to elongate but having a fan-shaped, flared neck and containing two diverging tubes leading to twin apertures; maximum diameter near centre of main chamber.



TEXT-FIG. 4A, B. *Gastrochaenolites lapidicus* ichnosp. nov. A, interpenetrating paratypes, BGS Kelly Collection Zn2232; B, holotype, same collection, Zu2230; both from Basal Spilsby Nodule Bed, Middle Volgian; Sand Pit, 200 m south-east of Top Barn, Nettleton, Lincolnshire. Phosphatic nodule substrate, $\times 1.5$. C, *G. ampullatus* ichnosp. nov. holotype, BM(NH) L15174, Last Collection, Tertiary (Neogene), 40 ft from surface; Mbwani, Zanzibar. One apertural tube damaged. Coral substrate, $\times 1$.

Remarks. The flared neck distinguishes *G. ampullatus* from other species. The main chamber may range from subspherical to elongate. The neck is thickly lined to produce two diverging siphonal tubes. The structure of the lining is complex, having arisen through migration of tubes with the growth of the animal (see text-fig. 2A-B). A common mode of preservation is shown in text-fig. 4C, where the fill was cemented prior to the loss of the lining, producing a combination mould of body fossil and boring. In these cases the true form of the neck is obscured. Borings of this type are produced today by *Spengleria rostrata* (Warne 1975, fig. 11.26; Bromley 1978, fig. 9 left).

Range. Neogene to Recent.

Gastrochaenolites cluniformis ichnosp. nov.

Text-figs. 3d, 5

Holotype. BM(NH) L21602, Hythe Beds, Lower Greensand, Aptian; Maidstone, Kent.

Derivatio nominis. Latin, *cluniformis* = buttock shaped.

Diagnosis. Smooth *Gastrochaenolites* having one principal ridge in the main chamber and a second

weakly developed one diametrically opposite. The base is rounded to bilobate. The neck and aperture are rounded to oval.

Remarks. The principal ridge and bilobate form distinguish *G. chuiiformis* from *G. dijugus*. Borings of this type are found in corals and are produced by *Botula* spp.

Range. Cretaceous to Recent.



TEXT-FIG. 5. *Gastrochaenolites chuiiformis* ichnosp. nov. Assemblage with holotype arrowed. BM(NH) L21602, Hythe Beds, Lower Greensand, Aptian, Cretaceous; Maidstone, Kent. Lithic substrate, $\times 1$.

Gastrochaenolites dijugus ichnosp. nov.

Text-figs. 2C-D, 3C, 6A-B

. 1980 *Teredolites clavatus* Leymerie; Bradshaw, p. 290, text-figs. A-E.

Holotype. BM(NH) L36922, Corallian, Oxfordian, Jurassic; Calne, Wiltshire, England; paratype, BM(NH) L71398, same horizon, Malton, Yorkshire, England.

Derivatio nominis. Latin, *dijugus* = having two ridges.

Diagnosis. Smooth *Gastrochaenolites* in which neck region is constricted in the form approaching a figure of eight by two opposed ridges.

Remarks. The boring is commonly lined in the neck region, the lining usually continuing above the surface as a fused pair of extension tubes. *Gastrochaena* is a known occupant from Jurassic to Recent; the carinate *Gastrochaenopsis* is also known from the Jurassic only.

Range. Jurassic to Recent.

Gastrochaenolites orbicularis ichnosp. nov.

Text-figs. 3H, 6C

Holotype. BM(NH) L8138, Damon Collection, mid-Cenomanian to early Turonian; Tourtia de Tournai, Belgium.

Derivatio nominis. Latin, *orbis* = orb.

Diagnosis. Smooth *Gastrochaenolites*, circular in cross-section throughout; main chamber orbicular; neck region elongate in type specimen but may be short.



TEXT-FIG. 6A, B. *Gastrochaenolites dijugus* ichnosp. nov. A, paratype, BM(NH) L71398 Corallian, Oxfordian; Malton, Yorkshire, England. Coral substrate, $\times 1$; B, holotype, BM(NH) L36922, Corallian, Oxfordian, Jurassic, Calne, Wiltshire. Coral substrate, $\times 1$. C, *G. orbicularis* ichnosp. nov. holotype, BM(NH) L8138, Damon Collection, mid-Cenomanian-early Turonian, Cretaceous; Tourtia de Tournai, Belgium. Lithic substrate, $\times 1$.

Remarks. The orbicular main chamber and circular cross-section to the neck distinguish this species from others. Borings of this type are produced by *Jouannetia*. There may be an inconspicuous thin lining.

Range. Jurassic to Recent.

Gastrochaenolites ornatus ichnosp. nov.

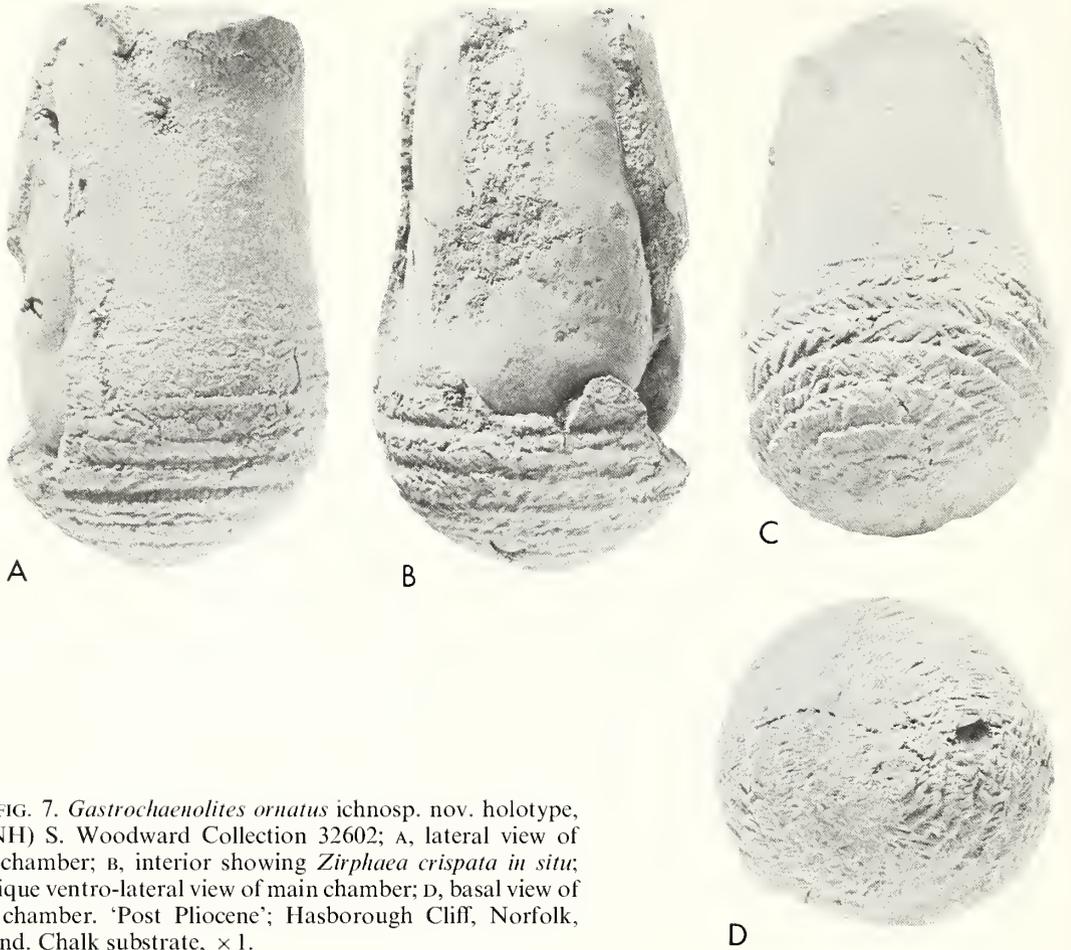
Text-figs. 3E, 7A-D

Holotype. BM(NH) S. Woodward Collection 32602. Originally figured S. Woodward (1833, p. 39, pl. 1, fig. 19) as: 'Pholas crispata; *auctor*. Imbedded in a pyritous cast of the cavity formed by the animal in the rock.' Post-Pliocene, from Hasborough Cliff, Norfolk, England.

Derivatio nominis. Latin, *ornatus* = ornamented.

Diagnosis. *Gastrochaenolites* that are circular in cross-section throughout. Deepest portion bears circular or spiral bioglyph, sometimes serrated grooves.

Remarks. These are unlined borings commonly found in association with pholad bivalves. The holotype contains the remains of *Zirfaea crispata*. The concentric grooves were formed by the serrated anterior portion of the shell rotating within the boring and grinding away the base of the boring, thus enlarging it. Although bioglyphic ornament may be present on other ichnospecies of *Gastrochaenolites*, the present form has such strongly developed bioglyph that it deserves distinction as a separate ichnospecies. The morphology otherwise resembles that of *G. turbinatus*. Warne and McHuron (1968) figure *Jouannetia* associated with such borings; Röder (1977, p. 136, fig. 15) figures



TEXT-FIG. 7. *Gastrochaenolites ornatus* ichnosp. nov. holotype, BM(NH) S. Woodward Collection 32602; A, lateral view of main chamber; B, interior showing *Zirphaea crispata* in situ; C, oblique ventro-lateral view of main chamber; D, basal view of main chamber. 'Post Pliocene'; Hasborough Cliff, Norfolk, England. Chalk substrate, $\times 1$.

Recent *Barnea* in association with these borings and (1977, pl. 3) figures Recent borings of this type which were constructed by *Pholas*.

Range. Pleistocene to Recent.

Gastrochaenolites torpedo ichnosp. nov.

Text-figs. 3F, 8A-B

Holotype. BM(NH) 56735, labelled Pliocene, but probably Jaffna Limestone, L. Miocene (Cooray 1967, 135; 1982); Kankasanturai, north of Jaffna, Sri Lanka.

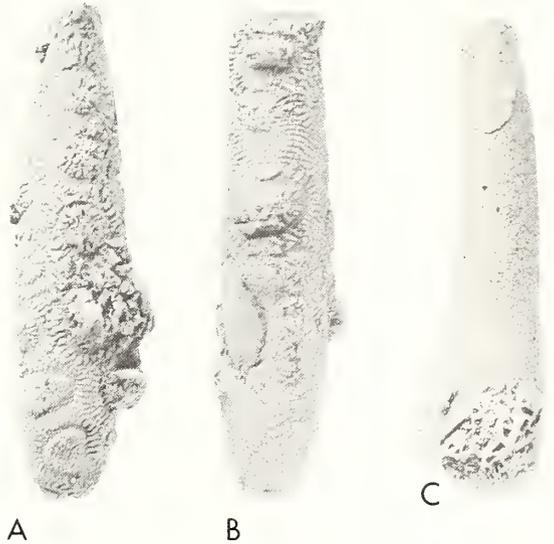
Derivatio nominis. Named after its similarity to the weapon.

Diagnosis. Elongate smooth boring, widest point close to mid-line with the base acutely parabolic. The neck region is markedly compressed but the aperture itself is oval or approaches a figure-of-eight shape.

Remarks. Differs from *G. lapidicus* by having a more elongate shape and a more compressed neck region. The borings are commonly lined. The lining thins towards the widest part of the boring and

may have a transverse wrinkled ornament internally. The lining thickens towards the aperture where the lumen of the boring is restricted to a figure-of-eight cross-section, and continues beyond the substrate surface as a chimney. Borings of this type are constructed today by some species of *Gastrochaena* (cf. Bromley 1978, fig. 9 right) and also of *Lithophaga*. Certain borings of polychaetes and sipunculids resemble this ichnospecies (See Bromley, 1970, p. 63, figs. 4b, 4c respectively), but are generally more slender.

Range. Jurassic to Recent.



TEXT-FIG. 8. *Gastrochaenolites torpedo* ichnosp. nov. A, B, holotype, BM(NH) 56735, two views of holotype, probably Jaffna Limestone, lower Miocene; Kankasanturai, north of Jaffna, Sri Lanka. Coral substrate, $\times 1$. C, *G. turbinatus* ichnosp. nov. holotype, BM(NH) L56724, probably Jaffna Limestone, lower Miocene; Kankasanturai, north of Jaffna, Sri Lanka. Coral substrate, $\times 1$.

Gastrochaenolites turbinatus ichnosp. nov.

Text-figs. 3G, 8C

Holotype. BM(NH) L56724, labelled Pliocene, but probably Jaffna Limestone, L. Miocene (Cooray 1967, 135; 1982); Kankasanturai, north of Jaffna, Sri Lanka.

Derivatio nominis. Latin, *turbinatus* = conical.

Diagnosis. Smooth *Gastrochaenolites*, acutely conical, having evenly tapered body and neck, the widest point close to the short rounded base; rounded cross-section throughout length.

Remarks. Distinguished from other ichnospecies of *Gastrochaenolites* by the evenly tapered main chamber which merges imperceptibly with the neck. No known linings. Holotype bears some traces of a coral substrate. *Gastrochaena* sp. has been seen occupying Jurassic examples. *Penitella* forms such borings in Recent examples (e.g. Warne 1970, pl. 4).

Range. Jurassic to Recent.

Ichnogenus *Teredolites* Leymerie, 1842

- 1841 *Teredolites* Leymerie, p. 341 (*nom. nud.*).
- * 1842 *Teredolites* Leymerie, p. 2, pl. 2, figs. 4, 5.
- 1852 *Teredolites* Herrmannsen, p. 131 (*nom. nud.*).
- . 1900 *Teredolites* Leymerie; Zittel, p. 424, fig. 787D.
- . 1913 *Teredolites* Leymerie; Zittel, p. 501, fig. 336D.
- . 1961 *Martesites* Vitalis, p. 124, pls. 1-2.

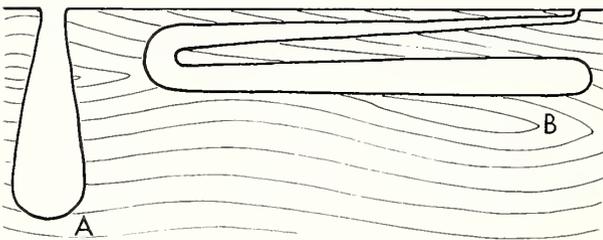
- p1972 *Trypanites* Mägdefrau; Bromley, fig. 1B, E only.
 1972 *Teredolites* Leymerie; Hatai and Murata, p. 7, pl. 1.
 1975 *Martesites* Vitalis; Häntschel, W129.
 1975 *Teredolites* Leymerie; Häntschel, W135.
 v non 1981 *Teredolites* Leymerie; Kelly in Balson 1981, p. 726.

Type species. *T. clavatus* Leymerie 1842 (see below).

Diagnosis. Clavate borings in woody substrates, acutely turbinate, evenly tapered from aperture to base of main chamber; neck region not separated from main chamber; cross-sections at all levels more or less circular; elongate to short.

Remarks. Borings are normally smooth, but may bear the xenoglyph of the grain of the lignic substrate. Faint bioglyphic ornament may also be preserved (Bromley *et al.* 1984). Axis of boring may be straight, sinuous, or contorted. The axis of the boring may change suddenly and cause a constriction in the pattern of the tube (Röder 1977, p. 147, fig. 21). Linings of these borings, as body fossils, fall within the group name *Teredolithus* Bartsch. Typical species are shown in text-fig. 9.

Range. Jurassic to Recent.



TEXT-FIG. 9. Range in morphology of *Teredolites*. A, *T. clavatus* Leymerie; B, *T. longissimus* ichnosp. nov., both generalized axial sections showing relationship to grain of lignic substrate. Cross-sectional shape round throughout length, $\times 1$.

Teredolites clavatus Leymerie, 1842

Text-figs. 9A, 10

- . 1841 *Teredolites clavatus* Leymerie, p. 341 (*nom. nud.*).
 * 1842 *Teredolites clavatus* Leymerie, p. 2, pl. 2, figs. 4, 5.
 . 1961 *Martesites vadaszi* Vitalis, p. 124, pl. 1, 2.
 . 1969 *Teredolites clavatus* Leymerie; Turner (*in* Moore, ed.), p. N740, fig. 214, 2a, b.
 . 1972 *Trypanites vadaszi* (Vitalis); Bromley, fig. 1B.
 . 1975 *Martesites vadaszi* Vitalis; Häntschel, p. W129, fig. W79, 1.
 v. 1983 *Teredolites*; Kelly and Rawson, p. 70.
 v. 1983 *Teredolites*; Kelly, p. 287.
 v. 1984 *Teredolites clavatus* Leymerie; Bromley, Pemberton and Rahmani, p. 488.

Type specimen: Untraced, Leymerie Collection, Calcaire à Spatangues, Hauterivian, lower Cretaceous, Aube, France.

Diagnosis. Clavate *Teredolites* predominantly perpendicular to the grain in woody substrates having length/width ratio usually less than 5.

Remarks. Such borings are produced today by species of *Martesia*. Fossil occupants include *Martesia* and *Opertochasma*.

Range. Jurassic to Recent.

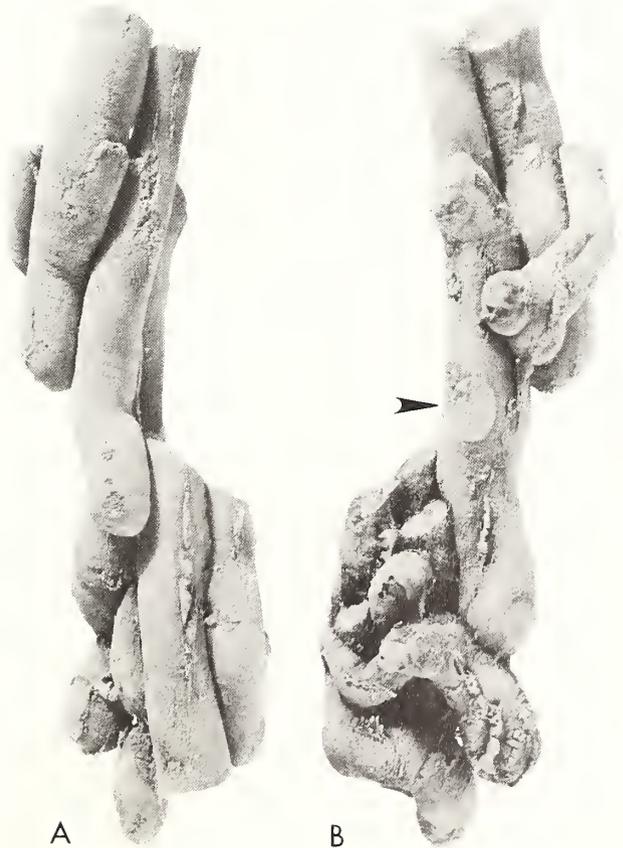
Teredolites longissimus ichnosp. nov.

Text-figs. 9B, 11A-B

Holotype. BM(NH) Bensted Collection, 38019, Kentish Rag, Aptian, Lower Cretaceous, Hythe, Kent, England.



TEXT-FIG. 10. *Teredolites clavatus* Leymerie. SMC B11389, Spilsby Sandstone, probably Ryazanian; Benniworth Haven (probably the Railway Cutting south-west of Donington-on-Bain), Lincolnshire. Borings perpendicular to surface of log of wood, $\times 2$.



TEXT-FIG. 11. *Teredolites longissimus* ichnosp. nov. Lateral views (A and B) of holotype (arrowed), with paratypes, BM(NH) Bensted Collection 38019, Kentish Rag, Aptian, lower Cretaceous; Hythe, Kent, England. Borings parallel to grain of lignic substrate, $\times 1$.

Derivatio nominis. Latin, *longissimus* = longest.

Diagnosis. Clavate *Teredolites* predominantly parallel to the grain in lignic substrate having length/width ratio usually greater than 5. Commonly sinuous to contorted.

Remarks. Commonly lined with calcite, the thickness of which increases towards the aperture. Borings of the teredine ship-worms which include those of *Teredo* itself, fall within this ichnospecies. Juvenile forms pass through a phase having the morphology of *T. clavatus*.

Range. Cretaceous to Recent.

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AN IMMATURE SPECIMEN OF THE CROCODILIAN *BERNISSARTIA* FROM THE LOWER CRETACEOUS OF GALVE (PROVINCE OF TERUEL, SPAIN)

by A. D. BUSCALIONI, E. BUFFETAUT and J. L. SANZ

ABSTRACT. An almost complete skeleton of a small crocodylian has been found in the Barremian-Aptian of Galve (province of Teruel, Spain). Its well preserved skull is described here. Several cranial features are very reminiscent of *Bernissartia fagesii* Dollo, from the Wealden of Belgium: general outline, proportions of the snout and of the posterior region, anterior outline of the orbits, relative proportions of the orbits and supratemporal fenestrae, absence of a maxillary depression. A few features are different in the Spanish and Belgian specimens, such as the relative proportions of snout, orbits, and cranial table. However, these divergences are explainable by the immaturity of the Galve specimen, which we refer to the genus *Bernissartia*.

THE genus *Bernissartia* was described by Dollo (1883) on the basis of crocodylian remains found in the Wealden beds of the famous coal mine at Bernissart (Belgium). Although a complete skeleton was found, anatomical details were poorly preserved: cranial sutures are hardly visible, and the ventral part of the skull is difficult to interpret (Buffetaut 1975). As a result, the systematic position of *Bernissartia* has been much disputed. Dollo (1883) considered it as a representative of a new family of the Mesosuchia (Bernissartidae), different from the Goniopholididae. Lydekker (1888) proposed its inclusion in a subfamily of the Goniopholididae, the Bernissartinae. Kälin (1955) referred *Bernissartia* to the modern suborder Eusuchia, and he has been followed by various authors, notably Steel (1973).

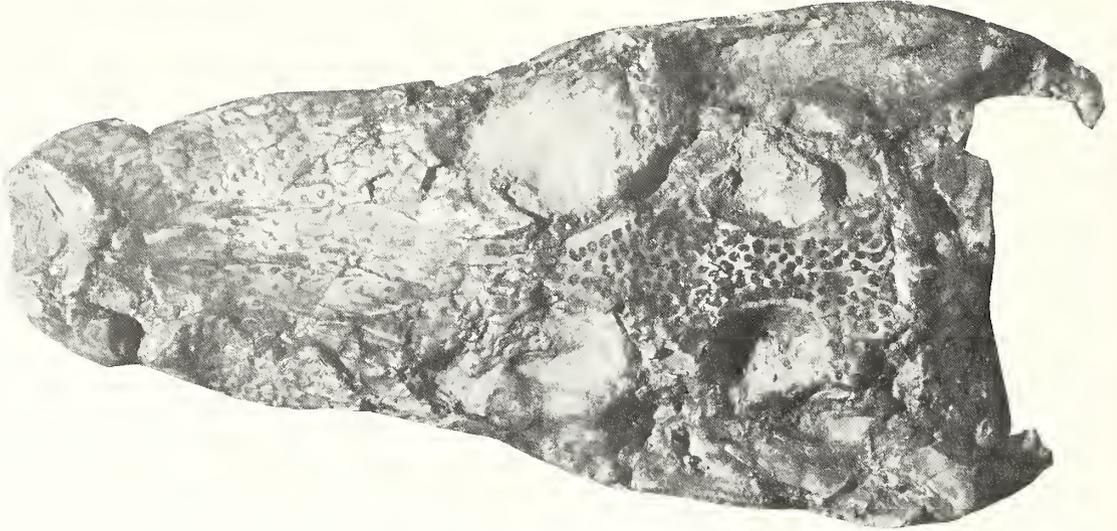
In 1975, one of us (E.B.) revised the original material of *B. fagesii*, and concluded that it still belongs to the mesosuchian level of crocodylian evolution, and that other crocodylians from the Purbeck and Wealden beds of England (notably *Theriosuchus* Owen 1879) are more progressive than *Bernissartia* and may be closer to the ancestry of the Eusuchia. Kälin's interpretation was thus rejected, and Dollo's systematic proposal was accepted. Since then, very incomplete remains of *Bernissartia* (mainly isolated teeth) have been reported from the Wealden of England (Buffetaut and Ford 1979).

We report here the discovery of a complete skeleton of *Bernissartia* in the lower Cretaceous of Spain, and give a preliminary description of its skull to justify its systematic allocation.

THE CROCODYLIANS FROM THE LOWER CRETACEOUS OF GALVE

Various crocodylian remains have already been reported from the lower Cretaceous of Galve (province of Teruel, Spain). Kühne (1966) reported crocodylian teeth and scutes. Crusafont-Pairó and Adrover (1966) and Berg and Crusafont-Pairó (1970) have referred blunt and rounded isolated teeth to the alligatorid *Allognathosuchus* Mook but they more probably belong to *Bernissartia* (Buffetaut and Ford 1979). Estes and Sanchiz (1982) have referred isolated teeth to the families Atoposauridae, Pholidosauridae, and Bernissartidae (cf. *Bernissartia* sp.). The specimen described in the present paper is much more complete than the isolated scutes and teeth hitherto reported from Galve. It is an almost complete skeleton, including the whole skull, which will require further preparation, and may eventually provide a better knowledge of the still problematic genus *Bernissartia*.

Together with the crocodylians, several types of dinosaurs also occur in the Galve deposits. They include an indeterminate brachiosaurine close to *Brachiosaurus* Riggs (1903) (Sanz 1982), *Iguanodon bernissartensis* van Beneden (1881) (identified by Lapparent 1960), *I. cf. mantelli*, and an indeterminate carnosaur (unpublished data). This reptilian fauna seems to be similar to that from the Wealden beds of England and Belgium. The age of the outcrops at Galve has been determined as Barremian–Aptian by means of charophytes (Crusafont-Pairó and Gibert 1976).



TEXT-FIG. 1. Young individual of *Bernissartia* from the lower Cretaceous of Galve (province of Teruel, Spain). Skull in dorsal view.

The *Bernissartia* skeleton was found in a clay pit called 'Cerrada Roya' by Mr. J. M. Herrero, who lives in Galve and kindly gave the specimen to the authors for study. The material is currently housed in the Zoology Department, Universidad Autónoma de Madrid.

DESCRIPTIVE PALAEOLOGY

The skeleton, enclosed in a clay matrix, is small, about 300 mm in length. The skull is slightly distorted due to dorsoventral crushing. The bones are thin, which may be linked to the immaturity of the animal (see below). The snout is short. The bones of the dorsal face of the skull are covered with regularly distributed pits of subcircular shape, easily observable in the frontoparietal region. The total length of the skull from the occipital complex to the anterior region of the premaxillae is 70 mm.

The supratemporal fenestrae are shorter than the orbits; they are bordered by a smooth, unsculptured rim. Their shape is ellipsoidal, with the longer axis parallel to the symmetry plane of the skull. The longitudinal axis is 9.5 mm in length; the transversal axis (width) is estimated to be *c.* 8.5 mm. The smallest distance between the supratemporal fenestrae is 5.5 mm. The orbits present a peculiar outline (text-fig. 1), with an anterolateral notch; their posterior part is definitely wider than the anterior one. A smooth rim borders the orbits especially in the medial zone. The orbits represent one quarter of the total skull length. The smallest interorbital distance is 4.6 mm, and it represents

54% of the length of the frontoparietal suture, both measurements being taken along parallel lines. The interorbital region is slightly concave. The longer orbital axis, measured from the anterior notch to the posterior border of the orbit, is 15.5 mm long. The shorter axis, as measured orthogonal to the longer axis, is 10.8 mm long.

The regions of the postorbital bars and of the external nares are damaged in the Galve specimen. The postorbital bars have been displaced by dorsoventral crushing. Despite this, the postorbital bar does not seem to be in a very internal position, but its interpretation is problematical. In the anterior region of the snout, part of the premaxillae is probably missing. This fact makes it difficult to interpret the external nares, which seem to be very large. The anterior point of the nasals may reach the posterior edge of the nares.

The dorsal outline of the skull displays two main constrictions. The first one is sharp and located at the level of the premaxilla-maxilla suture, while the second one, less sharp, is placed lateral to the orbits, at the level of their anterior notches, and affects the maxillae. Posterior to this level, the sides of the skull diverge toward the quadrate condyles. The posterior width of the skull, from quadrate to quadrate, is 36.7 mm. The skull is 25 mm wide at the posterior constriction, and about 18 mm at the premaxilla-maxilla constriction. The skull table is of subquadrangular shape, and not higher than the snout in lateral view.

Some sutures are difficult to trace (text-fig. 1). A sagittal suture separates the nasals and divides the frontal, and probably also parietal. The nasals form an anterior V-shaped apophysis which separates the premaxillae and seems to reach the external nares. The premaxilla-maxilla suture is clear. This suture is directed obliquely and reaches the nasals at their anterior third. The nasofrontal suture is V-shaped, the anterior point of the frontal separates the posterior regions of the nasals at the level of the orbital notches. The relation between the frontal and the parietal is clear, too: the sutural line separates them at the level of the anterior border of the supratemporal fenestrae. The maxillo-jugal suture appears to be located at the level of the middle region of the orbit. Finally, a suture parallel to the mediosagittal plane separates the parietal from squamosal. The supraoccipital seems to enter the cranial table with a slightly curved suture. The quadratojugal does not take part in the cranio-mandibular articulation.

DISCUSSION

There are many features in common to the crocodylian from the lower Cretaceous of Galve and *Bernissartia fagesii* which distinguish them from other Wealden crocodylians:

1. The general outline of the skull in dorsal view, especially the constriction at the level of the premaxilla-maxilla suture, and the relative proportions of the snout and posterior region. These traits differentiate the Spanish crocodylian from other Wealden forms such as the short-snouted *Theriosuchus* Owen 1879 and the long-snouted *Vectisuchus* Buffetaut and Hutt 1980.

2. The presence of a notch in the anterior border of the orbits.

3. The orbits are relatively larger than the supratemporal fenestrae. This character separates the Galve crocodylian from the Goniopholididae of the European Wealden, such as *Goniopholis crassidens* Owen 1842 and *G. simus* Owen 1878.

4. There is neither an antorbital fenestra nor a maxillary depression (as defined by Buffetaut 1982.) The latter feature is characteristic of the Goniopholididae.

5. The interorbital distance is relatively smaller than in the Goniopholididae; even young individuals of the latter family show a relatively wider interorbital space (cf. Joffe 1967, about *Nannosuchus*). The transversal frontal ridge between the orbits, present in the Goniopholididae (whatever their individual age) is absent in both the Galve crocodylian and *B. fagesii*.

6. The Goniopholididae have a frontoparietal suture in a more posterior position than the Galve crocodylian.

All these characters suggest that our specimen is closely related to *B. fagesii*. Nevertheless, there are also some differences:

1. In *B. fagesii*, the length of the orbit is one sixth of the total cranial length, while it is one quarter in the Spanish form.

2. The snout is relatively shorter, and the cranial table is relatively larger in the Galve crocodylian than in *B. fagesii*.

However, these differences probably indicate that the Galve specimen is an immature individual. Immature crocodylians are known to have relatively short snouts and large orbits (Kälin 1955; Joffe 1967; Webb and Messel 1978). This interpretation is in agreement with the small size of the specimen, and other features seem to corroborate this interpretation, e.g. the presence of an axial suture in the frontal, and possibly the parietal region (cf. Langston 1973). It thus seems legitimate to consider the Galve crocodylian as a juvenile specimen of *Bernissartia*. When preparation of the fossil is completed, a study of the whole specimen should indicate whether it belongs to the same species as the Belgian form.

Acknowledgements. We thank Mr. J. M. Herrero, owner of the specimen who kindly gave the specimen to the authors for study. Thanks to G. F. Kurtz for the fine photograph.

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ADDENDUM

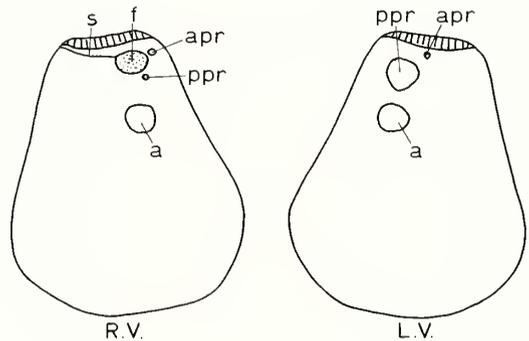
New geological and biostratigraphical evidence seems to indicate that the level of the Spanish young *Bernissartia* must be located in the early Barremian.

REVISION OF THE BIVALVE FAMILY PULVINITIDAE STEPHENSON, 1941

by T. J. PALMER

ABSTRACT. Reconsideration of the characteristics of all species referred to the three genera which have hitherto constituted the Family Pulvinitidae Stephenson, 1941, indicates that all should be accommodated in the nominate genus, *Pulvinites* Blainville, 1824. A new species, *P. mackerrowi* from the middle Jurassic of England (the earliest known representative of the family) is described.

THE bivalve family Pulvinitidae Stephenson, 1941, comprises a small, poorly known taxon with a discontinuous stratigraphic range from the Jurassic to the Recent. It appears to represent an offshoot of the Family Isognomonidae whose byssus has become enclosed by growth together of the dorsal and ventral margins of the right byssal notch (Cox 1969). The byssus thus appears, as in *Anomia*, to pass through a hole in the right valve. This hole is connected to the antero-dorsal shell margin by a suture (text-fig. 1).



TEXT-FIG. 1. Diagrammatic representation of the features observable on the inner surfaces of the valves of all species of the genus *Pulvinites*. s = suture; f = byssal foramen; a = adductor muscle scar; apr = anterior pedal retractor muscle scar; ppr = posterior pedal retractor muscle scar.

CONSTITUENT GENERA OF THE FAMILY PULVINITIDAE

The family was erected without a formal diagnosis by Stephenson (1941) as a repository for the best-known genus, *Pulvinites* Blainville, 1824. Species of this genus have been described from a number of upper Cretaceous localities in North America (Conrad 1858, 1860; Wade 1926; Stephenson 1914, 1926, 1941), Lebanon (Vokes 1941), and Antarctica (Zinsmeister 1978), and from the Palaeocene of California (Zinsmeister 1978). The American occurrences include exceptionally well-preserved material from the Maastrichtian Ripley Formation of Coon Creek, Tennessee. The only known occurrence in the European Cretaceous is that of the type material of *P. adansonii* Blainville, 1824, from the Maastrichtian Calcaire à Baculites (Craie de Valognes) at Frésville in the Cotentin peninsula, France.

Two other genera have hitherto been placed in the family (Cox 1969): *Hypotrema* d'Orbigny, 1853 from the French upper Jurassic and the extant *Foramulina* Hedley, 1914 from south-east Australia. The wide geographic and stratigraphic distribution of the three genera has led to confusion about their similarities and differences. The authors of many of the species, as well as of the later two genera, have suffered from inaccessibility to, and unfamiliarity with, appropriate comparative material from

the related taxa, and have been unable to gain a correct impression of the true characteristics and considerable variability of members of this family. As a result many misconceptions are stated in the literature, and the family is taxonomically over-split. Several workers (e.g. Bronn 1852, Stoliczka 1871, Freneix 1956) have claimed or suspected this state of affairs without the information to back their suspicions, but this is the first time that all the species in the family have been studied together. Their characteristics are summarized in Table 1.

MATERIAL STUDIED

Extensive material from all three above-mentioned genera has been examined. It includes the only known surviving specimens of *P. adansonii*, which are topotypes belonging to the de Gerville collection in the British Museum (Natural History); well-preserved topotypes of *P. argenteus* Conrad, 1858 from the Ripley Formation of Tennessee; the type suites of *H. rupellensis* d'Orbigny, 1853 and *H. triangularis* d'Orbigny, 1853 from the d'Orbigny collection in the Museum National d'Histoire Naturelle, Paris; additional topotypes of *H. rupellensis* in the Museum d'Histoire Naturelle at La Rochelle and in the Oxford University Museum (author's collection); the figured paratype of *F. exempla* Hedley, 1914; and one specimen from a recently discovered population of *F. exempla* (the only known soft-part occurrence other than the holotype).

SYSTEMATIC PALAEOLOGY

- Class BIVALVIA Linné, 1758
- Subclass PTERIOMORPHIA Beurlen, 1944
- Order PTERIOIDA Newell, 1965
- Suborder PTERIINA Newell, 1965
- Superfamily PTERIACEA Gray, 1847
- Family PULVINITIDAE Stephenson, 1941

Diagnosis. Shell ovate, orbicular or trigonal; externally lamellose and oyster-like; outer ostracum of prismatic calcite, inner ostracum nacreous; LV usually more inflated than RV, which is often planar or concave; hinge anterior to umbo, edentulous, but with wide ligamental area in each valve bearing series of narrow, elongate, sub-parallel, transverse ligamental pits which indent lower margin of area and which may become lachrymate in some species; RV of post-juvenile has byssal foramen just below middle of ligamental area, joined to antero-dorsal shell margin by suture representing line of ontogenetic closure of byssal notch; LV with enlarged posterior byssal retractor muscle scar opposite foramen; single adductor muscle scars located medially in each valve.

Discussion. Stephenson (1941) gave no diagnosis or description of the family when he erected it as a repository for the genus *Pulvinites*. Cox's (1969) definition of the family gave undue significance to the radial striation of the byssal retractor, which is only seen in some specimens. The above redefinition also excludes those characteristics such as size and convexity considered to be of only subsidiary importance, but includes shell structure.

Much unnecessary doubt has been thrown on the existence of the suture in fossil forms. Cox (1969) states that it has not been observed at all, and Zinsmeister (1978) states that it has not been observed in *P. argenteus*. Conrad (1858, 1867), however, clearly states that it is present in *P. argenteus*, and his figure (Conrad 1860) shows it. He also understood its significance and records (Conrad 1867) that juveniles of that species can be found in which the byssal notch is still open to the anterior. A suture is obvious in all specimens of *P. argenteus* examined in this study. Similarly, the suture is clearly shown in Sowerby's (1833) picture of the topotype of *P. adansonii* (BMNH L63618), and in the specimen itself. All the other right valves in the material examined in this study (see above) also clearly show the suture.

TABLE 1. Morphological characteristics and measurements of all species of the genus *Pulvinites*; junior synonyms in parentheses. Under lateral profile, O = oval; T = trigonal; st, conc, and conv = straight, concave, and convex posterior dorsal margin respectively.

Species; synonyms in inverted commas	Lateral profile	Inflation weak, moderate, or strong	Max. length (l) mm	Max. height (h) mm	l >, =, or < h	Length of ligament mm	Number of pits	Length of ligament	Length of ligament		Geographic occurrence
									No. of pits	No. of pits	
<i>adansonii</i>	T, st-conc	weak	53	46	l ≥ h	6-9	7-8	0.9-1.2	4.4-6.3	Maastrichtian	Frésville, Manche, Normandy
'auriculatus'	T conc	weak	51	47	l ≥ h	—	6	—	—	Cenomanian	Hajula, Lebanon
'antarctica'	O, T conc	weak	52	49	l > h	10-11	9-11	1.0-1.1	4.3-5.2	U. Campanian or Maastrichtian	Seymour Is., Antarctica
<i>argenteus</i>	T conv, O, st or conc	weak-mod. strong	53	52	l >, = or < h	9-15	10-15	0.9-1.0	2.9-3.9	Maastrichtian	Texas, Mississippi, Tennessee, Alabama
<i>rupellensis</i>	O-oval	mod.-strong	30	50	l < h	5-11	5-12	0.8-1.5	2.1-5.4	Kimmeridgian	nr. La Rochelle, Charente Maritime
'triangularis'	oval w. dorsal taper	mod.	—	—	l < h	8	6	1.3	—	Kimmeridgian	nr. La Rochelle, Charente Maritime
<i>mackerrowi</i>	O	strong	30	31	l = h	6-11	6-12	0.8-1.0	2.7-3.8	M. and U. Bathonian	Oxfordshire
<i>californica</i>	O, T st	weak	18.5	20	l ≤ h	3-5	5	0.7	4-6	uppermost Palaeocene	Ventura Co., California
<i>pacifica</i>	? O	weak	39	44	l < h	—	c.5	—	—	Palaeocene	Ventura Co., California
<i>exempla</i>	T conc	weak	131	111	l > h	36	20	1.8	3-7	Recent	Gabo Is., Victoria, Aus.

TABLE 1. Morphological characteristics and measurements of all species of the genus *Pulvinites*; junior synonyms in parentheses. Under lateral profile, O = oval; T = trigonal; st. conc. and conv = straight, concave, and convex posterior dorsal margin respectively.

Species; synonyms in inverted commas	Lateral profile	Inflation weak, moderate, or strong	Max. length (l) mm	Max. height (h) mm	l >, =, or < h	Length of ligament mm	Number of ligament pits	Length		Age	Geographic occurrence
								No. of pits	Length of ligament		
<i>adansonii</i>	T, st-conc	weak	53	46	l ≥ h	6-9	7-8	0.9-1.2	4.4-6.3	Maastrichtian	Fréville, Manche, Normandy
' <i>auriculus</i> '	T conc	weak	51	47	l ≥ h	—	6	—	—	Cenomanian	Hajula, Lebanon
' <i>antarctica</i> '	O, T conc	weak	52	49	l > h	10-11	9-11	1.0-1.1	4.3-5.2	U. Campanian or Maastrichtian	Seymour Is., Antarctica
<i>argenteus</i>	T conv, O, st or conc	weak- mod.	53	52	l >, = or < h	9-15	10-15	0.9-1.0	2.9-3.9	Maastrichtian	Texas, Mississippi, Tennessee, Alabama
<i>rupellensis</i>	O-oval	mod. — strong	30	50	l < h	5-11	5-12	0.8-1.5	2.1-5.4	Kimmeridgian	nr. La Rochelle, Charente Maritime
' <i>triangularis</i> '	oval w. dorsal taper	mod.	—	—	l < h	8	6	1.3	—	Kimmeridgian	nr. La Rochelle, Charente Maritime
<i>mackerrowi</i>	O	strong	30	31	l = h	6-11	6-12	0.8-1.0	2.7-3.8	M. and U. Bathonian	Oxfordshire
<i>californica</i>	O, T st	weak	18.5	20	l ≤ h	3.5	5	0.7	4.6	uppermost Palaeocene	Ventura Co., California
<i>pacifica</i>	? O	weak	39	44	l < h	—	c.5	—	—	Palaeocene	Ventura Co., California
<i>exempla</i>	T conc	weak	131	111	l > h	36	20	1.8	3.7	Recent	Gabo Is. Victoria, Aus.

Genus *Pulvinites* Blainville, 1824

Type Species. *Pulvinites adansonii* Blainville, 1824, by monotypy.

Synonymy. *Hypotrema* d'Orbigny, 1853; *Foramolina* Hedley, 1914

Original diagnosis. 'Coquille mince, ovale, équivalve, subéquilatérale, à sommets bien marqués et à peine inclinés en avant; charnière composée par huit ou dix dents un peu divergents du sommet et séparées par autant de fossettes pour les ligamens; impressions musculaires inconnues' (Blainville 1824, p. 316).

Amended diagnosis. Pulvinitidae of medium size; not auriculate. RV flat or slightly concave, with scar of anterior byssal (pedal) retractor muscle displaced posteriorly by migration of foramen to occupy position just posterior to foramen's dorsal margin; scar of posterior retractor lies just ventral to this, off the foramen's ventro-posterior margin. LV weakly to strongly convex, with anterior byssal (pedal) retractor scar lying just beneath centre of ligamental area, just postero-dorsally of the apex of the posterior retractor scar (text-fig. 1).

Discussion. All previous accounts have credited DeFrance with authorship of both the genus and the type species. However, DeFrance's (1826*a, b*) entry in the *Dictionnaire des Sciences Naturelle* under the entry 'Pulvinite' was preceded by that of Blainville (1824) under 'Mollusca', and it is as a subcategory of this entry that the above diagnosis, albeit using the name '*Pulvinites Adansonii* DeFr.', was first given. Blainville's entry refers to the volume of plates of the same work which bears a publication date of 1826. However, even if this date is wrong and the relevant plate (pl. 88, fig. 3) had in fact already been published by the time that Blainville's entry was published, it can still not be regarded as a valid description since the plate caption uses only the vernacular name 'Pulvinite d'Adanson. (Def.)'. There is no doubt, therefore, that Blainville, 1824, is the true author of both genus and type species.

The type material has been destroyed and is represented only by rather poor photographs (Freneix 1956). Some of these, however, show muscle impressions and were presumably collected after the original diagnosis, in which it is stated that the scars were unknown, was written. The de Gerville collection topotypes in the British Museum (Natural History) clearly show muscle impressions and details of the foramen and suture. Blainville and DeFrance seem not to have been aware of these features.

The material from the upper Jurassic ('Corallien', now known to be of Kimmeridgian age—see Arkell 1956) of La Rochelle, for which d'Orbigny (1853) created the genus *Hypotrema*, was discovered in 1826 (d'Orbigny 1853) and seems first to have been referred to in the *Palaeontologie Française* (d'Orbigny 1847) under the name *P. oblonga* (*lapsus calami*). In the *Prodrôme* (d'Orbigny 1850), however, this species is not mentioned and the La Rochelle material is referred to *Pulvinites rupellensis*. Presumably the names *Pulvinites oblonga* and *Pulvinites rupellensis* applied to the same material. D'Orbigny subsequently, however (1853), noting that the foramen had not been mentioned in the original description of *P. adansonii*, decided that *Pulvinites* was no more than an ordinary *Perna* (= *Isognomon*) and that the genus was therefore invalid. It was for this reason that *Hypotrema* was erected, to encompass *Isognomon*-like forms which, like the La Rochelle material, truly had an enclosed foramen in the right valve. Since d'Orbigny's reasoning was erroneous, and since examination of de Gerville's collection or of Sowerby's (1833) plate would have proved the validity of *Pulvinites* Blainville, *Hypotrema* d'Orbigny, 1853, is an unequivocal synonym. This has been suspected by other workers (Bronn 1852; Deshayes 1864; Stoliczka 1871; Fischer 1886; Stephenson 1941; Vokes 1941; Freneix 1956). Cox (1969) re-defined *Hypotrema* and distinguished it from *Pulvinites* on three points: (i) *Hypotrema* is taller and narrower; (ii) in *Hypotrema* the byssal retractor and adductor scars touch in the left valve, and (iii) the ligamental area is arched in *Hypotrema* but straight in *Pulvinites*. Examination of a representative suite of material shows that valve profile is variable in both forms, and that the taller, narrower condition seen in some *Hypotrema* is not fully diagnostic and only of specific importance. Similarly, the ligamental area is variably straight or

arched in both forms. This leaves the relative position of the muscle scars in the left valve: in *P. mackerrowi* sp. nov., they touch in some specimens and not in others from the same population. None of these features is therefore likely to be of generic significance.

Foramelina Hedley, 1914 was erected for the newly discovered *F. exempla*. Hedley was aware of the similarity of his shell to both *Hypotrema* d'Orbigny, and to *P. argentus* Conrad, 1858. However, *Hypotrema* was rejected as a possible genus because of d'Orbigny's (erroneous) opinion that the foramen served for passage of a muscle, not a byssus as in Hedley's shell in which an uncalcified byssus was preserved. *P. argenteus* Conrad was stated to be assigned to that genus only with doubt (Hedley 1914, p. 71), and this gave him justification for establishment of his new genus. In fact, *F. exempla* is very similar to both *P. adansonii* and *P. argenteus*, differing principally in its larger size (length c.130 mm, cf. not more than 60 mm in the other two *Pulvinites*; see Table 1), and the corresponding larger number and wider spacing of the ligament pits (both of which increase during ontogeny). Apart from size, the details of musculature, profile, foramen, and suture are virtually identical in both forms and there is no doubt that they are congeneric species. Zinsmeister's (1978) reservations on inclusion of *Foramelina* in the Pulvinitidae, based on his perceived differences between the 'sub-umbonal orifice and groove' described in *Foramelina*, and the narrow suture of *Pulvinites*, are unwarranted. The two conditions are identical, and wholly different from that shown by the species which Zinsmeister calls *Melina percrassa* Tate (and which he considers a possible relative of *Foramelina*), in which the byssal slit, though deep, is both open to the anterior and located in the left valve.

All the species considered in this study are represented by at least some specimens whose muscle scars are well-enough preserved to indicate the points of insertion of the byssal (pedal) retraction muscles, as well as the adductor muscle, in both valves (text-fig. 1). These insertion points are in equivalent positions in each species, and their identity is confirmed by examination of the soft parts of *P. exempla*.

Pulvinites adansonii Blainville, 1824

Plate 72, fig. 1

- 1824 *Pulvinites Adansonii* Blainville, p. 316.
- 1826a *Pulvinites Adansonii* DeFrance, p. 107.
- 1826b Pulvinite d'Adanson DeFrance, pl. 88, fig. 3.
- 1833 *Pulvinites Adansonii* DeFrance; Sowerby, pl. 104.
- 1941 *Pulvinites auriculus* Vokes, p. 8, figs. 14, 15.
- 1956 *Pulvinites adansonii* DeFrance (partim.); Freneix, fig. A, 1-6.
- 1978 *Pulvinites antarctica* Zinsmeister, p. 567, pl. 1, figs. 1-4.

Types. Syntypes: DeFrance Coll., University of Caen, destroyed in 1944, figured by Freneix (1956), figs. 1-4. Topotypes: Gerville Coll. figured by Freneix (1956), figs. 5, 6 (incorporated with DeFrance Coll. and destroyed with them); Gerville Coll., British Museum (Natural History), BML 63618, 63619, 65685; British Museum (Natural History), BMLL 40007.

Original diagnosis. As for genus (Blainville 1824).

Emended diagnosis and description. Orbicular, or trigonal with a straight, slightly convex or slightly concave postero-dorsal shell margin. In adult, LV weakly inflated with length around 53 mm; length usually slightly greater than height; c.7-11 ligament pits on ligamental area of length c.6-11 mm; ratio of valve length to length of ligament greater than 4 (Table 1). Scars of adductor and byssal retractor muscles do not touch in LV; division of adductor scar into quick and catch portions is sometimes discernable.

Discussion. Sowerby's (1833) figure of topotypes (BML 63618, 61619) remains the best published illustration of this species, those of Freneix (1956) being of poor quality. Vokes' (1941) *P. auriculus* was distinguished from *P. adansonii* on the basis of its being 'more regularly rounded anteriorly and ventrally, and in being somewhat more produced posteriorly'. Presumably he only had DeFrance's

original figure to go on which is somewhat pointed anteriorly and not particularly produced posteriorly. In fact, Sowerby's (1833) figure shows the typical outline of *P. adansonii*, which is identical to that shown in Vokes' figures of *P. auriculus*. Zinsmeister (1978) did not consider the characteristics of *P. adansonii* when he erected his species *P. antarctica*. The holotype of his species has a slightly more orbicular outline than typical *adansonii* (not diagnostic), but the paratype is well within the limits of variation of that species.

Pulvinites argenteus Conrad, 1858

Plate 72, figs. 3, 4

1858 *Pulvinites argentea* Conrad, p. 330, pl. 34, fig. 5.

1956 *Pulvinites adansonii* DeFrance (partim.); Freneix.

Types. Conrad's types from Owl Creek, 4 km north-east of Ripley, Tippah Co., Mississippi are stated by Stephenson (1941) to be lost. He further states that specimens USNM 20667 and USNM 73635 in the National Museum in Washington (Smithsonian Institution) are good topotypes. A topotype (USNM 32741) is also illustrated (Pl. 72, figs. 3, 4).

Original diagnosis. 'Transversely subovate, compressed; perforated valve slightly concave; foramen oval, from its upper margin a channel extends to the apex; substance of shell silvery, thin; cardinal plate broad, with about thirteen radii or teeth; the lower valve presents within the appearance of two muscular impressions, the one above the other, the former striated' (Conrad 1858, p. 330).

Amended diagnosis. Orbicular, or trigonal with a straight, convex, or slightly concave postero-dorsal shell margin. In adult, LV weakly or moderately inflated with a length of around 53 mm; length equal to, slightly greater than, or slightly less than height; 10–15 ligament pits on a ligamental area of length c.9–15 mm; ratio of valve length to length of ligament less than 4 (Table 1). Scars of adductor and byssal retractor muscles do not touch in LV.

Discussion. Freneix (1956) wrongly regards this species as identical to *P. adansonii*. Although similar, the hinge plate is consistently broader for the equivalent valve length (Table 1) as was stated by Conrad in the original description. Conrad's original figure showed a particularly orbicular specimen; the more typical outline is the trigonal one figured by Wade (1926) and reproduced in Cox (1969).

Pulvinites rupellensis d'Orbigny, 1850

Plate 72, fig. 2

1847 *Pulvinitis oblonga* d'Orbigny; p. 522 (*nomen nudum*).

1850 *Pulvinites rupellensis* d'Orbigny; p. 24.

EXPLANATION OF PLATE 72

Pulvinites spp.: s = suture; f = byssal foramen; a = adductor muscle; apr = anterior pedal retractor; ppr = posterior pedal retractor.

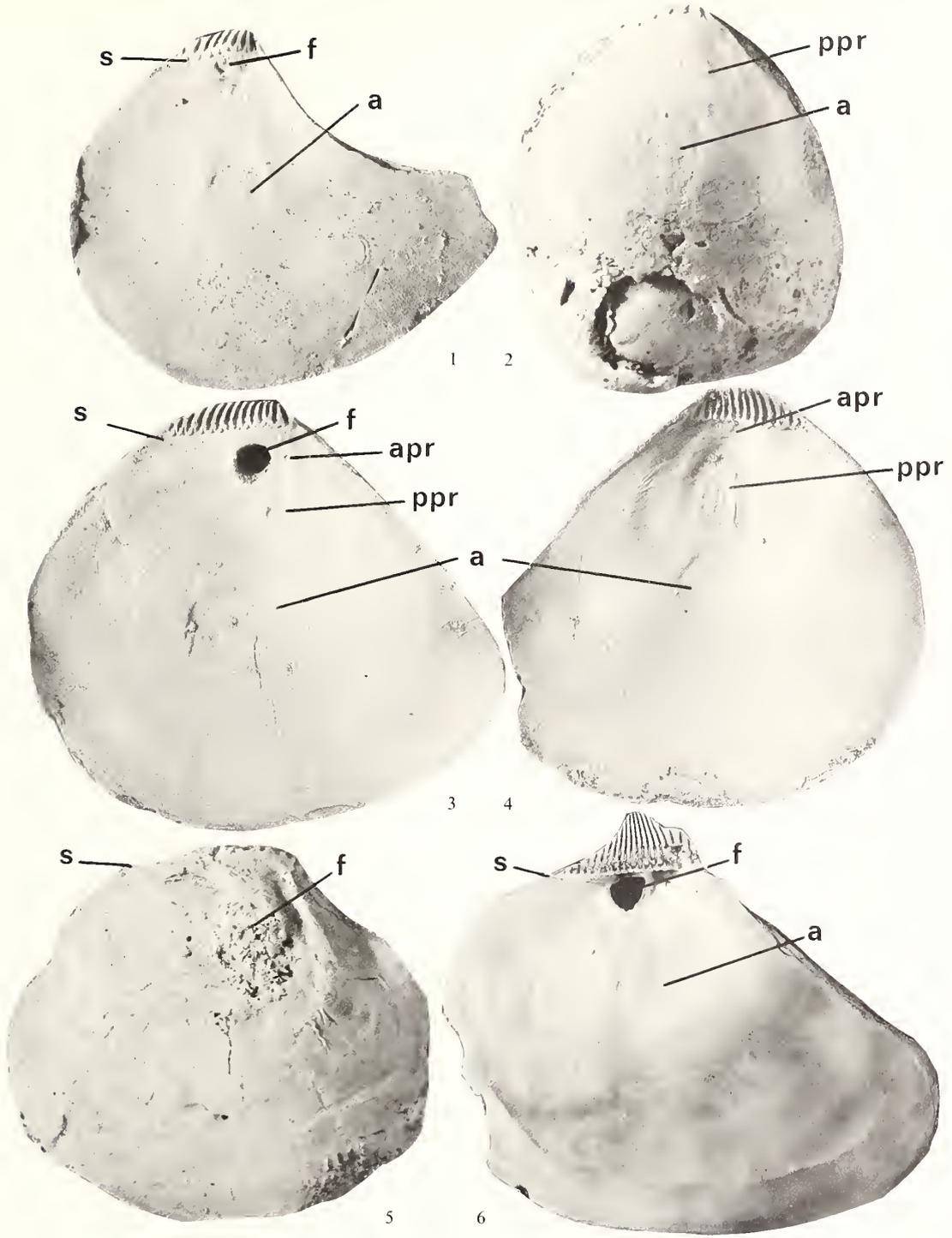
Fig. 1. *P. adansonii*, latex impression of mould of interior of right valve of topotype; Gerville Coll., British Museum (Natural History) BML 63618. $\times 1.3$.

Fig. 2. *P. rupellensis*, internal mould of left valve of topotype d'Orbigny Coll. Museum National d'Histoire Naturelle, I.P.M.—ORB 4314A. $\times 2.1$.

Figs. 3, 4. *P. argenteus*, internal views of right and left valves of hypotype; Ripley Formation, Coon Creek, Tennessee, USNM 32741. $\times 1.3$.

Fig. 5. *P. mackerrowi*, internal view of right valve from which the inner shell layer has been lost; holotype, $\times 2.7$. Wood Eaton quarry, nr. Oxford; Ardley Member of White Limestone Formation. Oxford University Museum J40183.

Fig. 6. *P. exempla*, internal view of right valve of paratype. Australian Museum, Sydney, C37004. $\times 0.5$.



PALMER, *Pulvinites*

- 1853 *Hypotrema rupellensis* d'Orbigny; p. 437, pl. 10, figs. 1–5.
 1853 *Hypotrema triangularis* d'Orbigny; p. 437, pl. 10, figs. 6–12.
 1929 *Hypotrema Rupellensis* d'Orbigny; Cottreau, pl. 20, figs. 17–19.
 1931 *Hypotrema Rupellensis* d'Orbigny; Cottreau, p. 1.

Types. Twenty-two specimens from d'Orbigny's collection are preserved in the Museum National d'Histoire Naturelle in Paris. These are now all labelled *H. rupellensis*, and come from La Rochelle (5 specimens, collective No. 4314) and Estré (17 specimens, collective No. 4314a). Estré is today a suburb of La Rochelle, called Aytré. The Paris specimens include those figured by d'Orbigny (1853) as *H. rupellensis*, and one of the figured syntypes of *H. triangularis* (labelled as *H. rupellensis*). The other figured syntypes of *H. triangularis* appear to be missing. Clearly, the material that d'Orbigny considered to constitute the second species has now been combined with that of the first. At the time of erection of the *nomen nudum*, *Pulvinitis oblonga*, d'Orbigny (1847) stated that he had only eight specimens. Whether this number constitutes the type suite of *Pulvinites rupellensis* d'Orbigny, 1850, and when the other specimens now in the d'Orbigny collection were added, are unknown. Other material from the La Rochelle region includes specimens nos. 255–258 in the collections of the Museum d'Histoire Naturelle at La Rochelle, and Oxford University Museum nos. JZ 1791–JZ 1801 from the coast at Marsilly just north of La Rochelle (author's collection). All specimens are of Kimmeridgian age.

Original diagnosis and description. 'Espèce remarquable, ovale ou oblongue, fixée sur le polypiers' (d'Orbigny 1850, p. 24).

Amended diagnosis and description. Orbicular, sub-trigonal, or, more commonly, dorso-ventrally elongated oval, with moderately or strongly inflated LV. Height in adult up to *c.*50 mm and usually much higher than long; 5–12 ligament pits on a ligamental area up to *c.*11 mm (Table 1). Adductor muscle scar in LV more dorsal than in Cretaceous species so that its dorsal edge is in contact with the ventral side of the main byssal retractor scar. Widely spread threadlike radial riblets on exterior of RV.

Discussion. The main component of growth in this species is in the ventral direction, rather than antero-posteriorly. The precise rate at which size increase in the anterior-posterior direction occurs is variable, so that some specimens are more or less symmetrically oval, whereas others have a more triangular profile like that of an egg. These latter specimens, with the shorter ligamental area (and thus less ligament pits), were separated into the species *triangularis* by d'Orbigny (1853) but in fact the range of variation is continuous. The most inflated specimens show the plane of the ligamental area rotated through 90° so that, as in *Anomia* with a similar lifestyle, the opening thrust of the ligament must have been dorsally directed.

Pulvinites mackerrowi sp. nov.

Plate 72 fig. 5; text-fig. 2

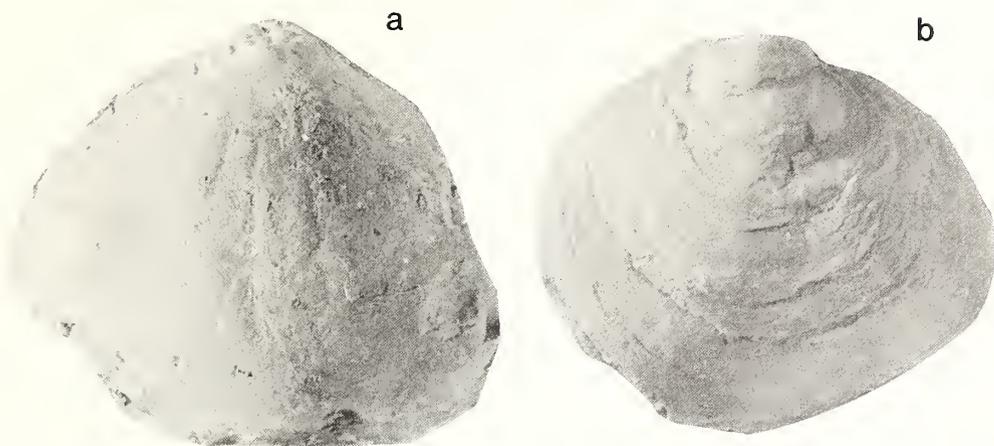
- 1969 *Nucula* sp.; McKerrow, Johnson and Jakobson, Table 8.
 1969 *Exogyra* sp.; McKerrow, Johnson and Jakobson, Table 8.
 1969 *Epithyris oxonica* Arkell (partim.); McKerrow, Johnson and Jakobson, Tables 8, 9.

Types. (Oxford University Museum Collections); holotype: J43401; paratypes: J43402–J43486, J28030, J28035–J28038, J28041.

Derivation of name. After Dr. W. S. McKerrow, who first collected large populations of the species.

Diagnosis. Orbicular to (rarely) trigonally suboval, opisthogyrate with strongly inflated LV and well-developed umbo; approximately equidimensional, with length and height up to *c.*30 mm (Table 1). Outer shell surface smooth, or with xenomorphic ornament. Scars of adductor and byssal retractor muscles in LV may or may not touch; see Table 1 for measurements.

Discussion. This species is found in the Bathonian White Limestone Formation of Oxfordshire, where it occurs commonly in beds with a high proportion of corals and other epifauna (Palmer 1979). It is often found in life position on coral fronds or brachiopods; the xenomorphic ornament is one reason why it has been overlooked in the past. The combination of strong inflation, relatively small size, and the orbicular outline distinguish it from other species.



TEXT-FIG. 2. *Pulvinites mackerowi* sp. nov., left valves of paratypes, both coated with ammonium chloride. *a*, sediment mould of internal, showing ligament pits and muscle scars, J43486, $\times 3.0$. *b*, external view, J43403, $\times 3.0$.

Pulvinites exempla (Hedley, 1914)

Plate 72, fig. 6

1914 *Foramulina exempla* Hedley, p. 71; pl. 11, fig. 6; pl. 12, figs. 7, 8.

Types. Australian Museum, Sydney, No. C37003 (holotype); C37004 (paratype).

Original diagnosis and description. 'Shell equivalve, equilateral, large, flat, discoidal, margin irregular in outline. Valves thick, composed of brittle, imbricating lamellae which both include and are overlaid by a thin membranous epidermis, where eroded of a silvery sheen, interior a dark bronze. Perforation in the right valve about 10 mm in diameter, median and subumbonal, internally with a raised margin, externally excavated as an oblique furrow ascending to the vertex. From the margin of the perforation a suture leads to the anterior extremity of the hinge plate. Byssus a dense bundle of threads about half an inch long. Hinge line about 43 mm long. Area much eroded above and traversed by about twenty-two narrow ligamental grooves which slightly radiate from above. Externally the hinge gapes when the valves are closed as in *Melina* [= *Isognomon* Lightfoot]. Adductor small, subcircular about its own breadth below the perforation. Byssal retractor rather larger than the adductor and immediately above it in the left valve. Pallial margin entire, about half an inch within the ventral margin. Height, 120 mm; length, 130 mm' (Hedley 1914, p. 71).

Amended diagnosis and description. Distinguished from other species of *Pulvinites* by its large size when adult, and by features related to size such as the greater number of ligament pits and their greater size and spacing (Table 1).

Discussion. *P. exempla* is identical to what would be expected in a scaled-up *P. adansonii*. Hedley (1914) was aware of the similarities of his species to *Hypotrema* d'Orbigny and to *P. argenteus* Conrad, but stated that reference of the latter species to the genus *Pulvinites* was doubtful. Now that the Cretaceous members of the genus are well known, it is clear that the inclusion of *P. exempla* in a genus of its own is quite unjustified.

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STEM MORPHOLOGY OF THE RECENT CRINOID *CHLADOCRINUS (NEOCRINUS) DECORUS*

by S. K. DONOVAN

ABSTRACT. The modern crinoid *Chladocrinus (Neocrinus) decorus* (Wyville Thomson) has a column which is divided into a short proximal growing region, and a longer distal portion in which the arrangement of columnals remains constant. Lumen shape is pentagonal just beneath the cup but is circular for most of the length of the stem. Articular facet morphology shows considerable variation proximally but is constant in the dististele except between nodals and infranodals, where articulation is synostiosial rather than symplexial. Cirri are quite different from the column, being elliptical with elliptical lumina and synarthrial articulation between cirral ossicles. Lumen shape is more constant than columnal outline or facet morphology, so it is concluded that the Russian system of naming morphogenera, which emphasizes lumen shape, is preferable to that of Moore (1939a), which stresses columnal outline.

It is possible to describe crinoid columnals and to group those of a similar morphology together, but the reconstruction of complete crinoid stems from dissociated ossicles is generally impracticable. New vertebrate taxa can often be described from minimal evidence (e.g. Rieppel 1982) because the number of bones in the skeleton and their arrangement remains reasonably constant throughout the group, despite the great variation in vertebrate morphology. Crinoid columns, however, differ from the vertebrate skeleton by showing great variation in the number, shape, and arrangement of units (i.e. columnals, which are broadly analogous to bones), even within members of the same genus (compare, for example, the columnals of *Colpodecrinus quadrifidus* Sprinkle and Kolata, 1982 and *C. forbesi* Donovan, 1983a). Dissociated columnals are not usually sufficiently distinct for them to be classified with confidence, and can usually only be named by inclusion within artificial morphogenera (Moore 1939a; Yeltysheva 1955, 1956).

Few detailed studies have been made of the variation shown within a crinoid column, so there is only minimal reference material available. Jeffords and Miller (1968) examined four columnal taxa for which numerous good specimens were available. Growth stages were determined by examination of internodal insertion, the relationship between columnal diameter and the number of culmina (radiating ridges on the articulation surface), and the nature of longitudinal sections. Each of the columnal types showed a distinct sequence of development. Comparison of columnal diameter with the number of culmina was shown to be a useful method of ontogenetic analysis, although good preservation is necessary for this to be applied to fossil material. Roux graphically determined the relationship between columnal height and diameter in the Bourgueticrinina (1977a) and the Millericrinidae (1978). This is reasonable if good material is available, but Ordovician columnals, for example, are often preserved as external moulds. Unless a counterpart is available, it is not usually possible to determine the height of columnals preserved in this manner.

A number of parameters were used in bivariate analyses of Devonian columnal morphospecies by Le Menn (1981); of these, graphs of articular facet diameter against columnal diameter, lumen diameter against articular facet diameter, and columnal height against columnal diameter are of the greatest general utility. Plots of columnal diameter against lumen diameter and against columnal height have proved most useful in the analysis of Ordovician columnals (Donovan 1983b, pp. 68-74).

The problem remains, however, that little detailed information is available concerning the morphology of columns in individual crinoids. In this paper the stem of the recent isocrinid *Chladocrinus (Neocrinus) decorus* (Wyville Thomson, 1864) (Breimer 1978, p. T9, footnote; Rasmussen 1978, p. T857) is considered. Reichensperger (1905) described the anatomy of this species

and determined the organization of soft tissues in the axial canal (see Jefferies 1968, p. 259, fig. 5, after Reichensperger). Roux (1977*b*), in his review of isocrinid stalk joints, described the articular facets of *C. decorus*. In the present study the whole stem of *C. decorus* is described; particularly the changes that occur between different parts of the column, so that comparison can be made when similar variations are detected in fossil columns. *C. decorus* is an articulate, and therefore in a different subclass to all Palaeozoic crinoids, but it is probable that the morphological variations which it shows are determined by stem function and that similar variations which occur in other pelmatozoans, regardless of age or systematic position, are also functional in origin.

A recent crinoid, rather than a fossil species, has been chosen for this study of gross stem morphology because of the ease with which the column can be disarticulated and sectioned, examined functionally (e.g. comparing the flexibility of the proxistele and dististele), and prepared for SEM study of the microstructure. Stem terminology follows Moore, Jeffords, and Miller (1968), Roux (1977*b*), Ubaghs (1978), and Webster (1974). Features of the articular facet of *C. decorus* are illustrated in text-fig. 3. Other terminology applied to the crinoid stem is explained in text-figs. 1, 5, and 6. Terminology of stereom microstructure follows Smith (1980). The stem is divided into two distinct skeletal systems: the column (composed of individual calcite plates called columnals) and associated cirri (jointed appendages, in this example adapted for attachment, composed of cirral ossicles).

MATERIALS AND METHODS

This study is based on two specimens exchanged with the Smithsonian Institution, Washington DC, USA. The exchange was initiated by Dr. David L. Pawson of the Department of Invertebrate Zoology at my request. Both specimens formed part of a group registered with the United States National Museum as USNM 12356 *Isocrinus decorus* and are referred to in the text as USNM 12356/1 and 12356/2. Labels attached to the specimens state '*Pentacrinus decorus* Wyv. Th. Off Havana, Cuba; Sta. 2,319-2,350. U.S. FISH COMMISSION, Steamer Albatross, 1885'. Both were damaged but the most complete specimen (USNM 12356/1) had an entire stem, broken into a number of pieces, which was disarticulated to obtain most of the ossicles shown in Plates 73-75. Ossicles from USNM 12356/2 are illustrated in Plates 73 and 76, and the 'whole' specimen in text-fig. 2. Both specimens are to be returned to the Smithsonian Institution.

Ossicles were disarticulated using Milton 2 sterilizing fluid diluted with an equal volume of water. The process was observed using a 'Wild' binocular microscope so that ossicles could be removed from the solution as they dissociated. This enabled ossicles to be selected for examination before complete disarticulation into a mass of plates. Columnals treated in this manner had all soft tissues dissolved. The ossicles were then washed and dried with a gentle heat source. Plates for examination under SEM were mounted on stubs using 'Durofix' glue or doubled-sided 'Sellotape.' Coating of stubs with 60% gold-palladium was carried out in the Department of Botany, University of Liverpool.

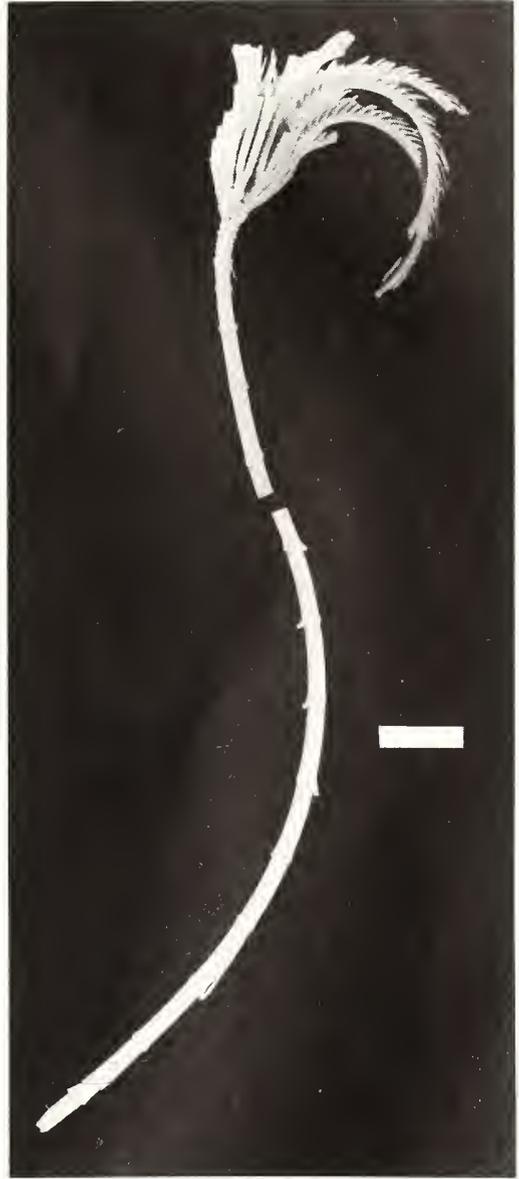
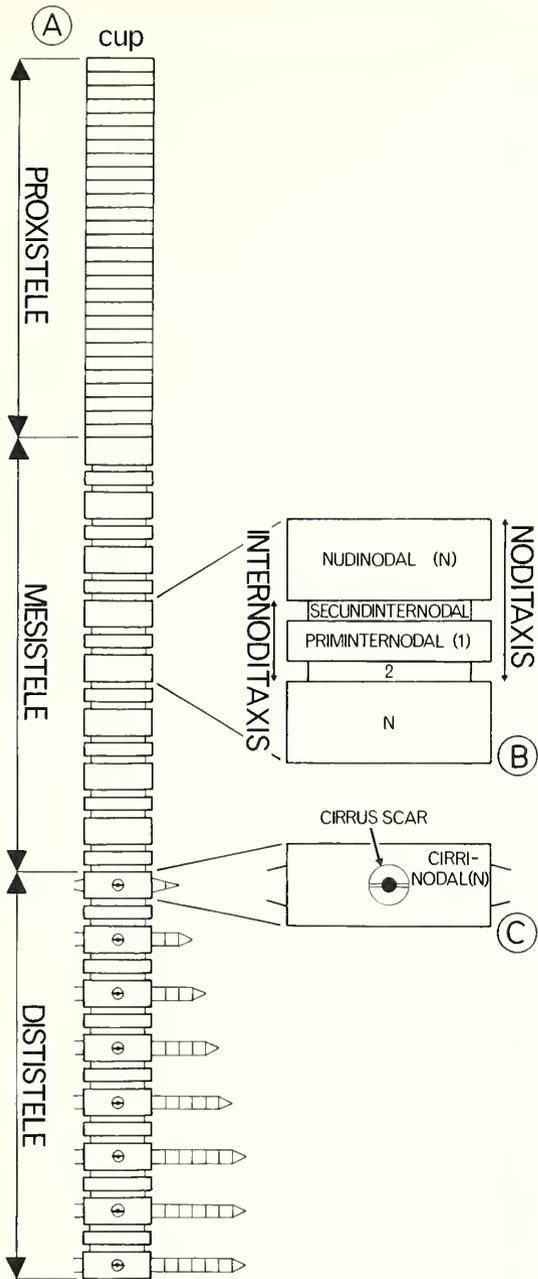
COLUMN AND COLUMNALS

The stem of *C. decorus* can be divided into two distinct regions, a proxistele (i.e. the stem proximal to the cup), and a relatively longer dististele (at least five times as long, although this is probably variable due to autotomy; Emson and Wilkie 1980) (text-fig. 1A). Stems such as this example, which can be divided into two or more morphologically distinct regions, are called xenomorphic. Using Webster's notation (1974; N = nodal, 1 = priminternodal, etc.; see text-fig. 5), and dividing the column into noditaxes (text-fig. 1B), the columnals which can be seen in the proximal region of USNM 12356/2, without sectioning, are:

(cup)-212N-212N (first cirrinodal)-212N-2123N-3231323N-3231434243N-3424341434243N (25.0 mm below base of cup)-3424341434243N-3424341434243N (54.5 mm).

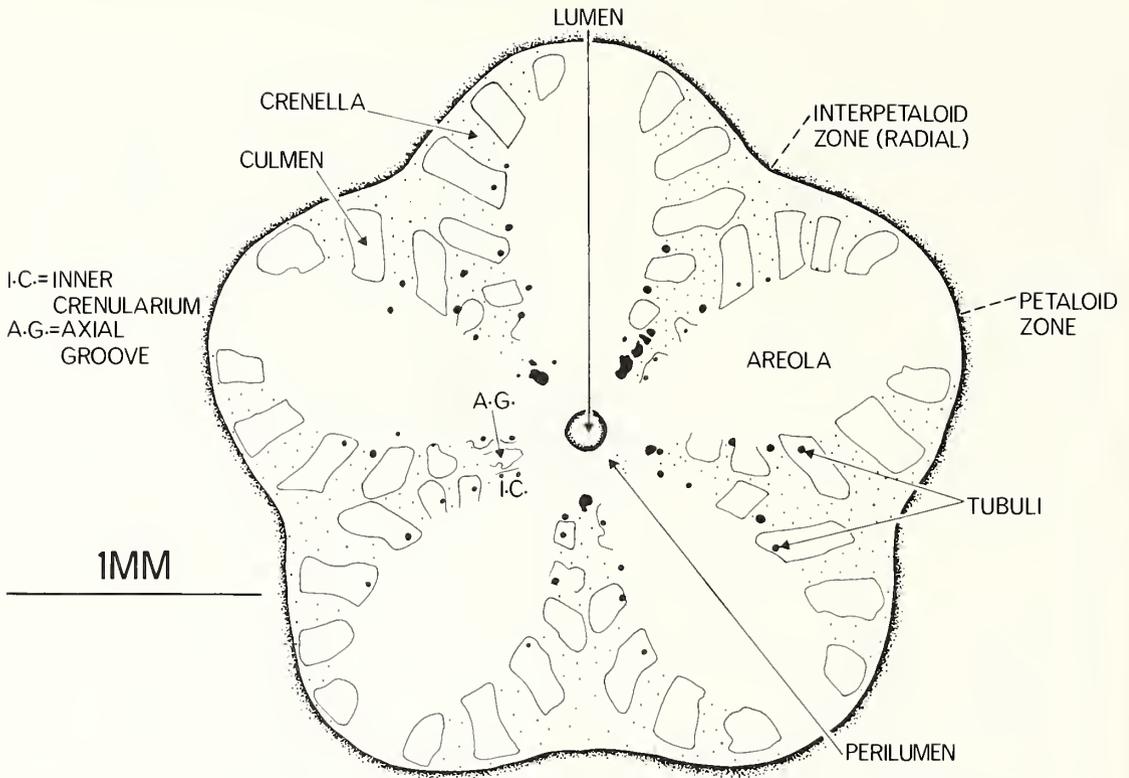
The proximal stem of USNM 12356/1 was (before disarticulation):

(cup)-?N-N-1N (first cirrinodal)-1N-1N-212N-212N-3231323N-3231323N (11.5 mm)-3424341434243N (19.0 mm)-3424341434243N (25.5 mm).



TEXT-FIG. 1 (left). A-C, hypothetical stem showing three morphologically distinct regions (only two are seen in *Chladorinus (Neocrinus) decorus*), the proxistele, mesistele, and dististele. A, schematic diagram of the complete stem; cirri (attachment structures) only occur in the dististele of this example, unlike the stem of *C. (N.) decorus*. B, part of the mesistele (middle stem). C, (*N.*) *decorus* has a column which can be divided into two distinct regions only, and is not regarded as having a 'middle stem' unlike many other crinoids. The largest columnals are nudinodals (i.e. nodals that do not bear cirri). Priminternodals are larger than secundinternodals. A taxis is a sequence of ossicles. The internoditaxis includes all ossicles (internodals) between two sequential nodals. The noditaxis comprises a nodal with associated internoditaxis. C, cirrinodal of the dististele; cirri articulate on small facets, called cirrus scars, on the nodal latera.

TEXT-FIG. 2 (right). *Chladorinus (Neocrinus) decorus* (Wyville Thomson). USNM 12356/2. The most distal part of the column, many of the cirri, and some of the arms are missing. Scale bar represents 2cm.



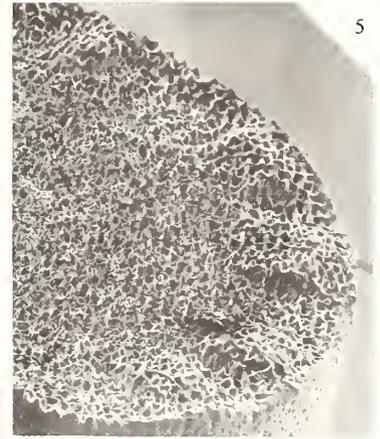
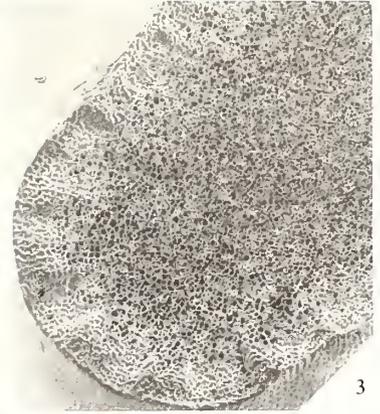
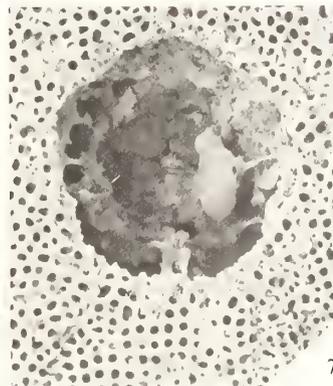
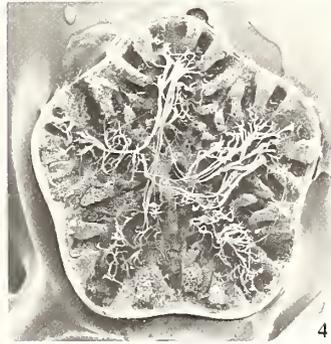
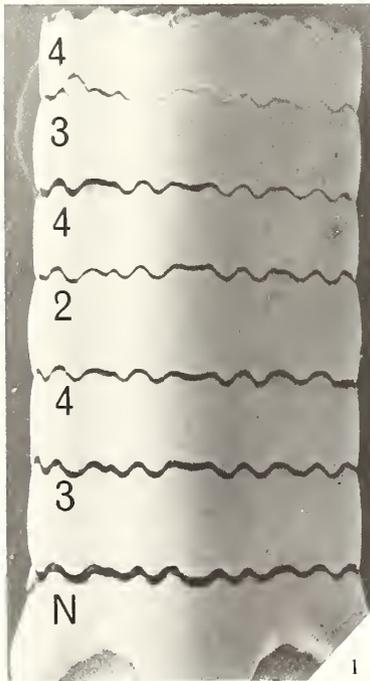
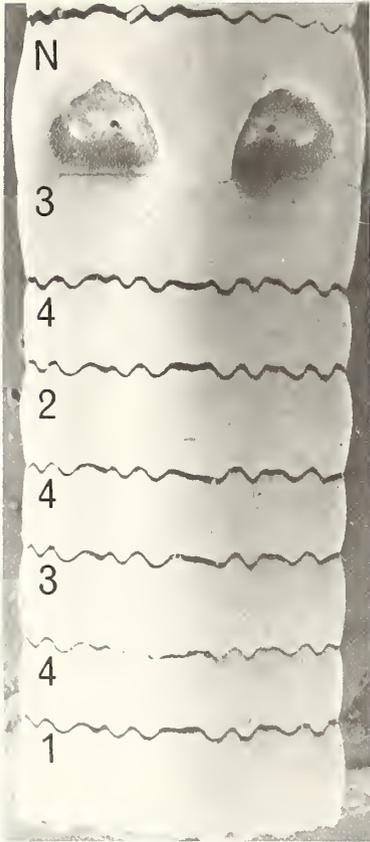
TEXT-FIG. 3. *Chladocrinus (Neocrinus) decorus*. USNM 12356/1. Proximal articular facet of a nodal (traced from an enlargement of Pl. 74, fig. 2).

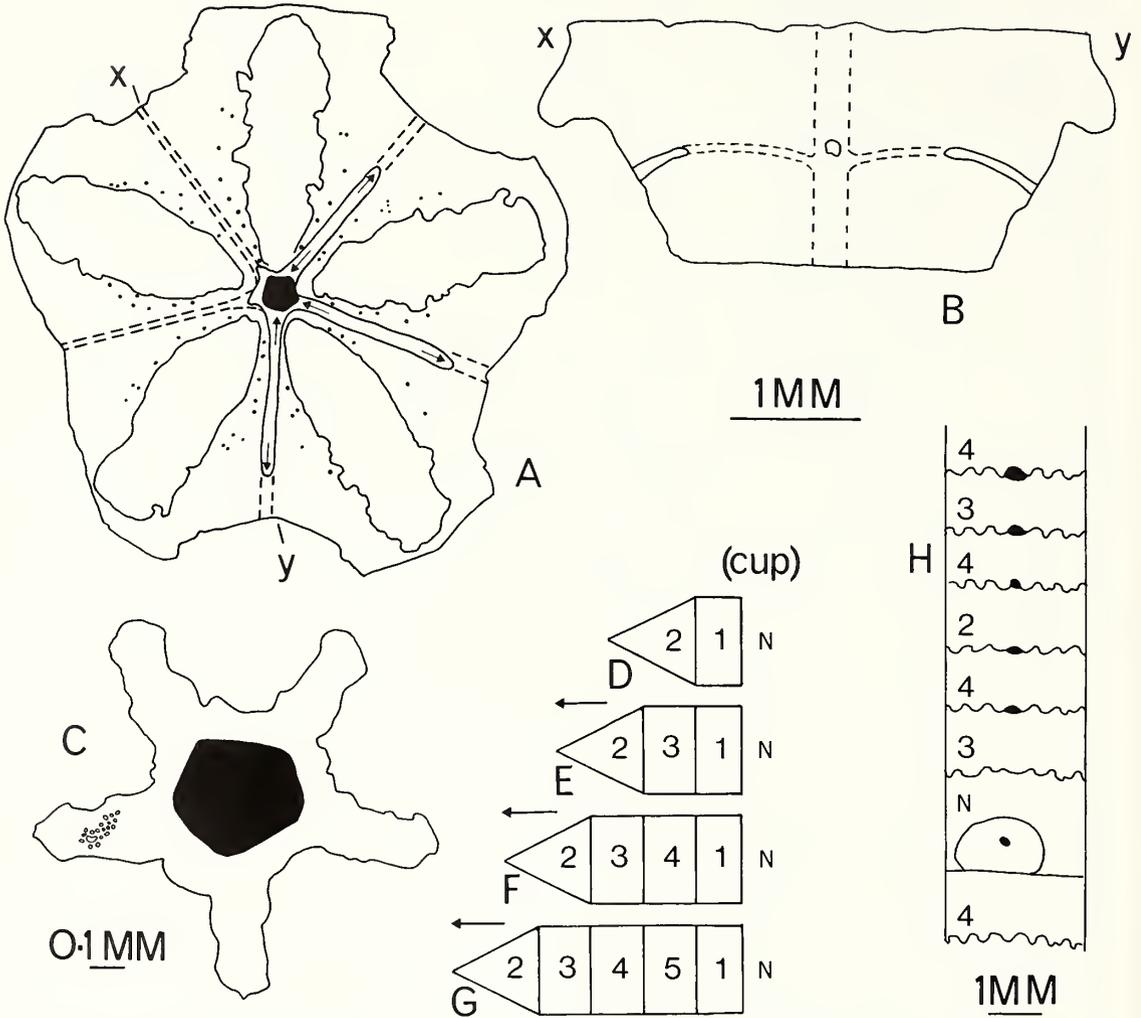
The Webster chart for USNM 12356/2 represents the entire proxistele, whereas the chart for 12356/1 is slightly less. The variation which can occur in the arrangement of columnals in the proxistele is apparent when the two charts are compared. Breimer (1978, p. T23, fig. 10) illustrates the most proximal part of the column of another specimen of *C. decorus*.

The most proximal columnals apparent are very thin. Between these and the base of the cup occur a number of cryptic ossicles (for example, three between the cup and ?N of USNM 12356/1) which are very small, pentastellate in outline, a single stereom layer thick, and extremely delicate; these are presumably incipient nodals. Similarly, internodals of the same appearance are formed in the proxistele between more mature columnals, and are also hidden from view until they are as wide as the adjacent columnals. These cryptic columnals are accommodated during their early growth stages in concave regions of the proxistele, either at the base of the cup (Pl. 73, figs. 2, 8) or in the petaloid zone of concave columnals (Pl. 74, fig. 7; the petaloid zone is the principle area of ligamentation of

EXPLANATION OF PLATE 73

Figs. 1-8. *Chladocrinus (Neocrinus) decorus* (Wyville Thomson). USNM 12356/1 (figs. 1, 2, 6-8) and 12356/2 (figs. 3-5). Scanning electron micrographs of the stem and cup. 1, noditaxis N3424341434243; the upper nodal is the more proximal, $\times 12$. 2, 7, 8, the base of the cup: 2, general view of the whole cup, $\times 6$; 7, lumen at the base of the cup, $\times 80$; 8, a single basal plate, $\times 25$. 3, 5, cryptosymplexes of distal nodal facets, $\times 56$ and $\times 120$ respectively. 4, articular facet showing ligament fibres concentrated in petaloid zones, $\times 12$. 6, poorly preserved proximal internodal (cf. text-fig. 4c), $\times 60$.





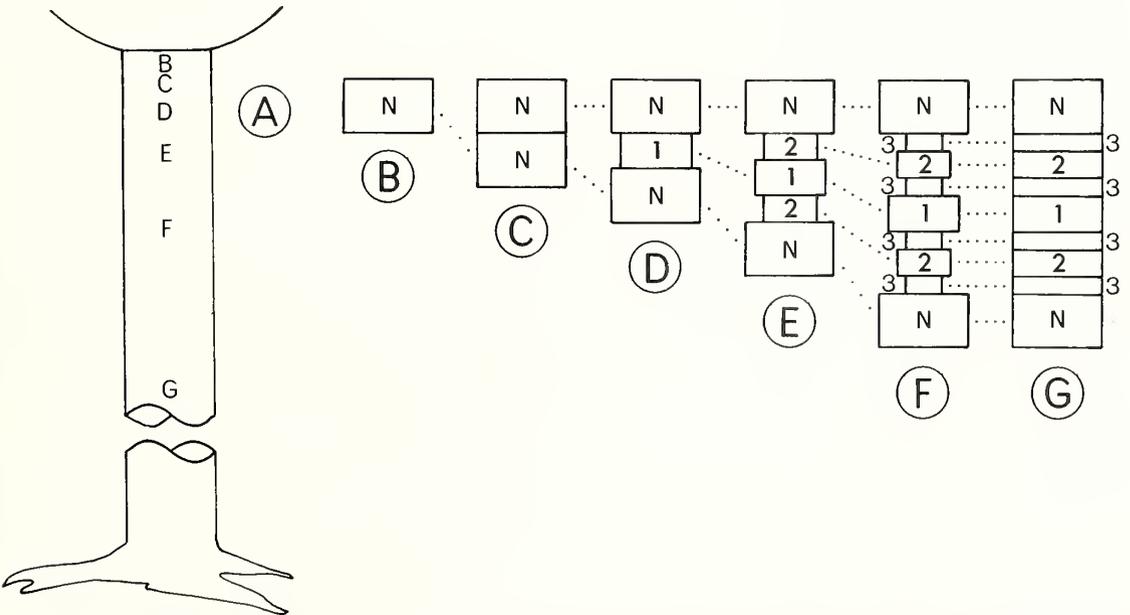
TEXT-FIG. 4. *Chladocrinus (Neocrinus) decorus*. A-C, USNM 12356/1. Transverse (A) and longitudinal (B) sections through nodals at the junction between the axial canal and cirral canals, i.e. canaliculi. A, three canaliculi cut by section, all five being completed as dashed lines. Arrows point down dip. Orientation of diagram looking distally, i.e. away from the cup. Tubuli shown as black dots and axial canal of the columnal shaded black. Irregular oval areas correspond to rectilinear stereom. B, longitudinal section x-y from A, showing the orientations of the axial canal and canaliculi (cup towards the top of the page). C, reconstruction of the facet of a proximal internodal (cf. Pl. 73, fig. 6); some stereom pores outlined (lower left). D-G, sequence of formation of new cirrals (numbers refer to order of formation, N = nodal). D, most proximal cirrus, formed of primary cirrals 1 and 2. E, cirral ossicle 3 intercalated between 1 and 2 on a slightly more distal nodal. F, cirral ossicle 4 appears between 1 and 3. G. cirral ossicle 5 is intercalated between 1 and 4. H, USNM 12356/2. Junction between the dististele (the first columnal of which is the lowest quartinternodal) and the proxistele; fossulae (between columnals) and canaliculi shaded black. A-C and H are camera lucida drawings. The longest scale bar refers to A and B.

a columnal facet). A damaged internodal in its early growth stages has been examined (Pl. 73, fig. 6) and a reconstruction of the columnal made (text-fig. 4c). A slightly more advanced columnal is also shown (Pl. 74, fig. 6). The crenularium (i.e. the alternating arrangement of ridges and grooves—culmina and crenellae, respectively—which interlock to provide a rigid suture between adjacent columnals) has yet to develop.

The proxistele is much more flexible than the dististele. This is because it is composed of thin columnals of variable height and diameter which are able to adjust to changes of orientation of adjacent columnals more easily than the thicker columnals of the dististele.

The number of internodals increases away from the cup until a maximum number of columnals in a noditaxis is attained i.e. fourteen columnals, 3424341434243N (Pl. 73, fig. 1). No further internodals are added after this configuration has been attained, and all noditaxes of the dististele have this arrangement of columnals. A theoretically perfect noditaxis would have two further quart-internodals, i.e. 434243414342434N. This is not the case, however, and the reason why this particular internoditaxis configuration is attained remains unknown. The internoditaxis (text-fig. 1b) pattern is symmetrical about the priminternodal, implying that formation of new internodals has occurred evenly throughout the noditaxis. The sequence of columnal insertion is similar (but not identical) to that of the Muschelkalk (middle Triassic) species *Encrinurus liliiformis* (text-fig. 5; Linck 1954; Raup and Stanley 1978, p. 48 fig. 3.2) and numerous other examples from the fossil record.

The first cirrinodals occur close to the bottom of the cup, although the nodals closest to the cup are nudinodals; therefore, cirrinodals develop from nudinodals. Columnal calcite is resorbed to form the axial canals (canaliculi) of the cirri which are then formed externally. The cirri are initially extremely short and non-functional as holdfast structures. The first cirri of USNM 12356/1 were composed of two ossicles only. The terminal cirral ossicle is conical and retains the same position throughout growth of the cirrus, becoming claw-like when mature (Pl. 76, fig. 5). The most proximal cirral ossicle

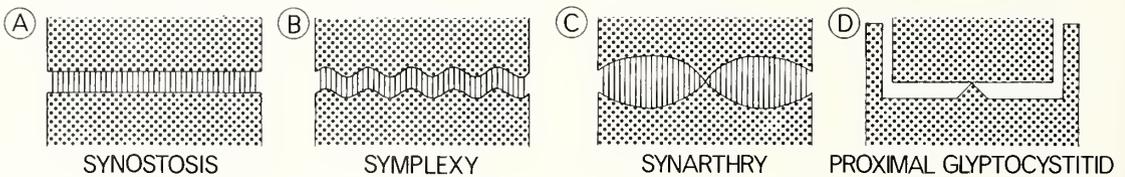


TEXT-FIG. 5. Idealized growth sequence of a heteromorphic stem, based on Raup and Stanley (1978, fig. 3.2) and Linck (1954, fig. 8). A nodal, N (B), is formed beneath the cup. A second nodal is intercalated (C). Prim- (D), second- (E), and tertinternodals (F) are intercalated between these two nodals (internodal orders labelled 1, 2, and 3, respectively). Further calcite secretion results in all columnals attaining a similar diameter (G). The parts of the stem where stages B-G occur are shown in A.

has a domed proximal facet (Pl. 76, fig. 4) which articulates on the saucer-like cirrus-scar (Pl. 74, fig. 8). The cirri most proximal to the cup do not seem to have this arrangement, but such domed proximal cirral ossicles have developed by the third cirrinodal beneath the cup in USNM 12356/2. If new cirral ossicles are added at the cirrus scar, the domed facet would have to become modified to a planar configuration as each new proximal plate is intercalated. This is unlikely, and it is more probable that new plates are formed between the first two cirral ossicles. These plates are thus of primary importance in cirrus formation, always remaining the most proximal and most distal ossicles, and are here called primary cirrals. The process of cirral ossicle formation is shown diagrammatically in text-fig. 4D-G.

The columnals of the proxistele are initially extremely thin, irregular pentastellate in outline, and lack a crenularium (Pl. 73, fig. 6; text-fig 4C). Columnals grow by increasing in thickness and becoming more regular in outline (Pl. 74, fig. 6). Such columnals are still thin and lack crenulae but show definite tubuli (broad stereom canals arranged around petaloid zones; text-fig. 3). Columnals become apparent externally only when a crenularium is developed, i.e. when the columnals are seen to articulate with adjacent ossicles. This is associated with a further thickening of the columnal and an alteration in outline from pentastellate to petaloid pentagonal (Pl. 74, fig. 1). The ossicle now shows all features of the mature, symplexial articular facet (text-fig. 6B) of all columnals of the dististele (some distal articular have a secondary synostosomal articulation, described below) (Pl. 74, fig. 2; text-fig. 3). This final stage of development is attained by further increasing the height and diameter of columnals, increasing the number and amplitude of the crenulae, and reducing the facet concavity of the early formed columnals.

The change from proxistele to dististele occurs after the last noditaxis in which adjacent columnals share five intercolumnal fossulae (Franzén-Bengston 1983). The fossulae of *C. decorus* are radially orientated, tubular passageways which lie at 72° to each other and are seen as grooves on the articular facet (Pl. 74, fig. 1), i.e. the grooves of adjacent articular combine to produce a tube. The positions of fossulae in the dististele are represented by the axial grooves. The last proximal columnal of USNM 12356/2 is the most distal nodal of the sequence described above (text-fig. 4H). It is also the first nodal to show a good synostosomal articulation (i.e. facets are smooth; text-fig. 6A) with the next distal internodal.



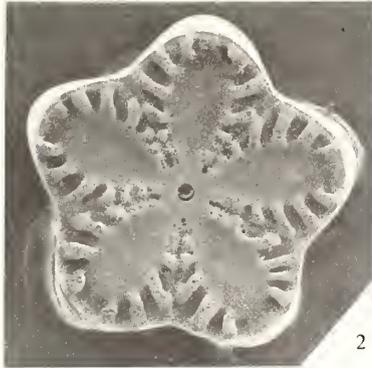
TEXT-FIG. 6. Articulations between columnals (ligaments shown as vertical rulings in A-C). A, a synostosis; adjacent facets are planar. B, a symplexy; two interlocking crenularia (text-fig. 3) composed of ridges (culmina) and grooves (crenellae). C, a synarthry; opposed faces rock on adjacent ridges. D, proximal glyptocystitid; a 'see-saw', in which a planar facet rocks on a fulcral ridge. (A-C, after Lewis 1980; D, after Paul 1968).

EXPLANATION OF PLATE 74

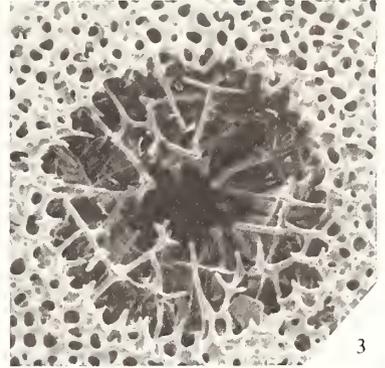
Figs. 1-10. *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson). USNM 12356/1. Scanning electron micrographs of columnals. 1, 6, 7, columnals from the proxistele: 1, articular facet, $\times 12$; 6, articular facet of a cryptic internodal, $\times 12$; 7, oblique view of a nodal facet showing the dish made by the interrays (note broad meshwork of lateral stereom which extends into the fossulae), $\times 25$. 2, proximal facet of a nodal of the dististele, $\times 12$. 3, 4, synostoses of the dististele: 3, stereom growth into the lumen of a nodal, $\times 200$; 4, nodal facet, $\times 12$. 5, 8, cirrus scars: 5, the left-hand scar encroaches on to the adjacent infranodal, the other being limited to the nodal, $\times 15$; 8, cirrus scar, showing the elliptical lumen and the synarthrial ridges, $\times 50$. 9, 10, stereom of the symplexial facet: 9, petaloid zone, $\times 50$; 10, interpetaloid zone (note tubuli), $\times 50$.



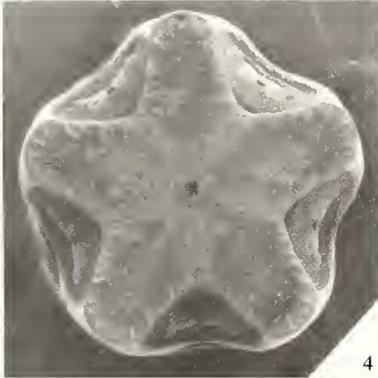
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2



3



4



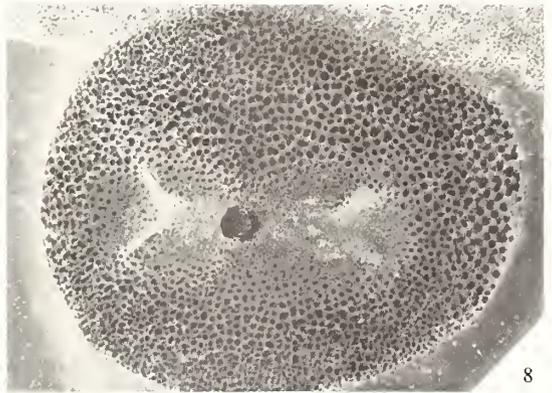
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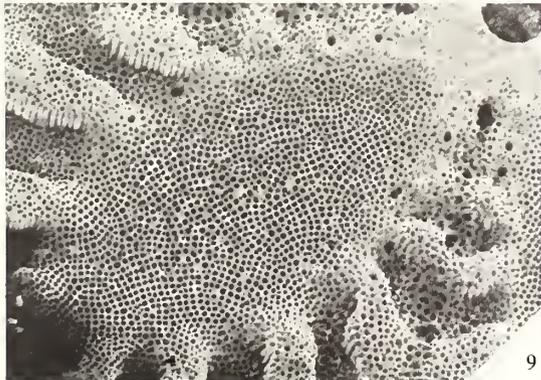
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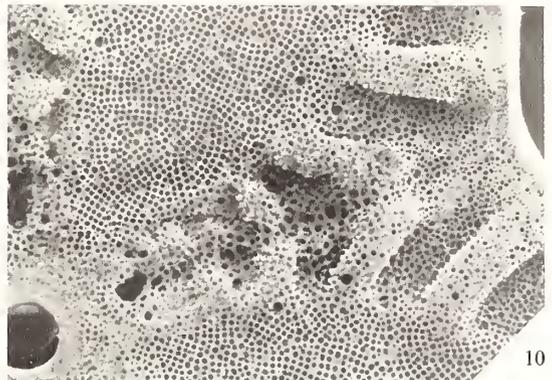
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8



9



10

The dististele is composed of noditaxes of a constant configuration i.e. 3424341434243N (Pl. 73, fig. 1). All internodals are pentagonal in outline, with well-rounded angles and sides infolded to give a flower-like appearance to the facet. Latera of internodals are gently convex. A reducing sequence of columnal heights from priminternodals to quartinternodals distinguishes the various internodal orders. The nodals are taller than the internodals, with latera that are more convex. Nodals are thus the widest columnals of the dististele. Nodals are further distinguished by having five distally orientated cirrus scars in radial positions on the lower half of the latus, i.e. they are cirrinodals (text-fig. 1C).

Almost all articularia of the dististele resemble those of Pl. 74, fig. 2 and text-fig. 3. The only exceptions are the distal facets of nodals and the proximal facets of adjacent internodals, which have a synostosomal articulation. The terminology used in text-fig. 3 follows Roux (1977*b*, p. 46) and Moore *et al.* (1968), except that the term 'large meshes' is replaced by tubuli (singular, tubulus; see explanation above). The petaloid zones are interradial.

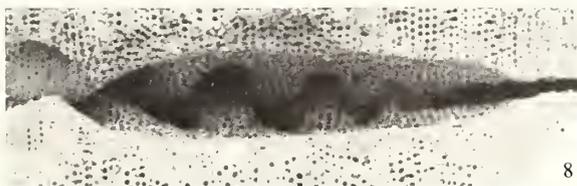
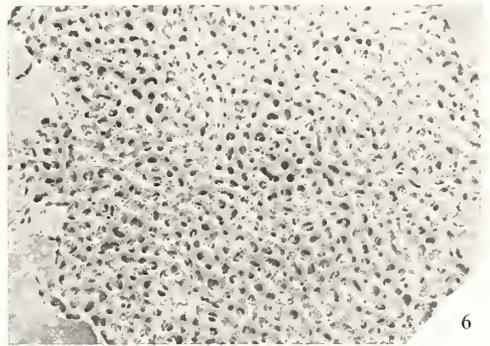
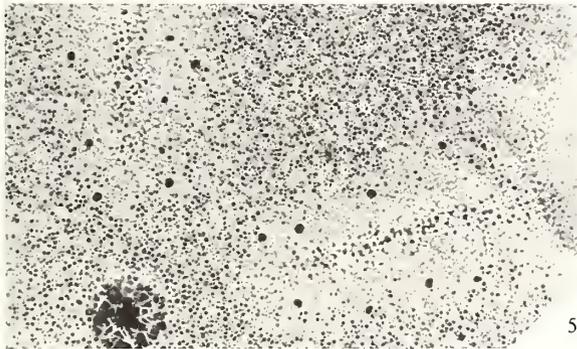
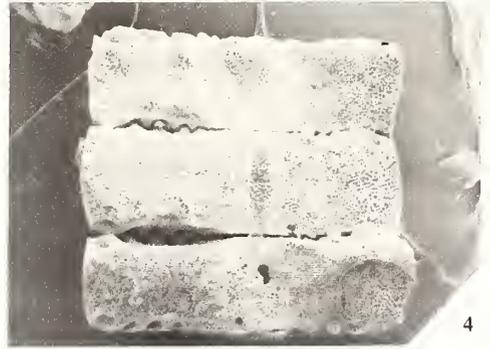
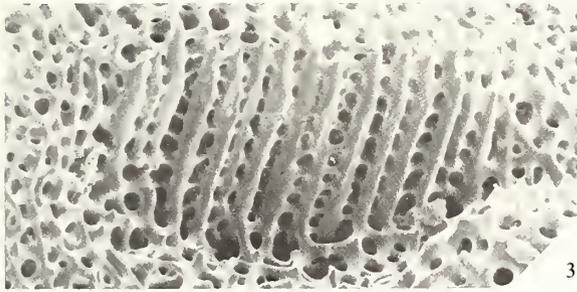
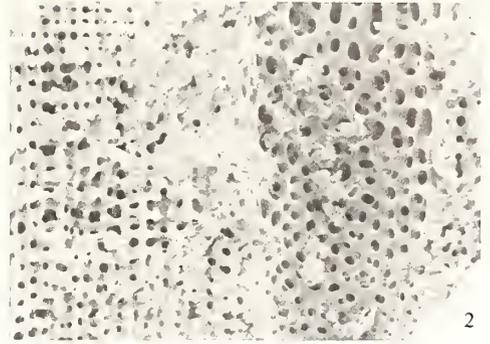
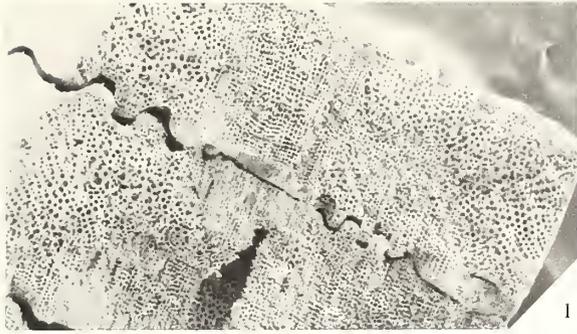
The configuration of the facets of my specimens does not agree completely with Roux's diagram of the same area (1977*b*, fig. 19); they have rectilinear stereom (Smith 1980) with diamond-shaped meshes in the five areola pits (Pl. 75, fig. 7). This is indicative of strong ligamentation in these areas. In transverse section the areas of rectilinear stereom of the columnal appear oval to pear-shaped in outline (text-fig. 4A). The areolar pits also have pear-like outlines. Nine to twelve crenulae border each petaloid zone. The tubuli form an irregular border around the areola petals but do not reach the margins of the columnal. The crenularium can be open or closed and an interpetaloid axial groove separates each pair of crenularia (Pl. 74, figs. 9, 10). Pl. 74, fig. 2 and text-fig. 3 show only areolae with open crenularia, but this is not always the case (Pl. 74, fig. 9; Roux 1977*b*, fig. 5c). Roux did not mention the possibility of open crenularia when discussing this species.

The distal articulum of each nodal, and the proximal facet of the sequential, distal tertinternodal (called the infranodal by Breimer 1978, p. T24), have synostosomal articulation facets (Pl. 73, figs. 1, 3, 5; Pl. 74, figs. 4, 5). These are secondarily modified from symplexial articulations (compare text-fig. 6A and B) by infilling with stereom (Roux 1974, p. 6) and have been called cryptosymplexes by some authors (e.g. Moore *et al.* 1968). Relict crenulae are apparent at the edge of some synostosomal articularia (Pl. 73, figs. 3, 5). It is almost impossible to break (mechanically) a column along such a stem joint; the stem will normally break through a symplexial suture, or partly through both suture and plate. Synostosomal joints therefore have extremely strong ligamentation. Such stem joints, however, are thought to be adapted for autotomy, i.e. self-mutilation as a defence mechanism (Emson and Wilkie 1980).

Lumina (singular, lumen: the intersection between the axial canal of the column and an articular facet) show little variation in shape or diameter along the whole column. The lumen at the base of the cup is pentagonal with rounded angles (Pl. 73, figs. 2, 7). This pentagonal outline is retained by columnals in the most proximal part of the stem (Pl. 73, fig. 6; text-fig. 4C) but most plates have circular lumina. For example, in USNM 12356/1 the most distal columnal with a pentagonal lumen is the second priminternodal beneath the cup. The transition from pentagonal to circular is gradual, not sudden.

EXPLANATION OF PLATE 75

Figs. 1-9. *Chladocrinus (Neocrinus) decorus* (Wyville Thomson). USNM 12356/1. Scanning electron micrographs of stereom microstructure. 1, 2, 4, 8, longitudinal section through a pluricolumnal of three internodals from the dististele: 1, rectilinear (centre) and labyrinthic stereom, the latter concentrated in the interpetaloid zones, $\times 30$; 2, rectilinear stereom adjacent to the axial canal (right), $\times 100$; 4, sequence of columnals (taxis) in section, $\times 15$; 8, section through a petaloid zone, showing the interlocking crenulae, $\times 60$. 3, rectilinear stereom of a crenula, $\times 60$. 5, interpetaloid zone of a synostosis, showing tubuli, $\times 55$. 6, stereom infilling axial canal at distal end of the most distal columnal, $\times 100$. 7, rectilinear stereom of a petaloid zone, $\times 400$. 9, stereom at the edge of a columnal, $\times 550$.



The shape of the lumen is modified in two areas of the dististele. The lumina of synostoses are partially infilled by long, spike-like, labyrinthic stereom fingers which grow into the axial canal (Pl. 74, fig. 3; Roux 1977*b*, fig. 8). This must limit the amount of soft tissue in the axial canal adjacent to synostoses (cf. Pl. 74, fig. 3 and Pl. 75, fig. 2). Such an ingrowth of stereom suggests that the axial canal can be infilled rapidly by calcite growth if autotomy occurs at a synostosomal stem joint. The axial canal of the synostosomal facet of the most distal columnal is completely filled by labyrinthic stereom (Pl. 75, fig. 6) and no suggestion of the outline of the lumen is preserved. In all other respects this columnal resembles the distal facet of any nodal of the dististele (e.g. Pl. 74, fig. 4). The axial canal is also modified in the regions within nodals in which the lateral extensions into the cirri arise (canaliculi; text-figs. 1, 4). In these regions the axial canal is pentagonal in outline, becoming pentastellate at the junction with the cirral canals.

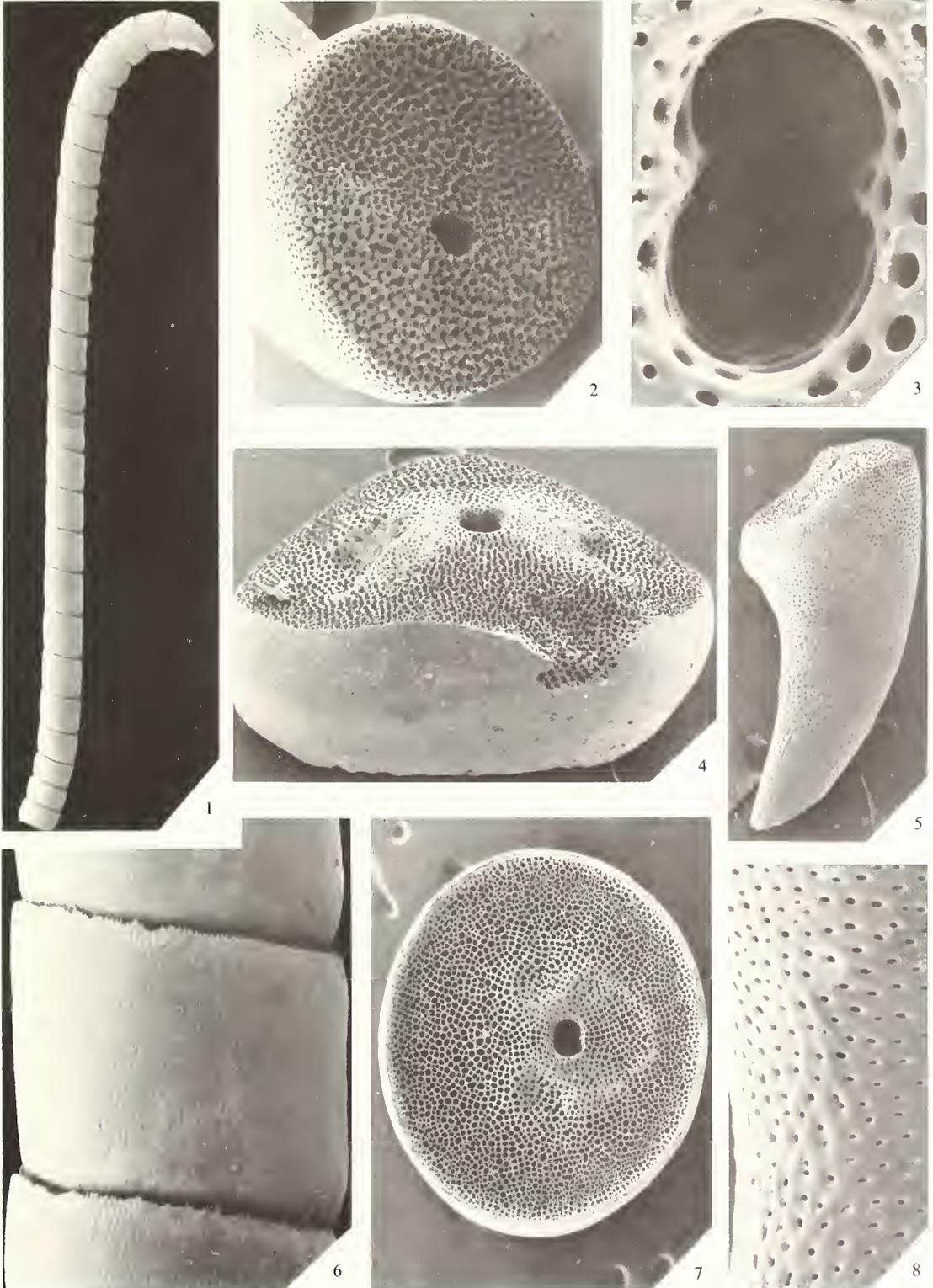
Cirri are attached to the column at the five cirrus scars which are present on each nodal (Pl. 73, fig. 1; Pl. 74, figs. 5, 8). These occur on the distal part of the latus and are orientated so that cirri always point away from the cup (Pl. 74, fig. 5; text-fig. 2; Breimer 1978, p. T24, fig. 11). Cirrus scars may be limited to the nodal or they may overlap on to the adjacent infranodal (Pl. 73, fig. 1; Pl. 74, fig. 5). They are elliptical in outline with a central, elliptical axial canal which is flanked by a pair of synarthrial articular ridges (Pl. 74, fig. 8). The ectoderm covering the column is probably continuous over the cirri.

The cirri of the proxistele have been discussed above. Cirri and cirral ossicles of the dististele are illustrated in Plate 76. An entire cirrus is approximately 17 mm long and is composed of twenty-six cirrals (Pl. 76, fig. 1). The most proximal and distal cirral ossicles (Pl. 76, figs. 4, 5, respectively) are the two primary cirrals, which were defined above. The proximal primary cirral has a domed proximal facet which fits the cirrus scar. The lumen is approximately elliptical (Pl. 76, fig. 3) but the axial canal of the cirral ossicle has two central ridges on the long sides which gives the appearance of a figure '8' to the aperture. The lumen is flanked on the articulum by two notches which articulate against the ridges of the cirrus scar. This differs from columnals with synarthrial ridges (text-fig. 6C), such as platycrinids (Moore 1939*b*) and *Ristnacrinus* (Chauvel and Le Menn 1972), in which the articulation is formed by two opposed ridges. It is, perhaps, more analogous with the 'see-saw' articulation of the glyptocystitid cystoids (text-fig. 6D; Paul 1968). The arrangement of ridge and groove is presumably more resistant (than two ridges) to a force acting to twist the cirral ossicle against the cirrus scar, e.g. eddy currents. The distal facet is approximately planar, with a slightly raised margin of stereom, so that the next distal cirral ossicle fits into it like a cup on to a saucer (Pl. 76, fig. 6). Similar articulation is shown by all cirral ossicles, except the distal primary cirral.

The proximal cirral ossicles are low but cirral height increases distally until they become slightly higher than wide (Pl. 76, fig. 1). The most distal cirral ossicles taper and are reduced in height, terminating in the claw-like, distal primary cirral (Pl. 76, figs. 1, 2, 5), i.e. cirral height is a maximum in the centre of the cirrus. The lumen becomes excentric in the middle cirrus (Pl. 76, fig. 7). The articulation surfaces are dorsal to the axial canal in this area, so that the cirrus has a preferred distal flexure. This effect is further aided by the articular facets being angled to the latera (Pl. 76, fig. 1). This excentricity and the nature of the stereom around the axial canal suggest unequal development of

EXPLANATION OF PLATE 76

Figs. 1-8. *Chladocrinus (Neocrinus) decorus* (Wyville Thomson). USNM 12356/2. Scanning electron micrographs of cirri. 1, complete, mature cirrus (proximal end at the bottom of the photograph), $\times 8$. 2, 5, 8, distal, claw-like primary cirral; 2, articular facet, $\times 120$; 5, latus, $\times 55$; 8, stereom microstructure of the latus, $\times 200$. 3, 4, proximal facet of the most proximal cirral: 3, lumen, $\times 400$; 4, oblique view of curved articular facet, slightly damaged to expose the internal stereom, $\times 55$. 6, articulation between sequential cirrals, $\times 55$. 7, facet of a cirral from the central part of the cirrus (note the excentric axial canal), $\times 55$.



DONOVAN, *Chladocrinus* (*Neocrinus*)

a contractile apparatus and a preferred flexure away from the cup, as in comatulids (Holland and Grimmer 1981). The distal primary cirral has an articular facet which is angled in the area of synarthrial articulation (Pl. 76, figs. 2, 5). The lumen is elliptical, excentric, and situated on the axis of articulation.

The five axial canals of the cirri are connected to the main axial canal of the column by curved canaliculi in the nodals (text-fig. 4A, B). The canaliculi are curved in the same direction as the preferred curvature of the cirri. It is possible that a swollen termination of nervous tissue exists in the zone where the cirral axial canals diverge. In the event of autotomy and loss of the stem distal to any nodal of the distal stem, the rapid growth of stereom is assumed to infill the axial canal up to the base of this termination.

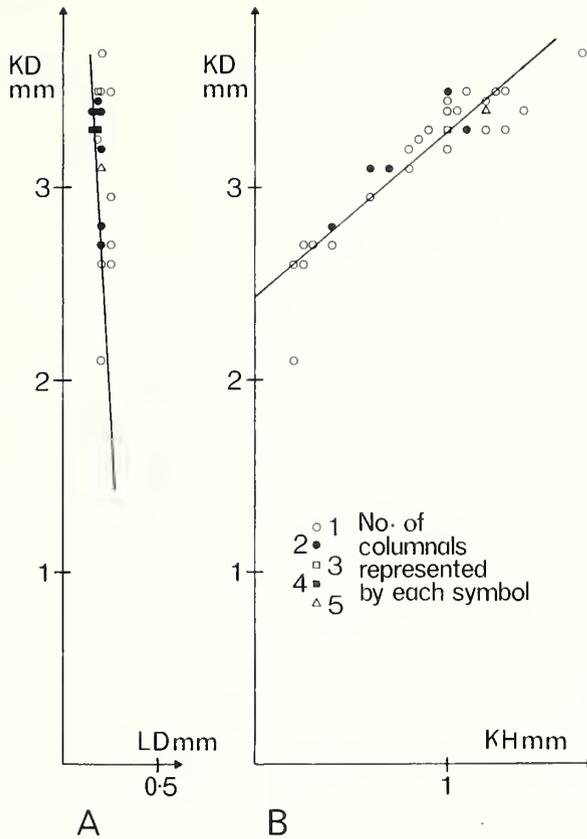
STEREOM MICROSTRUCTURE

Stereom microstructure was examined on cleaned ossicles (Pl. 75; the columnal illustrated in Pl. 73, fig. 4 shows the concentration of ligament fibres in the petaloid zones). The stereom of the petaloid zones (Pl. 74, figs. 9, 10; Pl. 75, figs. 3, 7, 8), cirrus scars (Pl. 74, fig. 8) and cirral facets (Pl. 76, figs. 2, 4, 7) is of the type called α -stereom by Roux (1970, 1975, 1977*b*). Smith (1980), in his revision of stereom microstructure, recognized two types of α -stereom: rectilinear and galleried. The stereom of the petaloid zones (Pl. 75, fig. 7) is rectilinear, although that of the culmina (Pl. 75, fig. 3) is apparently galleried. Latera (Pl. 75, fig. 9; Pl. 76, fig. 8) appear to be composed of the simple perforate stereom of Smith. The stereom of the interpetaloid zones (Pl. 74, fig. 10) is labyrinthic (= β -stereom of Roux). Longitudinal sections of pluricolumnals show that rectilinear stereom is concentrated in the region of the axial canal and of the petals (Pl. 75, figs. 1, 2, 4), while other regions are composed of labyrinthic stereom. Sectioning has also revealed the close contact between articulating crenulae (Pl. 75, fig. 8). The stereom of the synostiosal articularia (Pl. 74, fig. 4; Pl. 75, fig. 5) is a labyrinthic layer (synostiosal stereom of Roux 1977*b*, p. 47) which has overgrown a normal symplexy. Tubuli are present on these articularia, in similar positions to those of the symplexial articularia. It is probable that these canals penetrate the entire column.

BIVARIATE ANALYSIS OF COLUMNALS

Only three features discussed in previous columnal studies are considered in this section: columnal diameter (KD), columnal height (KH), and lumen diameter (LD). Features such as the length/breadth ratio of the petaloid zone show little variation, and the number of culmina varies in an irregular manner even between petals of a single articular facet (text-fig. 3; Roux 1977*b*, p. 62, fig. 19). In an attempt to generate an artificial 'palaeontological' sample, the KD/LD and KD/KH graphs (text-fig. 7A and B, respectively) are based on a random sample of columnals from the proxistele of USNM 12356/1 and the dististeles of both specimens. These graphs are somewhat artificial because the forty-one plotted points are based on information derived from only two individuals, whereas a similar collection of fossil columnals could come from forty-one individuals. The KD/LD plot (text-fig. 7A) shows that lumen diameter remains almost constant as columnal diameter increases, although there is a slight decrease in lumen diameter with columnal growth. This differs from many examples from the fossil record, in which lumen diameter increases with increased columnal diameter. The KD/KH plot (text-fig. 7B) gives a good linear grouping of columnals apart from one narrow, low columnal, an internodal from the proxistele. Such comparatively thin columnals are less likely to be preserved than the more robust, and plentiful, ossicles of the dististele. Lines of best fit have been calculated using the Bartlett method (Fryer 1966).

It is not intended to discuss here the functional morphology of the isocrinid column, which is summarized in Rasmussen (1977). Similarly, ecology of modern stalked crinoids is discussed by Macurda and Meyer (1974, 1983). Soft tissues of these specimens has deteriorated over the past hundred years and has not been studied in detail. The anatomy of modern crinoids has been reviewed by Breimer (1978).



TEXT-FIG. 7. KD/LD (A) and KD/KH (B) graphs for *Chladocrinus (Neocrinus) decorus*. KD, columnal diameter; LD, lumen diameter; KH, columnal height.

CONCLUSIONS

From the above survey of the column morphology of *C. decorus*, the following comments are made which may prove to be of general significance in all crinoids.

1. The diameter and shape in cross section of the axial canal is almost constant along the whole length of the stem. The only columnals which do not have a circular lumen are those of the most proximal part of the column and the distal facets of cirrinodals. This arrangement agrees with the intuitive conclusion that adjacent columnals must have lumina of similar morphology. It would not be expected that, say, a columnal with a pentastellate lumen would articulate with a columnal in which the lumen is circular. The shape of the axial canal, however, is not necessarily the same as that of the column.

2. Columnals change shape during growth, although their arrangement in the stem (of this example, at least) is regular. Adjacent articularia always have similar morphologies, e.g. symplexial and synostiosal articularia are never in direct contact with each other. This is true in both columnals and cirrals. Cirral facets are not necessarily the same as those of columnals from the same stem.

3. Noditaxes become regular and fixed in their arrangement of columnals, particularly away from the main growing area. Only nodals bear cirri. Only nodals and infranodals have different articularia on the same columnal, i.e. both have a symplexy on one articularium and a synostosis on the other.

4. Cirrus morphology is usually quite different from that of the associated column. Cirrus growth is different from that of crinoid arms (in which new ossicles are added at their tips) and columns, with new cirral ossicles being intercalated just distal to the most proximal primary cirrus.

5. Some columnals from the growing region (proxistele) are too small to be seen externally and can only be detected when the column is disarticulated or sectioned. Information about them will be lost in fossil pluricolumnals which are preserved as external moulds.

6. Some fine details which can be seen in *C. decorus* may be too delicate to be fossilized, e.g. the stereom infills of some axial canals (Pl. 74, fig. 3). However, good stereom is known to be preserved in some of the earliest echinoderm fossils (Donovan and Paul 1982).

The observation that axial canal outline is less variable than the columnal shape is important when assessing the relative merits of the two existing systems for naming dissociated crinoid columnals. That of Moore (1939*a*; Wright 1983) is based on both columnal and lumen outline, the name which is generated describing these features, e.g. a columnal with a pentagonal outline and a circular lumen would be placed in the morphogenus *Pentagonocyclopa*. In this system the first part of the generic name describes the columnal outline, which is presumably regarded as being more important than the lumen outline. The method of columnal naming used by Russian authors (Yeltysheva 1955, 1956) is similar, but the lumen outline is regarded as being the more important of the two parameters, e.g. the above columnal would be placed in the morphogenus *Cyclopentagonalis*. The stem morphology of *C. decorus* suggests that the latter system is to be preferred. The lumen outline and facet articulation are more important than columnal shape in columnal classification, and for reconstruction of stems from dissociated ossicles.

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ARTHROPLEURA TRAILS FROM THE WESTPHALIAN OF EASTERN CANADA

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ABSTRACT. The trace fossil *Diplichnites cuithensis* Briggs, Rolfe and Brannan, 1979 is described from the Tynemouth Creek Formation of southern New Brunswick, and is interpreted as a trail of the giant Carboniferous myriapod *Arthropleura*. The arthropod was weaving through a forest of calamites which formed a single species stand on a sheetflood deposit in an alluvial fan environment. Comparison with other *Arthropleura* trails suggests that, in this case, drier conditions prevailed, supporting the interpretation of an essentially terrestrial habit for the arthropod. This trail is the first of *Arthropleura* to be described in detail from North America, and provides evidence that the myriapod's mode of turning was similar to that of modern myriapods, and unlike trilobites. The ichnogenus *Diplichnites* should not be applied to trilobite trails.

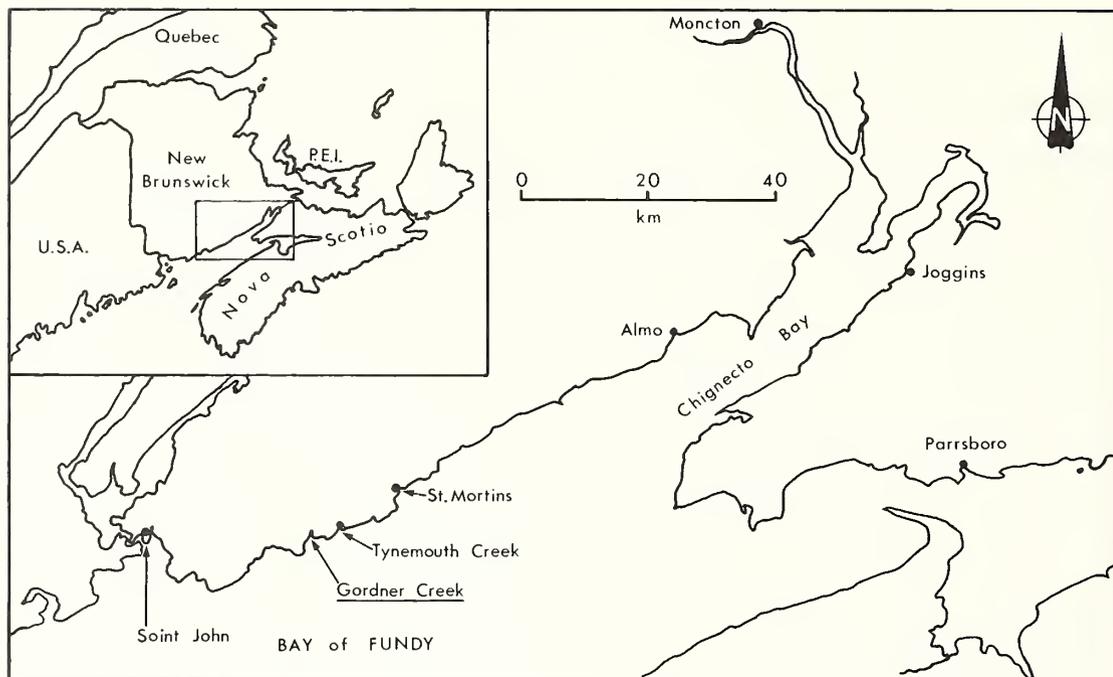
TRACE fossils can rarely be ascribed with confidence to a particular organism, but when this is possible they provide otherwise unavailable evidence of its mode of life and habitat. They can prove particularly important in interpreting the degree of terrestrialization achieved by arthropods in transitional environments, such as eurypterids (Briggs and Rolfe 1983) and the giant Carboniferous myriapod *Arthropleura*, because, unlike body fossils, traces are not transported (Rolfe 1980, p. 131). The first trails attributed to *Arthropleura* were reported and figured by Ferguson (1966, 1975) from the celebrated Joggins section (Westphalian B) in Nova Scotia (text-fig. 1). An analysis of an older Namurian example from Arran, Scotland, by Briggs *et al.* (1979) revealed details of the morphology and locomotory capability of the arthropod. Smaller arthropleurid trails are known from the Stephanian of Montceau-les-Mines, France (Langiaux and Sotty 1977a; Rolfe *et al.* 1982). The new example described here, however, is the first to preserve evidence of the arthropod making a pronounced change in direction, its path being constrained by calamite 'trees' growing in sheetflood deposits near the margin of an alluvial fan. The resultant trail provides information on the mode of cornering employed by *Arthropleura*, and its habitat. It also extends the geographical range of the trace fossil to New Brunswick, where unequivocal body fossils of *Arthropleura* have yet to be reported (Briggs *et al.* 1979, p. 287).

The trace fossil locality was discovered by A.G.P. in 1981; he and R.K.P. made a latex cast of the best-preserved part of the trail in August 1982. Unfortunately, most of the bedding plane was buried by a landslip the following winter. The trail was mapped (text-fig. 3B) using both a mosaic of enlarged photographs (cf. text-fig. 3A), and the latex cast. The position of the calamite stems was also recorded in the field. The latex cast (GSC 76665) is housed in the Geological Survey of Canada, Ottawa; sets of photographs of the trace fossil are held by the Department of Geology, University of New Brunswick, and the Hunterian Museum, University of Glasgow.

GEOLOGICAL SETTING

The trace fossil occurs in the Tynemouth Creek Formation (Plint and Poll 1982) which outcrops in the area around Tynemouth Creek, on the south coast of New Brunswick (text-fig. 1). The locality is about 200 m south-west of Gardner Creek Bridge. The trail horizon lies 28.5 m above the base of the section exposed on the shore, immediately to the west of Gardner Creek (text-fig. 1; cf. Plint and Poll 1982, fig. 2). A less well-preserved example, about 1 m long, occurs at approximately the same horizon about 100 m along strike to the north-east. The succession shown in text-fig. 2A is approximately

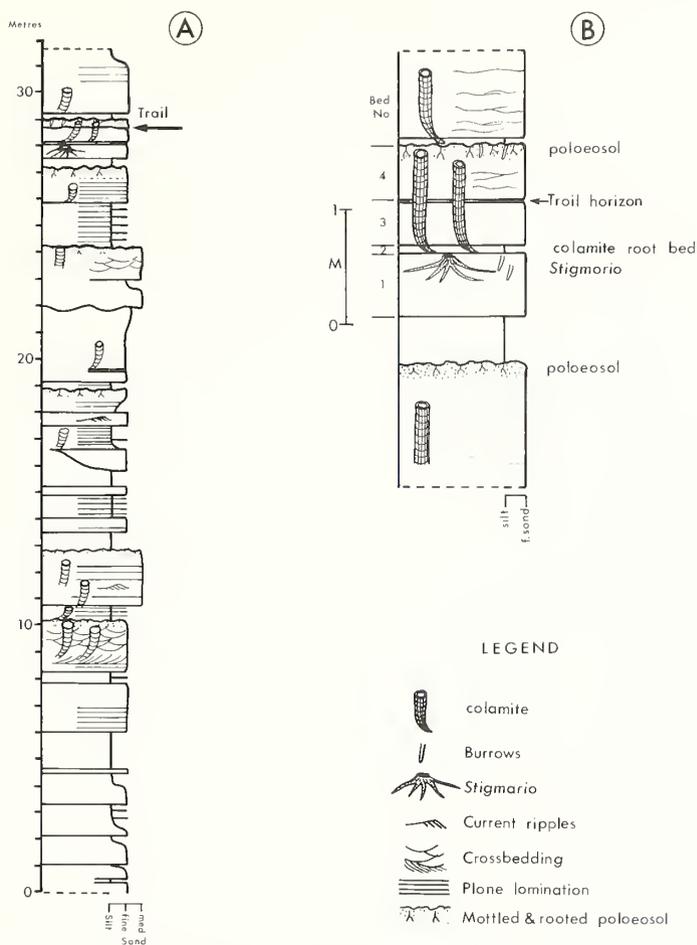
equivalent (along strike) to the lowest 30 m shown by Plint and Poll (1982, fig. 3). Spore analysis (Barss *in* Plint and Poll 1982, p. 106) indicates a Westphalian A or B age for the trace fossil; poor preservation of the spores makes a more precise age determination impossible. Two similar poorly preserved trails occur in a cliff exposure 300 m east of Tynemouth Creek (text-fig. 1). Both lie at the top of channel sandbodies beneath overbank sediments, 75 m and 90 m respectively above the base of Section 2 of Plint and Poll (1982, fig. 18). The trail horizons at Gardner Creek and Tynemouth Creek cannot be accurately correlated, but it seems likely that they are approximately contemporaneous.



TEXT-FIG. 1. Location map.

The Tynemouth Creek Formation consists predominantly of red siltstones, red and grey sandstones, and coarse conglomerates, and shows an overall upward-coarsening. Rare freshwater limestones are locally present. The sequence containing the trace fossil consists of fine, red, slightly silty, tabular sandstones, interbedded with red and green siltstones (text-fig. 2A). The sandstones are dominantly massive, but include plane and cross-laminated units, and vary in thickness from thin laminae within siltstones to units up to 2 m thick. The thicker units are usually composed of several decimetre-thick sandstone beds, separated by silt laminae. The top 10–20 cm of the thicker sandstone units are usually mottled pale green and bioturbated. Both siltstone and, in particular, sandstone beds contain numerous upright and obviously *in situ* calamite stems, up to 10 cm in diameter.

The best-preserved myriapod tracks at Gardner Creek occur within a 1.5 m sandstone which rests on 40 cm of siltstone. Bed 1 (text-fig. 2B) comprises fine, grey sandstone, containing large calamite 'tree stumps' and *Stigmara* (otherwise rare in the Tynemouth Creek Formation) which radiate to a distance of about 5 m. It was not possible to determine whether the *Stigmara* trees project above this bed, due to insufficient exposure. Bed 1 is overlain by 12 cm of siltstone (Bed 2), and 40 cm of fine sandstone (Bed 3) with numerous *in situ* calamites rooted in Bed 2. The top of Bed 3 grades up into a few millimetres of siltstone, and it is on this surface that the trace fossil is preserved. The trail surface undulates slightly but shows no evidence of sedimentary structures (e.g. ripple marks) or other trace

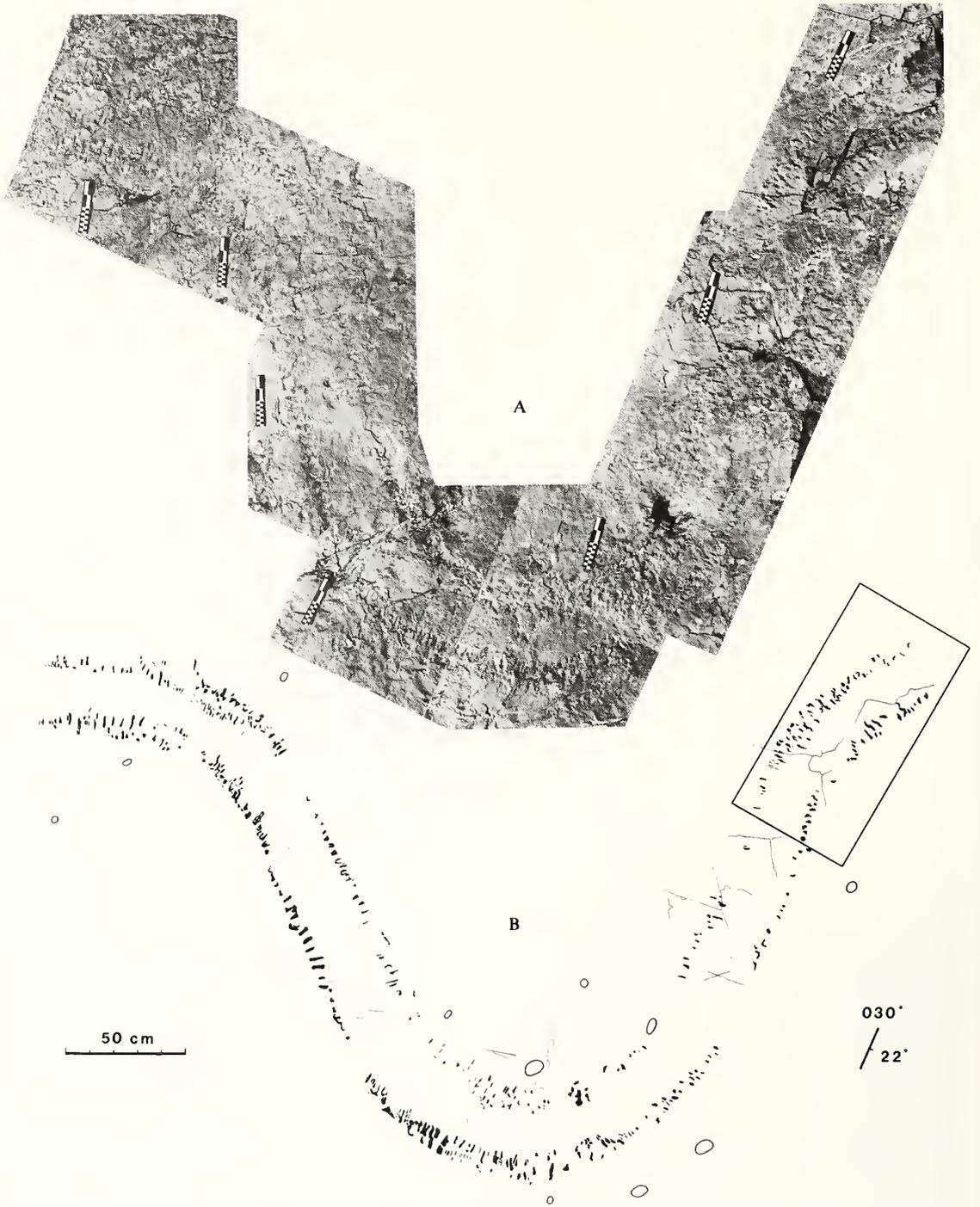


TEXT-FIG. 2. Stratigraphic sections: A, lowest 30 m immediately west of Gardner Creek, showing position of trail horizon; B, detail of beds including trail horizon.

fossils. Bed 4 comprises 50 cm of fine sandstone, at the top of which is a green-mottled palaeosol. The calamites in Bed 3 can be traced up *through* the trail horizon into Bed 4.

The sandstones are interpreted as the deposits of major sheet floods; palaeocurrents indicate a flow toward the north and north-west. The intervening siltstones were probably deposited during less vigorous floods. Thin sandstone laminae within the siltstones suggest a pulsatory flow. Green-mottled and bioturbated horizons at the top of sandstone units are interpreted as palaeosols which probably formed during prolonged breaks in sedimentation. The upper trail east of Tynemouth Creek occurs on the top of a highly bioturbated sandstone palaeosol which contains *Stigmario* and locally displays low-amplitude, straight-crested wave ripples, suggesting periodic shallow immersion. The environment, therefore, appears to have been stable for relatively long periods, favouring colonization by plants, except for short intervals of very rapid sedimentation during major floods. The depositional area was of low relief and gradient, and lay towards the margin of a major alluvial fan that was prograding toward the north-west (Plint and Poll 1982).

The large numbers of calamites, and the apparent absence of other plants (except for rare



TEXT-FIG. 3. *Diplichnites cuthensis* Briggs, Rolfe and Brannan 1979, Tynemouth Creek Formation (Westphalian A or B), 200 m south-west of Gardner Creek Bridge, near Tynemouth Creek, New Brunswick. A, photomosaic of the trail as it was in 1982 (20 cm scale bar). B, plan of the trail to show the position of the preserved tracks and calamites (represented by subcircular outlines); box marks position of text-fig 4.

Stigmaria), suggest that calamites alone were well suited to colonizing this type of sedimentary environment, and formed essentially single species forests. Pfefferkorn and Zodrow (1982) recorded similar standing forests of calamites in the Pennsylvanian of Nova Scotia; they concluded that calamites and lycopods grew where sedimentation rates were high, in areas 'that were generally not occupied by other plant groups'.

DESCRIPTION OF THE TRACE FOSSIL

The most extensively exposed trail follows a sinuous course, over 5.5 m long, between calamite stems (text-fig. 3). The trail varies between 29.5 and 36.5 cm in total width (the trails at Tynemouth Creek are 30 and 27 cm wide), and is preserved in a layer of siltstone about 5 mm thick grading into the underlying sandstone (text-fig. 2B). The siltstone parts readily along planes parallel to the bedding, and the effects of differential erosion were quite evident even after one winter (1981-1982). Thus the majority, if not all, of the imprints are preserved as undertracks (Goldring and Seilacher 1971), and in places erosion has removed short sections of the trail completely. The detailed morphology of individual imprints is not preserved (contrast Briggs *et al.* 1979, pl. 30, figs. 5, 6), and the tracks vary in size and shape. This may result from: (1) the superimposition or coalescing of two or more footfalls; (2) the water content of the sediment; (3) slight erosion during deposition of the overlying fine sand.

The maximum width (normal to the axis) of both the entire trail (36.5 cm) and of the right and left rows of tracks (*c.* 11 cm) is reached roughly at the points of maximum curvature of the trail. Here the lateral spread of right or left tracks is over twice that in the straight sections of the trail (although the number of footfalls remains the same). Thus the proportion of the total width of the trail occupied by imprints increases from less than 50 to about 60 %. The curve at the bottom of text-fig. 3A, B displays a linear density of about twenty imprints in 20 cm, i.e. about 1 per cm (text-fig. 4). There appears to be a lower density in the straight sections of the trail, but this is due to the superimposition of a greater proportion of footfalls. The pronounced elongation of some of the tracks transverse to the trail is also due to the coalescing of adjacent footfalls. A deep depression hidden in shadow (text-fig. 3A, bottom right) marks the site of a calamite which appears to lie only just on the edge of the trail. There is some equivocal evidence that its close proximity to the course taken by the arthropod may have prompted slight 'side stepping' by the limbs on the side in question. The surface has been eroded in the vicinity of the depression, however, and the critical imprints either lost or impaired as a consequence. There is no reliable evidence for the direction of progress of the arthropod (cf. Briggs *et al.* 1979, p. 278).



TEXT-FIG. 4. Well-preserved portion of the trail (down-dip; position marked on text-fig. 3B) showing increase in the lateral spread of tracks in curve (20 cm scale bar).

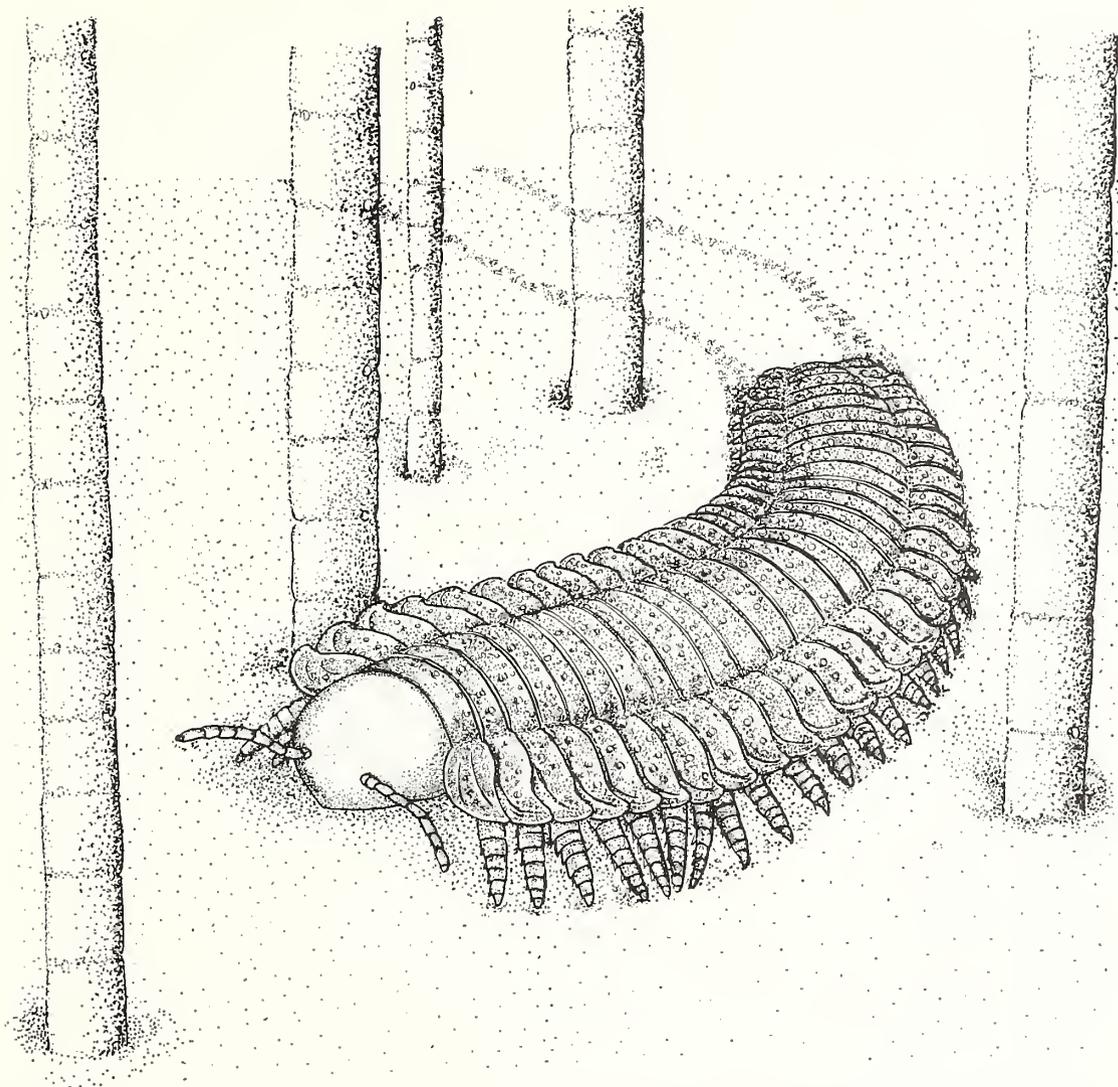
INTERPRETATION AND DISCUSSION

The trailmaker. The size of the trace fossil, the large number of regularly spaced tracks, and the sedimentary environment all indicate that the trail was made by *Arthropleura* (see Briggs *et al.* 1979, p. 278 for a fuller discussion).

Environmental setting. Following the deposition of Bed 1 (text-fig. 2B), probably by sheetflooding, a *Stigmaria* 'forest' was established. Low-energy floods deposited the siltstone of Bed 2 in which stands of calamites later rooted. A subsequent sheetflood deposited Bed 3, burying the lower parts of the calamites. A thin layer of silt accumulated on the top of Bed 3, probably during the waning phase of the flood. *Arthropleura* then walked through the area, following subaerial emergence, perhaps searching for food among the detritus carried in by the floodwaters. The cohesive nature of the mud was probably essential for preservation of the tracks which would have been easily eroded by the next flood had they been made in sand alone. Calamites in Bed 3 extend *through* the trail horizon into Bed 4. There is evidence of syndepositional scour of the sediment of the trail horizon around some of the stems. There is no sign of upward disruption of the bedding, such as would have occurred if the calamites had grown up through the trail horizon after it had been deposited. It is highly unlikely that the bed could have preserved the trail while remaining sufficiently wet to allow a large calamite to grow through it without causing disruption. It is also improbable that the calamites grew in positions flanking the trail by chance. The 'trees' were therefore standing when the trail was made. The sinuous course represents *Arthropleura* picking its way through this 'forest' of calamite stems.

Number of limbs and size. Due to the small number of complete specimens known, the ontogeny of *Arthropleura* is poorly understood. The apparent variation in the number of somites in near complete specimens (Rolfe 1969, p. 608) may indicate that development was partially anamorphic. If somites were indeed added during growth, estimating the dimensions of the trail-maker (apart from width) from the trace-fossil is not straightforward, particularly in the absence of evidence for the number of appendage-bearing somites. A reconstruction by Rolfe and Ingham (1967, p. 121, fig. 2) was based on the largest, most complete specimen known (Rolfe 1969, p. 607). Their reconstruction shows an individual 85 cm long with twenty-eight limb-bearing somites, which would produce a trail about 24.5 cm wide, assuming that Rolfe and Ingham have reconstructed the attitude of the appendages correctly (note that the magnification of $\times 0.2$ given for the same figure reproduced in Rolfe 1969, p. 609, fig. 387, is extrapolated for an animal 1.8 m long). The *Arthropleura* trail from the Namurian of Arran (Briggs *et al.* 1979) was made by an individual with only twenty-three limb-bearing somites (assuming that all the limbs were used in walking) but is none the less much wider (36 cm) than predicted by Rolfe and Ingham's (1967) reconstruction. Reducing the length of the reconstruction by five somites (assuming anamorphic development) indicates that the Arran individual was about 105 cm long. The near-complete juvenile figured by Rolfe (1969, p. 608, fig. 386), however, has at least twenty-three postcephalic (and presumably limb-bearing) somites although it is only 65 mm long. The smallest *Arthropleura* known (Rolfe *et al.* 1982, p. 426) is 29 mm long and appears to have twenty to twenty-two somites (Secretan 1980, p. 32). The data available, although unsatisfactory, therefore suggest some variability in rates of development in different examples (or species) of *Arthropleura*. The number of body segments commonly varies in living adult myriapods with more than twenty (Lawrence 1952).

Preliminary observations by John Almond (pers. comm.) suggest that two rather than one pair of limbs correspond to each of the more posterior tergites (at least) of small *Arthropleura* from Montceau-les-Mines (see Secretan 1980). If true, this does not necessarily imply a return to Waterlot's (1934) interpretation of *Arthropleura* limbs as biramous (see discussion in Rolfe and Ingham 1967, p. 118); it may, however, indicate that each tergite of *Arthropleura* corresponds to some sort of diplosegment. If Almond's observation can be confirmed and shown to apply to large arthropleurids, the basis for the reconstruction in text-fig. 5 (Rolfe 1969, p. 609) will require revision. In addition, a reconsideration of the estimate of the number of tergites in the individual which made



TEXT-FIG. 5. Reconstruction of *Arthropleura* making the trail. The detailed morphology of the head is unknown. The arthropod is depicted walking around the corner at the bottom of text-fig. 3A, B in a northerly direction (toward the left of the page). There is no evidence, however, to indicate that this was the more likely direction of progress. The position of the calamites is somewhat schematic; that in the left foreground has been displaced to one side to avoid concealing part of the arthropod. (For discussion see text; drawing by Annemarie Burzynski.)

the Arran trail (Briggs *et al.* 1979) will be necessary. Twenty-three pairs of walking limbs would then imply about half that number of tergites—an unlikely total for such a large individual.

Determination of the number of walking appendages from the trace-fossil depends on identifying two successive imprints of the same limb (i.e. evidence of a stride) and counting the number of footfalls between them (Briggs *et al.* 1979, p. 282). Unfortunately, the preservation of the present trail is inadequate to provide the necessary evidence. For the purpose of reconstruction (text-fig. 5) the number of walking limbs (twenty-eight pairs) and relative proportions of the Rolfe and Ingham

(1967) reconstruction are assumed; the arthropod is unlikely to have exceeded 102 cm in length (based on the 29.5 cm width of the straight sections of the trail).

Gait. Evidence for the gait employed by the arthropod is largely circumstantial, but provides a basis for the reconstruction (text-fig. 5). The trace-fossil provides no unequivocal evidence that the limbs on opposite sides of the body moved in phase, but an out-of-phase mode is highly improbable (Rolfe and Ingham 1967, fig. 2; Briggs *et al.* 1979). Rolfe and Ingham (1967) reconstructed a slow gait of 3.0 : 7.0 (ratio of duration of forward to backstroke; Manton 1977), i.e. with 70% of limbs in contact with the ground, suitable for pushing through the vegetation and plant debris on the coal-forest floor. Analysis of the Arran trace fossil (Briggs *et al.* 1979) revealed a gait of 5.5 : 4.5 (45% of limbs on the ground), when the arthropod was apparently unimpeded by vegetation. An intermediate pattern of 4.0 : 6.0 is adopted here (text-fig. 5) as a likely gait for the arthropod on open ground walking between calamite stems. A phase difference between limbs of 0.1 gives the most even spacing (cf. Briggs *et al.* 1979, pp. 283–284), hence *Arthropleura* is reconstructed (text-fig. 5) with ten limbs in a metachronal wave.

Mode of cornering. This trace fossil provides direct evidence for the cornering capability of *Arthropleura*. The configuration of imprints suggests that it changed direction in a fashion similar to living myriapods. The series of papers on arthropod locomotion by Manton (1977 and references therein) does not include a detailed discussion of cornering in the Myriapoda, but her observations on turning in the onychophoran *Peripatus* (1950, p. 561) explain how this is achieved. When the arthropod changes direction the body follows a turn of the head—‘the legs of both sides are displaced



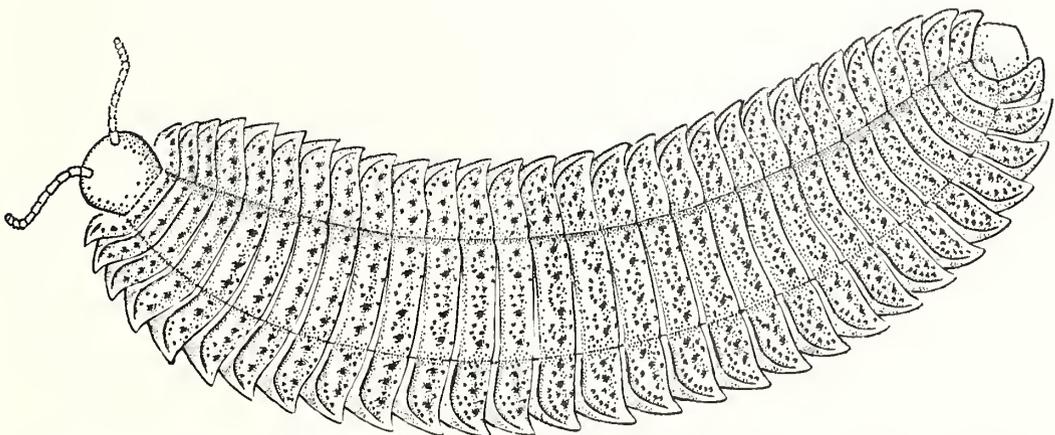
TEXT-FIG. 6. Trails of a recent millipede *Scaphiostreptus seychellarum* (130 mm long) made in wet mud, $\times 0.7$. A, curved, to show the increase in the lateral spread of tracks. B, straight. (Research and photographs by E. F. Walker.)

laterally in the direction of the turn, and the angle of swing of the legs on the outer side is increased without alteration of the pattern of the gait. If the turn is acute . . . the posterior part of the body does not follow the path of the anterior end but becomes progressively displaced towards the side.'

Although Manton's studies of the locomotion of myriapods were based in part on records made by the arthropods walking on smoked paper, very little work has been done on the traces produced by living arthropods walking on soft substrates. Some preliminary work by Rolfe (1980, p. 135, fig. 5) and Elaine Walker (Manchester University) has emphasized what a range of trails an individual arthropod can produce. Walker has provided photographs (text-fig. 6) of trails produced by the millipede *Scaphiostreptus seychellarum* which, although made by an individual a mere 130 mm long with about one hundred pairs of limbs, provides a basis for comparison with *Arthropleura*. Walker describes (pers. comm.) how the less dense part of the curved trail (text-fig. 6A) is made by the anterior limbs of the millipede as it probes forward, while the more pronounced lineation is the product of the overlapping imprints of the posterior limbs. The apparent 'doubling' of the right and left rows of prints on the corners of the *Arthropleura* trail (text-fig. 3A, B, left curve) indicates that, in this case also, the posterior part of the body did not precisely follow the anterior as the arthropod probed ahead to find a course between the calamite stems.

Briggs *et al.* (1979, p. 287) noted that the Joggins *Arthropleura* trails (Ferguson 1966, 1975) showed a wider spacing of imprints across the width of the right and left rows than the Arran example, and they considered that this suggested 'a greater variation in appendage length and flexibility in the smaller Joggins arthropleurids'. It is perhaps more likely that this wider spacing is the result of the arthropod 'probing' forward with the anterior appendages, although the figured examples from Joggins (Ferguson 1966, fig. 2; 1975, fig. 4) do not show as pronounced a change of direction as the example described here.

Lateral flexure. The deduced length of the trailmaker indicates that significant lateral flexure of the body must have taken place. Stormer (1976, p. 111, fig. 43) figured a posterior axial doublure on the tergites of *Arthropleura* extending forward about 25% of the length of each somite (a length equivalent to the overlap between tergites reported and reconstructed by Rolfe 1969, p. 608, fig. 387). Lateral flexure of the trunk would have been limited by the length of this doublure, and by the pronounced anterior keel on the paratergal folds (cf. Richardson 1959, fig. 43). Text-fig. 7 shows that sufficient curvature could be achieved within these constraints to allow *Arthropleura* to produce the trace fossil.



TEXT-FIG. 7. Reconstruction of *Arthropleura armata* displaying the lateral flexure required to produce the trail (after Rolfe and Ingham 1967, fig. 2), $\times 0.14$. Both the telson and the detailed morphology of the head are unknown.

DISTRIBUTION OF ARTHROPLEURA TRAILS

Arthropleura trails have been reported from both North America and Europe, and range in age from Namurian (Pendleian) to Stephanian B (Table 1). In addition to those figured in the literature (Table 1), large, poorly preserved trails from the Westphalian D north of Florence, Cape Breton Island, Nova Scotia, have been attributed to *Arthropleura* (Baird in Carroll *et al.* 1972, p. 54). M. Gibling (pers. comm.) also reported an example from the upper Westphalian-Stephanian Morien Group in the Sydney Basin, Cape Breton Island.

TABLE 1. *Arthropleura* trails figured in the literature

Locality	Age	Width of trail	Source
Arran, Scotland	Namurian (Pendleian)	36 cm	Briggs <i>et al.</i> 1979
Gardner Creek, New Brunswick	Westphalian A or B	29.5-36.5 cm	This paper
Joggins, Nova Scotia	Westphalian B	Up to 26 cm	Ferguson 1966, 1975
Montceau-les-Mines, France	Stephanian B	Up to 10.8 cm	Langiaux and Sotty 1977a Rolfe <i>et al.</i> 1982

The sedimentary environment of the Montceau-les-Mines trails has yet to be described (Langiaux and Sotty 1977b; Rolfe *et al.* 1982), but they appear to occur in fluvial flood-plain overbank deposits (J. E. Pollard, pers. comm.). The environment of the New Brunswick locality described here and those at Joggins and in Scotland are similar, but the New Brunswick occurrence differs in detail. The specimens at Joggins occur in a sheet sandstone that thickens laterally into a channel-filling sandstone (Bed 39/S2 of Duff and Walton 1973). The sheet sandstone possibly represents a crevasse splay that was subaerial at the time the tracks were made. The overall sedimentary environment was interpreted by Duff and Walton (1973) as an upper delta plain, characterized by laterally migrating fluvial channels with intervening low-lying floodbasins, lakes, and coal-swamps. In Arran, the well-preserved trail also occurs in a proximal deltaic environment, near the top of a fluvial channel-fill, in rippled, flaser-bedded, and rooted sandstones that were probably deposited in shallow water, close to the channel margin. The relatively good preservation of the tracks suggests that they were made subaerially, after the water level in the channel had dropped (Briggs *et al.* 1979).

The Tynemouth Creek Formation (Plint and Poll 1982) contrasts with the previously described depositional settings in that it apparently represents a much drier alluvial fan environment characterized by periodic sheetfloods across an otherwise quiescent area of relatively slow deposition. Desiccation, bioturbation, and weathering considerably modified the sediments under these conditions of intermittent deposition. Although smaller *Arthropleura* may have sought the relatively humid environment provided by hollow trunks (Rolfe 1980, p. 149), this refuge was presumably not as readily available to larger individuals such as the trail-maker in this case. The occurrence of *Arthropleura* in this environment thus provides additional evidence for an essentially terrestrial rather than amphibious or aquatic habitat (Rolfe 1969; Briggs *et al.* 1979). A specimen of an *Arthropleura* limb with *Monoletes* pollen grains attached has recently been reported from the middle Pennsylvanian Mazon Creek biota (Richardson 1980). This suggests that the arthropod may have pollinated medullosan seed ferns while brushing flood-plain scrub (Scott and Taylor 1983; Taylor and Scott 1983), thus supporting a terrestrial habitat.

TAXONOMY

Briggs *et al.* (1979) referred the *Arthropleura* trail from Arran to *Diplichmites* Dawson, 1873, pointing out that this genus was originally described from a similar non-marine environment in the Westphalian at Joggins.

The holotype of the type species, *D. aenigma* Dawson, 1873, has not been located, and the details of the specimen are not clear on the original woodcut (Dawson 1873, fig. 3). Briggs *et al.* (1979) established a new species, *D. cuithensis* for the Arran example, in recognition of the morphology of the individual tracks, and the size attained by the trace. Although in agreement with the need to maintain a morphological rather than biological basis for trace fossil taxonomy, they (1979, pp. 288-289) argued against the current tendency to extend the concept of *Diplichnites* (Seilacher 1955) to include what are obviously *marine* trails and probably the work of trilobites. In doing so they pointed out that such a restriction would not necessitate the erection of new taxa for these marine trace fossils, as a number have long been available in the literature (see Osgood 1970; Anderson 1975).

The ichnogenus *Diplichnites* has been applied to non-marine traces made by animals other than arthropleuroids and myriapods (Tevesz and McCall 1983). Savage (1971) described traces from later Carboniferous or early Permian periglacial lake sediments in Natal which he assigned to *Diplichnites* and interpreted as trails of syncarid or peracarid crustaceans. Bromley and Asgaard (1979, p. 64) referred traces from Triassic freshwater sediments in East Greenland to *D. triassicus* which they also considered to be the work of crustaceans (branchiopods). Detailed study of well-preserved examples of such traces should reveal the number of walking limbs employed by the animal. This would provide a means of distinguishing crustacean walking trails from those of the more numerous-limbed myriapods.

Dawson (1862), in his first report of the trails which he subsequently named *Diplichnites*, observed that 'their direction curves abruptly'; the original concept for the ichnogenus therefore included curved trails. The straight portions of the trail described here widen gradually into the curved portions which are characterized by a greater width of the rows of tracks (text-figs. 3, 4). In part of the trail (text-fig. 3A, B, left curve) the lateral spread of imprints in the opposing rows of tracks appears to divide for a short distance where the posterior end of the arthropod has not precisely followed the anterior. Examples of arthropod trace-fossils are known where different sections are referable to different ichnotaxa; Crimes (1970, pl. 12, figs. *a, b*), for example, figured specimens of *Rusophycus* continuous with *Cruziana*. These traces normally occur separately, however, are clearly distinct morphologically, and represent different behaviour patterns. In the present example it would seem unnecessary and counterproductive to assign the curved portions of the trail to a new ichnogenus, separate from the straight portions. It would be impossible to decide exactly where one taxon ends and the next begins! Thus the diagnosis of *Diplichnites* is emended below, as Dawson (1862, 1873) presumably intended, to include the curved parts of trails. The trail described here is referred to *D. cuithensis* Briggs, Rolfe and Brannan, 1979.

This more complete diagnosis of *Diplichnites* reinforces the observation of Briggs *et al.* (1979) that the ichnogenus should not be applied to traces attributed to trilobites. The opposing rows of imprints in trilobite traces differ in showing no obvious tendency to expand in width on corners (see Osgood 1970, for example). The articulation of the trilobite thorax does not permit significant lateral flexure. Thus unlike myriapods, including *Arthropleura* (as evidenced by this trail), the anterior of trilobites could not 'probe' forward and follow a slightly different line to the posterior.

SYSTEMATIC PALAEOLOGY

Ichnogenus DIPLICHNITES Dawson, 1873 (emended)

Type ichnospecies. *D. aenigma* Dawson, 1873, by original monotypy.

Emended diagnosis. Morphologically simple trail, up to 37 cm wide, consisting of two parallel rows of tracks (each up to 11 cm wide); width of opposed rows increasing on curves corresponding to greater lateral separation of individual tracks; each row may divide into two on acute curves; individual tracks elongate roughly normal to trail axis, spaced closely and regularly at as few as one per cm in large examples.

Diplichnites cuithensis Briggs, Rolfe and Brannan, 1979

Text-fig. 3

Type locality. Salt Pans harbour quarry, Laggan, Arran, Scotland.

Additional localities. Gardner Creek, Tynemouth Creek, southern New Brunswick, Canada.

Horizon. Carboniferous. Namurian, Pendleian Stage (E₁) to Westphalian A or B.

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NEW EVIDENCE OF A SPIRIFERIDE ANCESTOR FOR THE THECIDEIDINA (BRACHIOPODA)

by P. G. BAKER

ABSTRACT. Investigation of the microstructure of the ventral interarea of a juvenile denticulate spiriferacean assignable to *Unispirifer* reveals rod-like structures which, apart from a difference in size, are structurally almost identical with the tubercle cores of a recently discovered Aalenian thecideidine species *Mimikonstantia sculpta* Baker and Elston, 1984. The coincidence of cyrtomatodont teeth, shell resorption, and secondary fibrous shell, together with rod-like granular calcite structures ensheathed in secondary fibres, links the thecideidines with denticulate spiriferaceans. Comparison of the thecideidine shell microstructure with that of a stropheodontid strophomenide *Amphistrophia* has failed to reveal comparable microstructural elements. The new evidence indicates that the spiriferacean denticle is a structural homologue of the thecideidine tubercle and, from a systematic point of view, removes any remaining objection to the formal assignment of the Thecideidina as a suborder of the Spiriferida. The morphological similarity between thecideidines, suessiacean spiriferides, and certain davidsoniacean and productidine strophomenides is now regarded as an expression of homoeomorphy.

IN recent years attention has centred on the question of whether the thecideidine brachiopods share affinity with the Strophomenida or the Spiriferida. The main arguments in favour of derivation from strophomenide stock were advanced by Rudwick (1968) and Baker (1970) who supported the idea of descent from the Davidsoniacea. Pajaud (1970) and Grant (1972) similarly argued for a strophomenide ancestor but were in favour of derivation from productidine stock. The only strong dissent was voiced by Williams (1968, 1973) who, on the basis of shell microstructure, suggested that the thecideidines were derived from spiriferide stock and, more specifically, from the Suessiacea. The importance of neoteny in thecideidine evolution has been repeatedly stressed (Elliott 1953; Pajaud 1970; Williams 1973). If neoteny has exerted the profound influence which most workers believe to be true, the early thecideidines are likely to bear a much closer resemblance to juveniles of ancestral forms than to their adult counterparts. Unfortunately, early juveniles are not only less common than adults of the species but also more difficult to identify. After reviewing the morphological and microstructural evidence, Williams (1973, p. 466) concluded that certain persistent characters in the various thecideidine lineages were of fundamental phylogenetic significance. He identified shell microstructure as probably the most important character. The question posed, therefore, is whether the shell microstructure of early middle Jurassic thecideidines represents an ontogenetic ancestral character which through neoteny became 'frozen' into an adult shell fabric.

Work in progress on the preservation of ontogenetic relics in the shell fabrics of adult articulate brachiopods pinpoints the umbonal region of the brachial valve and, where no shell resorption has occurred, the pedicle valve also, as an area of great importance in the determination of phylogeny. However, because of the effects of neoteny, the solution to the problem of thecideidine affinity may never be reached through study of adult shell fabrics of even immediate potential ancestors. The aim of the current investigation has been, therefore, to establish whether the shell fabrics of juvenile representatives of Palaeozoic spiriferide and strophomenide genera provide unequivocal evidence of spiriferide or strophomenide affinity. Unfortunately, within the Thecideidina the shell microstructure exhibits such a bewildering variety of detail that it becomes difficult to isolate those characters which are of major significance. However, in spite of the drastic changes which affected the shell microstructure of the later representatives of the group, studies have shown that tubercles and secondary fibrous shell are characteristic and persistent features of the thecideidine shell (Baker 1970; Baker and Laurie 1978; Smirnova 1979; Williams 1973). When traced back to early representatives of the group, the tubercles are found to originate as cored structures in forms with a normal (*sensu*

Williams 1968) secondary fibrous layer. Since tubercle cores seem to be a fundamental feature of the thecideidine shell structure, persisting throughout the history of the group, it seems reasonable to assume that similar structures would be a character of the ancestral stock. The shell microstructure of juveniles of certain spiriferide and strophomenide genera was investigated with this in mind.

Registration of material. The material investigated in this study is to be housed in the British Museum (Natural History) as BB81115–81119. The BM(NH) specimens referred to in the discussion are relocated as numbers BB84702 (complete shell *ex* tubed specimens B32375D) and BB84703 (pedicle valve *ex* tubed specimens B32376B).

Preparation of material. Sufficiently large specimens were cut at the required orientation using a Logitech 'Trimsaw'. The cut face was then finished, using F800 C6 black silicon carbide abrasive powder, followed by etching for ten seconds in 5% hydrochloric acid. Small specimens were mounted in cold-setting resin before being subjected to the above preparation technique. All material selected for stereoscan electron microscopy was gold-coated before photography.

SHELL MICROSTRUCTURE

Spiriferide shell microstructure. The shell microstructure of spiriferide brachiopods has been the subject of a detailed study by MacKinnon (1974) and it is not necessary to add to his account of the general shell fabric encountered. He appears, however, to have overlooked aspects of the shell microstructure of denticulate spiriferaceans such as *Unispirifer*. This is unfortunate as investigation of the umbonal region of juveniles of lower Carboniferous specimens has provided the first clear evidence of structures in spiriferides which, apart from differences in size and orientation relative to the external surface of the shell, are otherwise identical with the tubercles found in the pedicle valve of certain basal middle Jurassic thecideidines.

The general shell microstructure of *Unispirifer* is identical with that of other spiriferacean genera studied by MacKinnon (1974). Study of the surface of the ventral interarea of well-preserved juveniles, however, reveals the presence of a parallel series of granular calcite-filled grooves aligned perpendicular to the hinge line (Pl. 77, fig. 1). Unfortunately, the umbonal regions of all the available specimens have suffered some abrasion or exfoliation so that the primary shell is nowhere complete. The best-preserved material, however, clearly shows that on the ventral interarea the striae, orientated at right angles to the hinge axis, are really in-sunk areas of primary shell which become more pronounced as the primary layer is lost (Pl. 77, fig. 2). Sections parallel with the hinge axis and perpendicular to the surface of the interarea show that the grooved areas are underlain by trough-like invaginations around which the secondary shell mosaic is deflected (Pl. 77, figs. 3, 4), indicating that the intervening ridges are an artefact produced by removal of shell material from the grooves.

EXPLANATION OF PLATE 77

Figs. 1–8. *Unispirifer* sp., juvenile specimens, north Derbyshire (precise horizon and locality unknown), Viséan limestones, lower Carboniferous. BB81117 (figs. 1–5), BB81118 (fig. 8), and BB81119 (figs. 6, 7). 1, oblique view of ventral interarea, hinge-line upper right, showing the ridges and grooves formed by removal of the majority of the primary shell layer, $\times 45$. 2, surface view showing the granular calcite-filled troughs which deflect the secondary shell fibres, $\times 80$. 3, transverse section, parallel with hinge axis, through ventral interarea to show detail of the way in which the granular calcite filling a trough deflects the secondary shell fibres, $\times 400$. 4, exfoliated region, same orientation as fig. 3, showing detail of a trough from which the granular calcite has been removed, $\times 250$. 5, oblique view, ground surface top right, to show the rod-like (accentuated by etching) nature of the granular calcite body occupying the trough, $\times 250$. 6, section parallel with surface of ventral interarea showing the granular calcite, together with traces of a gross pseudo-fibrous mosaic, of a denticle and its associated core in longitudinal section, $\times 400$. 7, detail of the granular calcite of the denticle core in fig. 6, location as indicated, $\times 3000$. 8, surface view of ventral interarea showing detail of primary layer (left) overlying a denticle core, and the fibrous secondary shell (right) adjacent to it, $\times 800$. Stereoscan photomicrographs.



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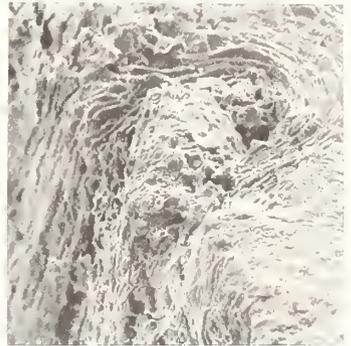
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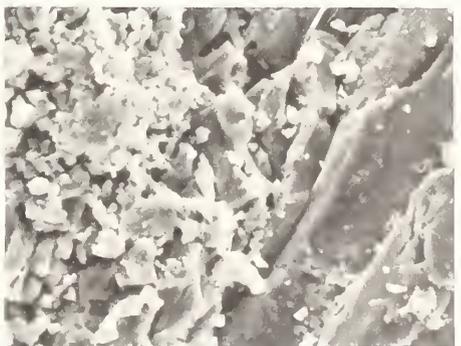
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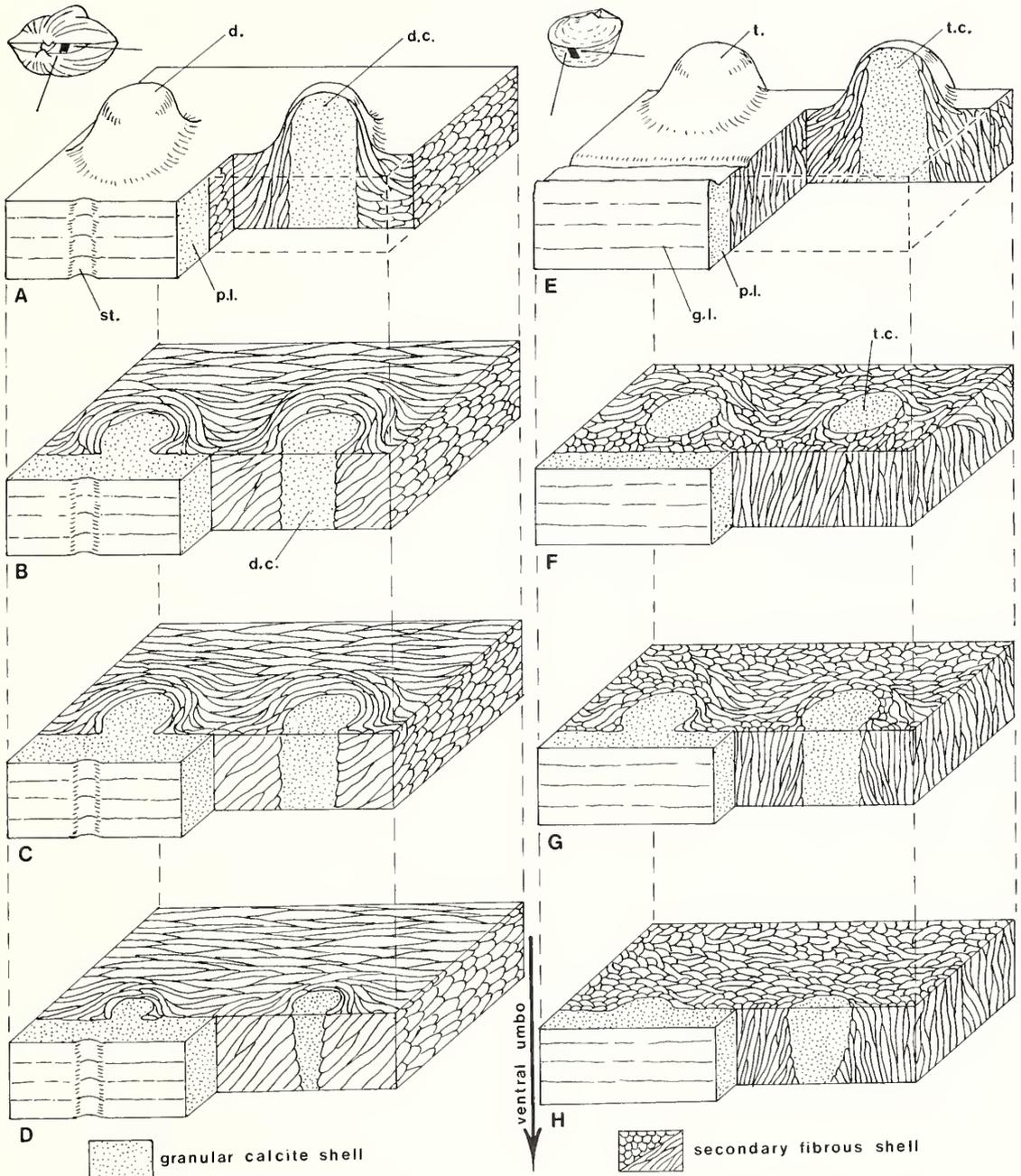
Specimens in which the structures are partially exfoliated (Pl. 77, fig. 5), and sections parallel with the surface of the interarea (Pl. 77, fig. 6), show that the troughs are occupied by rod-like bodies of granular calcite approximately 80 μm in diameter, whose outer surface remains in contact with the primary layer along their length (text-fig. 1B-D). Longitudinal sections through the rod-like bodies (Pl. 77, fig. 6) show them to be continuous with the denticles developed along the hinge margin. Although the shell material of the denticle core is clearly granular calcite (Pl. 77, figs. 7, 8), a gross fibrous mosaic appears to be discernible (Pl. 77, fig. 6) and is discussed later. The in-sunk condition of the denticle cores of *Unispirifer* is apparently different from that of the upper Devonian *Tenticospirifer* whose denticles were depicted by Williams and Rowell (1965, p. H94, fig. 100C, E) as forming denticular ridges on the surface of the interarea.

Thecideidine shell microstructure. The presence of cored tubercles in both valves of the shell of *Moorellina granulosa* (Moore) has been demonstrated by Baker (1970). The tubercles of the brachial valve were shown to have granular cores aligned almost perpendicular to the primary shell layer, whilst those of the pedicle valve had cores of conically arranged fibres aligned almost parallel with the inner surface of the primary layer (Baker 1970, p. 91, text-fig. 6). Williams (1973), in his detailed and comprehensive study of Recent and the majority of fossil thecideidine taxa, demonstrated that the evolution of the group was characterized by the neotenus suppression of the fibrous secondary layer; he identified the main onset of the sporadic secretion of secondary shell as a late Jurassic or early Cretaceous event. The recent discovery of a new genus (Baker and Elston 1984) clearly shows that in one stock at least the suppression of secondary shell was well advanced by basal middle Jurassic times. *Mimikonstantia sculpta* possesses cored tubercles and those of the brachial valve have granular calcite cores (Baker and Elston 1984, pl. 71, fig. 2) almost identical with those found in *Moorellina granulosa*. The tubercles of the pedicle valve of *Mimikonstantia sculpta*, however, have attenuated granular calcite cores (Baker and Elston 1984, pl. 71, figs. 6, 7) approximately 40 μm in diameter, in sharp contrast with the fibrous cores of *Moorellina granulosa* although their orientation approximates even more closely to an alignment parallel with the primary layer (text-fig. 1F-H). A significant difference between the shell fabric of *M. granulosa* and *Mimikonstantia sculpta* is that in the latter species the secondary fibrous shell layer is greatly reduced in thickness and is underlain by granular calcite. In this respect the shell of *M. sculpta* very closely resembles that of Cretaceous genera such as *Thecidiopsis*.

Strophomenide shell microstructure. Laminar shell (Williams 1968) is, with few exceptions (Williams 1970), a fundamental character of the strophomenide shell although, as Williams concluded (1970, p. 339), the strophomenides must have evolved from fibrous-shelled ancestors. It was important therefore, because of the possibility of a pedomorphic origin of the thecideidine shell fabric, to examine the shell microstructure of certain juvenile strophomenides to try to ascertain whether any of the characters could be correlated with those observed in the thecideidine shell. The discovery of the granular calcite core in the denticles of the spiriferacean ventral interarea necessitated an investigation of the interareas of stropheodontid strophomenaceans, in order to establish whether the microstructure of the stropheodontid denticle exhibited characters correlateable with the thecideidine tubercle. Horizontal and transverse sections through the ventral interarea of an upper Silurian juvenile *Amphistrophlia* show that the denticles are cored structures (Pl. 78, figs. 1, 2). Like pseudopunctae, however, the denticles have a core of crystalline calcite enveloped in typical laminar shell in which the laminae are deflected distally (Pl. 78, figs. 3-5). The denticles, therefore, appear to originate in the same way as pseudopunctae and, in view of the distribution of the occurrence of pseudopunctae throughout the Strophomenida, may be regarded as modified pseudopunctae.

DISCUSSION

If the thecideidines arose neotenusly (Elliott 1953; Pajaud 1970; Williams 1973) or pedomorphically (Williams and Rowell 1965), the validity of conclusions drawn from comparison of morphological



TEXT-FIG. 1. Exploded block reconstructions (not to scale). A-D, *Unispirifer*, small section of the ventral interarea (location as indicated) of a juvenile to show the relationship between the primary shell layer and the denticle cores. E-H, *Mimikonstantia*, small section of the free ventral wall (location as indicated) of the pedicle valve to show the relationship between two comparable tubercle cores and the primary shell layer. d., denticle; d.c., denticle core; g.l., growth line; p.l., primary shell layer; st., striation; t., tubercle; t.c., tubercle core.

characters may be considerably weakened. There is also an explanation other than genetic relationship for the morphological similarity between thecideidines, davidsoniacean strophomenides, and suessiacean spiriferides. Work by Cooper and Grant (1974) on the beautifully preserved reef-associated Permian faunas of West Texas showed that many of the Permian forms which most closely resemble thecideidines were an abundant element of patch reef faunas. Other studies (Baker 1981, 1983) established that middle Jurassic thecideidines were characteristically associated with patch reefs or coralliferous debris adjacent to patch reefs. Among the brachiopods there is a clear correlation between typically conical pedicle valves, loss of pedicle, complete delthyrial covers, weakly convex brachial valves, and the association with reefs. In short, the characters may be regarded as a response to environmental pressure, a view which is confirmed by the characteristic morphology of richthofenid brachiopods and rudistid bivalves. Williams (1973) drew attention to the danger of ascribing genetic significance to characters of convergent origin. It now seems probable that the morphological similarity between davidsoniaceans, suessiaceans, and thecideidines is environmentally induced; in which case, the davidsoniacean and suessiacean genera previously regarded as genetic relatives of the thecideidines are nothing more than heterochronous homoeomorphs. Therefore, in attempting to trace affinity, attention must be focused on characters which are likely to be less susceptible to environmental pressure.

Although morphological comparison is suspect, there are certain characters which appear to be so fundamental to thecideidines and their ancestral stock that none of the caenogenetic changes contributing to the emergence of the thecideidines (Williams 1973, p. 469) was sufficiently profound to be able to mask them. Jaanusson (1971) noted that brachiopod teeth were either deltidodont or cyrtomatodont, and that with only two exceptions forms with deltidodont teeth did not acquire the ability to use resorption for the construction of their shells. This frequently overlooked observation has profound implications for any proposed strophomenide (deltidodont) line of descent because the ability to resorb shell material is of such crucial importance for the construction of thecideidine (cyrtomatodont) shells that it is almost certain to be a capability shared by their immediate ancestors. Similarly, tubercles are such a persistent feature of the thecideidine shell that they should, together with fibrous secondary shell, be traceable back to the ancestral stock.

Baker (1970) concluded that a better knowledge of the Triassic genus *Thecospira* was critical to an understanding of thecideidine systematics. Three significant contributions (Dagis 1973; Williams 1973; MacKinnon 1974) were soon forthcoming and it is perhaps unfortunate that they served only to polarize still further the views already held. Dagis (1973) supported the views of Rudwick (1968,

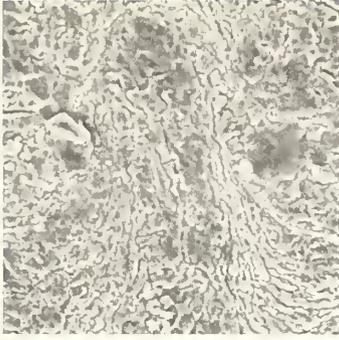
EXPLANATION OF PLATE 78

Figs. 1-5. *Amphistrophia funiculata* (M'Coy), juvenile specimens, Wren's Nest, Dudley, Much Wenlock Limestone Formation, upper Silurian. BB81115 (figs. 1, 4, 5), BB81116 (figs. 2, 3). 1, transverse section through hinge area showing crystalline calcite denticle core in longitudinal section, flanked by laminar shell, $\times 400$. 2, horizontal section through hinge area showing crystalline calcite denticle core in transverse section, flanked by laminar shell, $\times 1000$. 3, horizontal section through lateral region showing crystalline calcite taleola in transverse section, flanked by laminar shell, $\times 1000$. 4, transverse section through the shell showing laminar shell deflected by a taleola, $\times 400$. 5, detail of laminar shell in transverse section, $\times 1000$.

Figs. 6-8. Aff. *Moorellina*. BB84702, Dundry Hill, Bristol, Inferior Oolite (precise horizon and locality unknown). 6, brachial view, showing striations on ventral interarea, $\times 15$. 7, angled view (tilt angle 25°) of ventral interarea with ridge and groove structure perpendicular to hinge axis, $\times 35$. 8, part of ventral interarea showing detail of ridge and groove structure, and granular nature of the shell, $\times 400$.

Figs. 9-12. Cf. *Moorellina*. BB84703, Dundry Hill, Bristol, Inferior Oolite (precise horizon and locality unknown). 9, angled view (backward rotation 50°) showing row of small tubercles along hinge-line, $\times 12$. 10, part of hinge-line showing tubercles in more detail, $\times 100$. 11, broken hinge tubercle showing its apparently granular structure, $\times 1000$. 12, surface view of part of hinge tooth showing clearly defined fibrous structure, for comparison with hinge tubercle in fig. 11, $\times 1500$.

Stereoscan photomicrographs.



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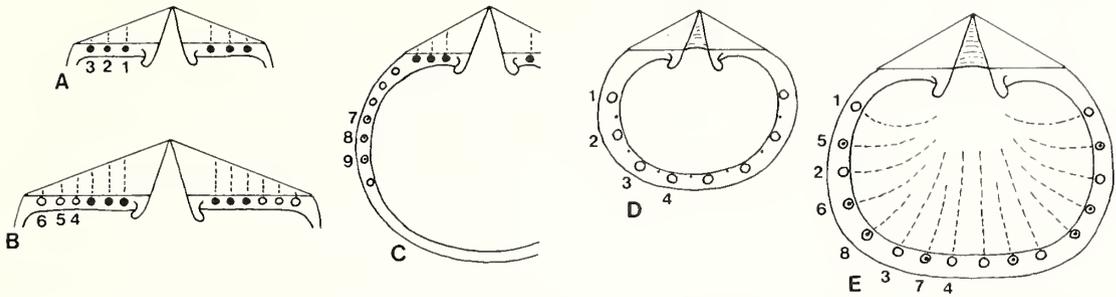
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1970) and Baker (1970) that *Thecospira* was of strophomenide affinity. Williams (1973), however, reiterated his earlier (1968) view that *Thecospira* was of spiriferide affinity. Williams's view was supported by MacKinnon (1974) in his comprehensive survey of spiriferide shell structure which included a detailed study of the microstructure of *Thecospira* from the Triassic St. Cassian Beds of northern Italy. Dagus (1973) studied a wider range of material than was available to MacKinnon and established beyond doubt that the shell structure of thecospirids is almost identical with that of middle Jurassic thecideaceans, such as *Moorellina* and *Minikonstantia*, even to the extent of the dissimilarity of the structure of the brachial and pedicle valves. Thecospirids, therefore, both morphologically and in the organization of their secondary shell fabric, are much closer to thecideidines than they are to any undoubted spiriferides and there can be little doubt that the relationship is a genetic one. Dagus (1973, p. 367) concluded that among the thecospirids *Hungaritheca* is in all probability ancestral to the Thecideidina. I agree that *Hungaritheca*, if not actually ancestral to the thecideidines, is certainly very close to the thecideidine line of descent. The plexus of descent of the thecideidines is thus inextricably linked with the derivation of the thecospirids also. Prior to Dagus's (1973) evidence, I had previously expressed the opinion that thecideidine tubercles might be the functionally modified homologue of the strophomenide pseudopunctae (Baker 1970, p. 97). This opinion must now be revised as granular calcite appears to be the primitive tubercle core material in thecideidines. The evidence is also weak from a paedomorphic point of view as the strophomenide taleola, even at a very early age, is characteristically flanked by laminar shell (Pl. 78, fig. 5). It now seems, therefore, that the strophomenide pseudopunctae have no counterpart among the Thecideidina. Consequently, the contention that the thecideidines might be descended from strophomenide ancestors is not supported by the present study.

In view of the demonstrable link between thecideidines and thecospirids, an important consideration arising from the new evidence is whether a similar link exists between the thecideidines and the spiriferaceans. In both *Unispirifer* and *Mimikonstantia* the rod-like granular calcite bodies possessed a distal accretion zone that remained slightly in advance of the secretion of secondary fibres which were subsequently deflected. Their growth pattern caused them to emerge along the hinge line as a row of tiny denticles in *Unispirifer* (text-fig. 1A) and along the inner margin of the valve edge as a row of small tubercles in the pedicle valve of *Mimikonstantia* (text-fig. 1E). In *Unispirifer* the denticle cores maintain a connection with the primary layer throughout their length (text-fig. 1B-D). Such cores would most easily have been formed by an invagination of the primary layer which, in the case of *Mimikonstantia*, may be regarded as having become 'pinched off' from the primary layer during their development (text-fig. 1F, G) to become totally ensheathed in secondary fibres. In *Unispirifer* the orientation of the denticles must mean that they were generated consecutively (text-fig. 2A, B) as the hinge line increased in length. Once initiated, the structures apparently continued to develop during the life of the animal. In *Mimikonstantia* on the other hand the tubercles show a systematic intercalary generation pattern (text-fig. 2D, E) which may be reconciled with the need to ensure the effective maintenance of the continuity of arrangement and location of the tubercles along the inner margin of the pedicle valve as growth proceeded. The difference in the location of the structures in the two genera is not a serious problem. Both sets of structures are sequential, with early and later representatives, and the arrangement of the tubercles bears the same relationship with the ventral umbo (text-fig. 1) irrespective of whether the structures are located in the ventral interarea or in the wall of the ventral valve. All that is required is a slight change in the growth pattern of the shell. Thecideidines have a relatively much shorter hinge line than spiriferaceans; therefore, if the trend towards the shortening of the hinge line was independent of the tubercle generation pattern, a slight change in the growth pattern of the shell could have resulted in the development of the structures along the lateral (text-fig. 2C) and, ultimately, the anterior margin of the valve. The same development pattern may have been triggered by a slight change in functional requirements (e.g. reef-association), in which case the change to an intercalary development pattern and the elimination of denticles and the appearance of tubercles in thecideidines may be explained as an evolutionary development.



TEXT-FIG. 2. Generalized diagrams to compare consecutive development patterns. A, B, *Unispirifer*, denticles in the ventral interarea as the hinge-line increases in length. D, E, *Mimikonstantia*, essentially intercalary pattern of the tubercles round the anterior border of the pedicle valve as the shell increases in size. C, cf. specimen BB84703 (Pl. 78, figs. 9, 10) hypothetical transitional stage with denticles along the hinge-line and tubercles on the lateral margins of the valve.

The above argument would obviously be strengthened if any early thecideidines showing some of the juvenile *Unispirifer* characters could be located. A search of the British Museum (Natural History) collections has revealed two specimens from the Inferior Oolite (horizon uncertain) of Dundry Hill near Bristol. BB84702 is a complete shell, 3.3 mm in width and assignable to aff. *Moorellina*, which has a ventral interarea (Pl. 78, figs. 6–8) showing clearly developed striations perpendicular to the hinge axis. BB84703 is a pedicle valve, 4 mm in width and assignable to cf. *Moorellina*, with a row of tubercles (denticles?) along the hinge line (Pl. 78, figs. 9, 10) in a position similar to that occupied by the denticles of *Unispirifer*. A broken tubercle (Pl. 78, fig. 11) appears to be composed of granular material, whereas the hinge tooth (Pl. 78, fig. 12) clearly displays a fibrous structure. This evidence, considered in conjunction with the microstructure described, convinces me that the spiriferacean denticle is homologous with the thecideidine tubercle. With regard to the thecospirids, Dagis (1973) described a pseudo-fibrous texture for the tubercle cores of the pedicle valve of *Thecospira communis* in which the individual fibres were composed of acicular grains of calcite. Williams (1973) described a similar arrangement in the secondary fibres of the teeth of *Thecidellina barretti* (Davidson). It is interesting that the granular denticle cores of the *Unispirifer* studied here have the appearance of a gross pseudo-fibrous fabric (Pl. 77, fig. 6) which may be correlated with the thecospiriid tubercle cores described by Dagis. Nalivkin (1976, p. 70) noted the presence of low narrow ridges and striae on the interareas of a number of spiriferides and concluded that during life the structures were associated with a covering of byssal attachment filaments. None of Nalivkin's material is available for study but the evidence from the British lower Carboniferous material, which enables the external ridges and grooves to be correlated with underlying structural elements of the interarea, is incompatible with his (1976) interpretation.

CONCLUSIONS

Characteristic though all the features evaluated by Williams (1973) are, the evidence indicates that cyrtomatodont teeth, secondary fibrous shell, tubercles, and the ability to resorb large tracts of shell material must be regarded as criteria of paramount importance in the indication of thecideidine ancestry. The morphological similarity previously cited as evidence of strophomenide or spiriferide affinity may simply reflect homoeomorphy. Shell microstructure, however, demonstrates unequivocally that the thecideidines are genetically related to the thecospirids and it is here recommended that the thecospirids should be assigned, as a taxon of superfamily rank, to the Thecideidina. The establishment of a genetic link between the shell microstructure of early middle Jurassic thecideidine and lower Carboniferous spiriferacean brachiopods leads to the conclusion that, however unlikely it may seem on morphological grounds, spiriferacean forms probably include the ancestral stock from

which the thecideidines and the thecospirids were derived. In this respect it is noted that the upper Devonian *Tenticospirifer* with its hemipyramidal pedicle valve and relatively flattened brachial valve is beginning already to approximate to thecideidine external morphology.

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PYROTHERIUM, A LARGE ENIGMATIC UNGULATE
(MAMMALIA, INCERTAE SEDIS) FROM THE
DESEADAN (OLIGOCENE) OF
SALLA, BOLIVIA

by BRUCE J. MACFADDEN and CARL D. FRAILEY

ABSTRACT. A well-preserved sample of *Pyrotherium* is described from at least two stratigraphic horizons in the Salla Beds of Bolivia. This sample is essentially indistinguishable from, and therefore conspecific with, the species *P. romeri* from Argentina. This represents the first description of this large herbivorous mammal outside of the classic 'Pyrotherium Beds' of Argentina. The presence of this biochronologically diagnostic taxon further supports previous assignments of a Deseadan (Oligocene) age for the Salla Beds of Bolivia.

THE Age of Mammals in South America is characterized by a highly unique and endemic fauna. The pyrotheres, or 'fire-beasts' (in reference to their occurrence in volcanic ash deposits), which are known from the late Palaeocene to the Oligocene in South America, are among the most enigmatic of eutherian mammals. Although of uncertain affinities, the Oligocene terminal member of this group is so distinctive and commonly encountered that it gave rise to the term 'Pyrotherium Beds' to characterize the Deseadan land mammal age as it was originally defined from Argentina (e.g. Ameghino 1895).

The original description of pyrotheres was based on the Deseadan genus *Pyrotherium* which has a diagnostic suite of characters including prominent upper and lower tusks, bilophodont cheek teeth, and large, graviportal limbs. Subsequently, more primitive forms have been described from earlier Tertiary localities in Argentina (see Simpson 1968), Colombia (Hoffstetter 1970), and Venezuela (Patterson 1977). The present paper describes new material from the Deseadan (Oligocene) Salla Beds of Bolivia. This paper is principally based on specimens collected during the 1960s by L. Branisa (then of LaPaz, Bolivia) for Princeton University. Other, more fragmentary, specimens were collected by the authors and associates during our 1981 and 1983 field seasons. The latter specimens do not contribute to an increased understanding of the morphology of Salla *Pyrotherium*. However, they are associated with precise stratigraphic data and they extend the palaeobiogeographic range of this distinctive taxon outside the classic Deseadan localities of Argentina.

The 'Estratos de Salla' have attracted much attention in the literature because of a very diverse and abundant Deseadan fauna (text-fig. 1). A general introduction to the geology of the Salla-Luribay basin has been presented by Hoffstetter (1968, 1976), Hoffstetter *et al.* (1971), and Villarroel and Marshall (1982). Various parts of the mammalian fauna have been presented including rodents (Hoffstetter 1976; Patterson and Wood 1982), marsupials (Villarroel and Marshall 1982), the earliest South American primate *Branisella* (Hoffstetter 1969; Wolff, in press, *b*), Argyrolagidae (Wolff, in press, *a*), and ungulates (Cifelli and Soria 1983*a, b*). The remainder of the rich Salla fauna presently is undescribed.

In early descriptions of *Pyrotherium* from the Deseado of Argentina, Ameghino (1895, 1902) believed these mammals to be similar and closely related to primitive proboscideans like *Palaeomastodon* from the late Oligocene Fayum of Egypt and *Deinotherium* from the early Miocene of the Old World. He believed that pyrotheres were the stem group from which the Old World proboscideans were ultimately descended. Loomis (1914) also considered *Pyrotherium* to be most



TEXT-FIG. 1. Location of the Salla Beds (triangle) of western Bolivia.

closely related to proboscideans. Gaudry (1909) concluded that *Pyrotherium* was unlike any known large mammal and did not fit into any then existing family. Patterson (1977), based on several basicranial characters, concluded that pyrotheres are notoungulates, although the characters used for this assessment have been criticized elsewhere (Simpson 1978, 1980; McKenna 1980). Other work (e.g. on tarsal bones) suggests similarities between pyrotheres and the Embrithopoda or Proboscidea (Cifelli 1983). All of the above mentioned hypotheses of relationships between pyrotheres and other eutherians require rather interesting palaeobiogeographical speculation. In the absence of any

unambiguous diagnostic characters, the pyrotheres are considered here as a separate order of eutherian mammals *incertae sedis*. Although the sample of *Pyrotherium* from Salla does not elucidate the phylogenetic affinities of this group, it is nevertheless important to place on record a description of this material from this relatively new and significant locality.

The following abbreviations are used in the text: LACM, Natural History Museum of Los Angeles County, Vertebrate Paleontology Collection; PU, Princeton University, Vertebrate Paleontology Collection; R, right side; L, left side; \bar{x} , mean; *s*, standard deviation; *V*, coefficient of variation; OR, observed range; mm, millimeters.

For relevant cheek teeth, the following measurements were taken: (1) greatest anteroposterior length including cingulum; (2) greatest transverse width across anterior loph and lophid; and (3) greatest transverse width across posterior loph and lophid. Because the dental homologies of advanced pyrotheres are uncertain, topographic names for dental characters are used in this paper (e.g. anterior loph rather than protoloph).

SYSTEMATIC PALAEOLOGY

Class MAMMALIA Linnaeus, 1758

Order PYROTHERIA Ameghino, 1895

Family PYROTHERIIDAE Ameghino, 1895

Pyrotherium romeri Ameghino, 1889

Text-figs. 2-3

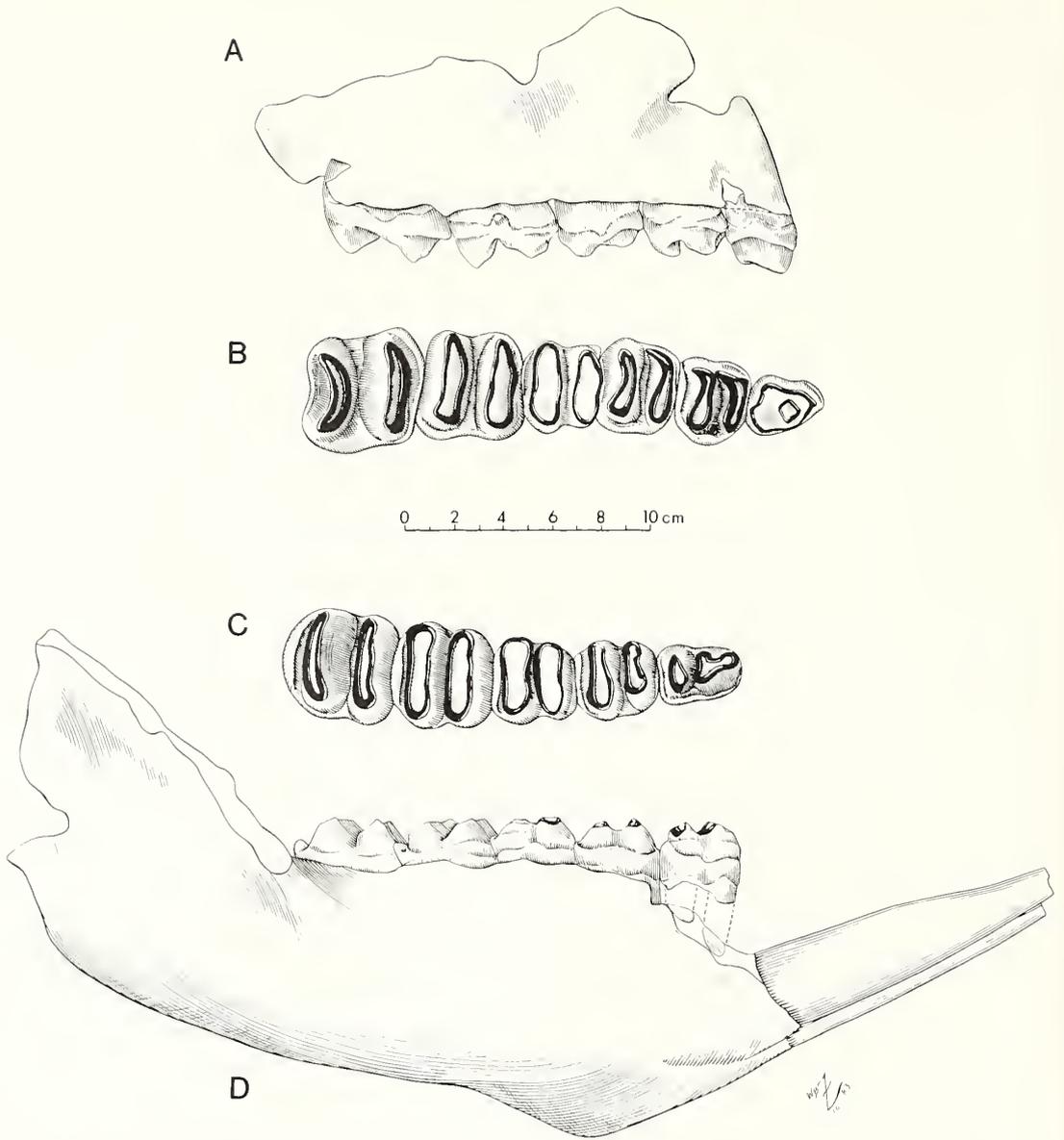
Referred material. Uppers: PU 20693, maxillary fragment with RP²-M³, LP², P²-M¹; PU 21919, LP³-M¹; PU 21917; RM¹-M³; PU 22146, anterior part LM³; PU 22143, LM³ fragment; PU 22143, posterior loph of M² or M³; PU 22144, posterior loph LM³; PU 22145, LM²; PU 22142, 21917, upper cheek teeth; PU 20683, premaxilla with parts of four incisors.

Lowers: PU 20679, mandible with fragment LI, R and LP₃-M₃; PU 20695, mandible with alveoli and RM₃; PU 21918, L ramus with M₂, M₃; PU 21989, R ramus with alveoli P₄, M₁, fragmentary M₂, M₃; PU 21921, fragmentary ramus with partial ?M₃; PU 22141, RP₃ fragment; PU 22147, LM₃ fragment; PU 20694, ramus with LP₃-M₃; PU 20684, mandible with R and LI, RP₃-M₃, LM₁-M₃ (also see uppers above); PU 20692, mandible with fragment R and LI, RP₃-M₃, LP₃, M₁-M₃; LACM 117571, LP₃-M₃; LACM 117572, RP₃, RM₃; LACM 117573, LP₃.

PU 22096, PU 22097, PU 22148; cheek tooth fragments. Also numerous uncatalogued specimens mostly consisting of tooth and postcranial fragments. There also are several uncatalogued fragments in the University of Florida—Servicio Geologia de Bolivia collection.

Stratigraphic distribution and age. Based on our field collecting and from specimens with relevant locality data in the PU Branisa collection, *Pyrotherium* occurs from at least two zones within the Salla Beds: (1) the lower part of the section above the Luribay Conglomerates (Branisa's Quebrada Chala Jahuira, Anchallani, V-12) and from the same general area, but *c.* 100 m below the base of the principal guide level, or 'Nivel Guia' (also see Villarroel and Marshall 1982); (2) the middle part of the section, which based on our field-work, includes the most fossiliferous concentrations (V-3, Tapial Pampa; also see Villarroel and Marshall 1982). Some of the better-preserved specimens in the Branisa collection come from Pasto Huarante. Unfortunately, the exact stratigraphic position of this locality is unknown (Branisa, pers. comm. 1983).

Description. As also noted for *Pyrotherium* from Argentina, the premaxillary region has four tusks; two on each half side and one behind the other. They emerge from the alveoli almost horizontally and curve downward to end almost vertically. The enamel is relatively thin, e.g. in contrast to proboscideans. The upper dentition consists of six cheek teeth, which are probably P²-M³. Relative to other Oligocene mammals from South America, *Pyrotherium* is very large as is reflected in its dental measurements (see Table 1). The P² is triangular in shape and consists of an anterior cone and two posterior cones connected by a loph (text-fig. 2). The P³ and P⁴ are molariform, i.e. they consist of well-developed anterior and posterior lophs as do M¹ to M³. There is a well-developed 'heel' on M³. On P³-M³ the lophs nearly comprise the total occlusal area of the tooth. In the premolars, these lophs sometimes merge at the external portion of the tooth almost forming an ectoloph. The enamel is breached during early wear exposing the dentine (this character persists throughout later wear stages). In the upper cheek teeth, the plane of shear on the lophs is antieriad. The cingulum varies from well developed to



TEXT-FIG. 2. *Pyrotherium romeri* from the Salla Beds. A, PU 20693, lateral view of R maxillary fragment with P³-M³. B, PU 20693, occlusal view P²-M³. C, PU 20694, occlusal view of R P₃-M₃. D, PU 20694, lateral view of mandible with anterior tusks and R P₃-M₃.

absent; characteristically it is strong on the anterior and internal parts of the teeth and poorly developed, rudimentary, or absent on the external and posterior portions of the teeth. In both the upper and lower dentitions the enamel is frequently crenulated, particularly on the cingulum.

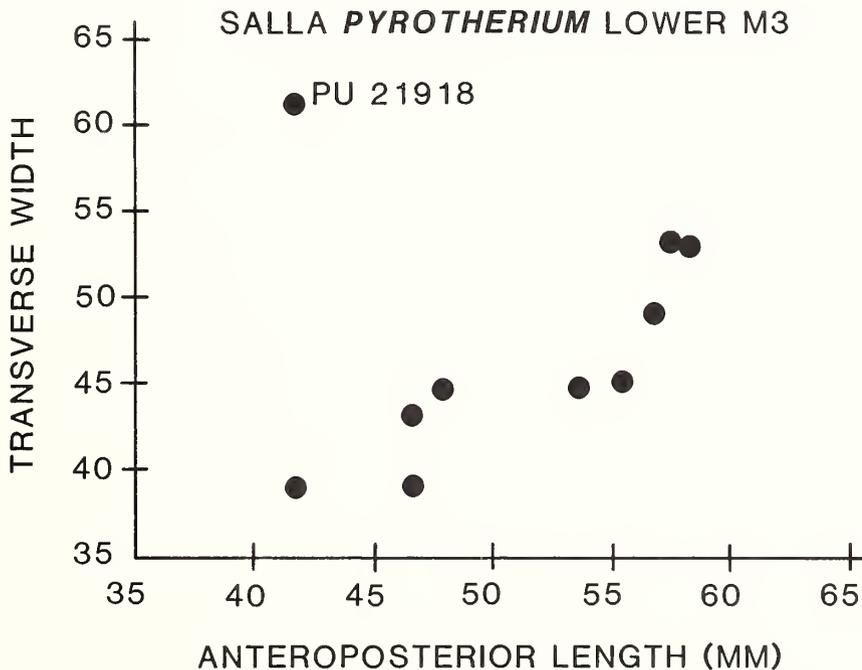
The mandible is relatively robust (text-fig. 2). The bony portion of the symphysis extends posteriorly to a position below P₄. The ascending portion of the ramus is dorsally abbreviated. Anteroventrally, the mandible is enlarged at the symphysis to accommodate the large pair of incisor tusks. The tusks are relatively robust and elongated with enamel only on the ventral side; dorsally dentine is exposed. The antermost tip of the incisor

tusks is characteristically flattened by wear. The lower dentition consists of five teeth, presumably P_3 - M_3 . P_3 consists of an antermost conid followed posteriorly by two lophids. P_4 - M_3 are generally similar in the presence of well-developed anterior and posterior lophids. As is also seen in the upper dentition, the enamel is breached during early wear exposing the dentine. The principal shear on the lophids is posteriad. The cingulum varies from well developed and continuous, particularly on the posterior portion of the teeth, to rudimentary or absent. In M_3 and, to a lesser extent in M_2 , there is a well-developed heel which seems to consist of an inflated cingulum.

DISCUSSION

The genus *Pyrotherium* was originally proposed by Ameghino (1889) to include the species *P. romeri* based on material from Patagonia, southern Argentina. As was characteristic of his taxonomic philosophy, Ameghino (1895, et seq.) later named at least four other species of *Pyrotherium* of which *P. soroudoi* has been most commonly cited in the literature. Although all of these 'species' were of roughly similar size, Ameghino and some later workers (e.g. Loomis 1914) mistakenly believed that *P. romeri* could be distinguished from the other species by the presence of P^1 . In a recent summary of pyrotheres, Patterson (1977) concluded that: (1) the ' P^1 ' of *P. romeri* is actually a deciduous tooth; and (2) all the Descadan species of *Pyrotherium* are synonymous. Therefore, *P. romeri* stands as the senior species and it is used in the present report.

So far as can be determined, in all characters of the dentition, the Salla sample of *Pyrotherium* is indistinguishable from that of Argentina. Therefore, the Bolivian material is confidently referred to *P. romeri*. In the Salla sample of *P. romeri* there is considerable variation in size as evidenced by V 's greater than 10 for certain characters (Table 1; text-fig. 3). With possible exception of one seemingly aberrant specimen (PU 21918, text-fig. 3), the Salla *P. romeri* corroborates Patterson's (1977) idea of a single morph. Comparisons of this sample with the measurements of three specimens of *P. romeri* from Argentina (Loomis 1914, p. 181) suggest that the Bolivian sample might be slightly smaller than



TEXT-FIG. 3. Bivariate plot of anteroposterior length versus transverse width of anterior loph for M_3 of Salla *Pyrotherium romeri* in the PU and LACM collections.

that of Argentina. However, more specimens and consistent measuring regimes would be necessary before any definite conclusion could be drawn from this possible difference.

In his preliminary faunal list Hoffstetter (1968) indicated a Deseadan age for the Salla Beds. One of the diagnostic taxa that he cited for this age assignment was *Pyrotherium* which Hoffstetter stated was common throughout the stratigraphic section. Our field-work confirms the presence of *P. romeri* from at least two horizons within the Salla Beds. However, it is neither as common nor as stratigraphically widespread as was observed by Hoffstetter. Perhaps the relative rarity during our recent field-work represents a collecting bias that has removed some of the more common, larger mammalian taxa during the two decades of prospecting in the Salla-Luribay basin. Of relevance to some of the allochthonous Salla taxa (i.e. rodents and *Branisella*), our field-work indicates that the principal fossil-bearing levels are concentrated in a relatively narrow stratigraphic interval some 75 m thick (between the Calabozo Pata I and Cebadal Churu/Huichinca levels of Villarroel and Marshall 1982) in the middle of our measured section (MacFadden, unpublished field-notes, 1981). These taxa co-occur with *P. romeri* within this zone thereby supporting a Deseadan age for the rodents, *Branisella*, and the other elements of the Salla fauna.

Acknowledgements. We thank Dr. Donald R. Baird of Princeton University for permission to study and borrow the Salla *Pyrotherium* and Patrick Leiggi, also of Princeton, for his curatorial assistance. The specimens described here were collected by L. Branisa and subsequently prepared at Princeton as a result of funds provided by the Gordon Barbour bequest. An enhanced understanding of the biostratigraphic framework of the Salla Beds resulted from our recent field-work in Bolivia that was supported by the U.S. National Science Foundation grants DEB 78-03122 and 79-05861. We thank the other members of those field parties and the Geological Survey of Bolivia (GEOBOL) for their significant contributions to successful expeditions. Drs. Kenneth E. Campbell, Jr., R. Hoffstetter, S. David Webb, Ronald G. Wolff, and Carlos Villarroel provided helpful comments that improved the manuscript. Mrs. Terri Anthony prepared the LACM specimens. Ms. Wendy Zomlefer skillfully prepared the text-fig. 2. This is University of Florida Contribution to Vertebrate Paleontology number 232.

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A NEW ACTINOLEPID ARTHRODIRE FROM THE LOWER DEVONIAN OF ARCTIC CANADA

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ABSTRACT. Actinolepid material from the lower Devonian of Prince of Wales Island, Arctic Canada, described as *Eskimaspis heintzi* gen. et sp. nov. closely resembles *Kujdanowiaspis* and *Heightingtonaspis*, especially in the pattern of the head shield. In comparison with *Baringaspis* which is associated with it, it differs mainly in the short nuchal plate and the ornamentation of scattered tubercles.

THE actinolepid arthrodires from the lower Devonian of Arctic Canada were first given palaeontological description by Miles in 1973, at which time *B. dineleyi* was established. Afterwards, a large amount of actinolepid material was collected in the same area by members of the Department of Geology, University of Bristol, in the summer of 1973. Recently, when we prepared this collection a distinct new form, *E. heintzi* gen. et sp. nov. associated with *B. dineleyi* was found. Meanwhile the new material suggests that some specimens designated as *B. dineleyi* by Miles in his description belong to *E. heintzi* too. The main purpose of the present paper is to give *E. heintzi* a brief description. Thus, only details of *B. dineleyi* not previously known are given here.

With the exception of the complete head shields, the remains consist mainly of disarticulated plates together with a few partial trunk shields. Most of the photographs included below are of the rubber casts following negative preparation with dilute hydrochloric acid.

The arthrodires occur in the Upper Member of the Peel Sound Formation at three localities: locality A at the bank of Porolepis Brook (= Miles's localities D + H); (Miles 1973, fig. 1); locality B at the bank of Forsyth Brook, about 1.5 km south of Baring Channel and 4.5 km west of locality A; locality C at the bank of Ermine Creek about 2 km south of locality A (text-fig. 1). The material is housed in the collections of the Palaeobiology Division of the Canadian National Museum of Natural Sciences, Ottawa, and bears National Museum catalogue numbers, prefixed NMC.

DESCRIPTION

Order EUARTHRODIRA
Suborder DOLICOTHORACI
Family ACTINOLEPIDIDAE
Eskimaspis gen. nov.

Etymology. After *Eskimo*, the aboriginal of the Canadian Arctic.

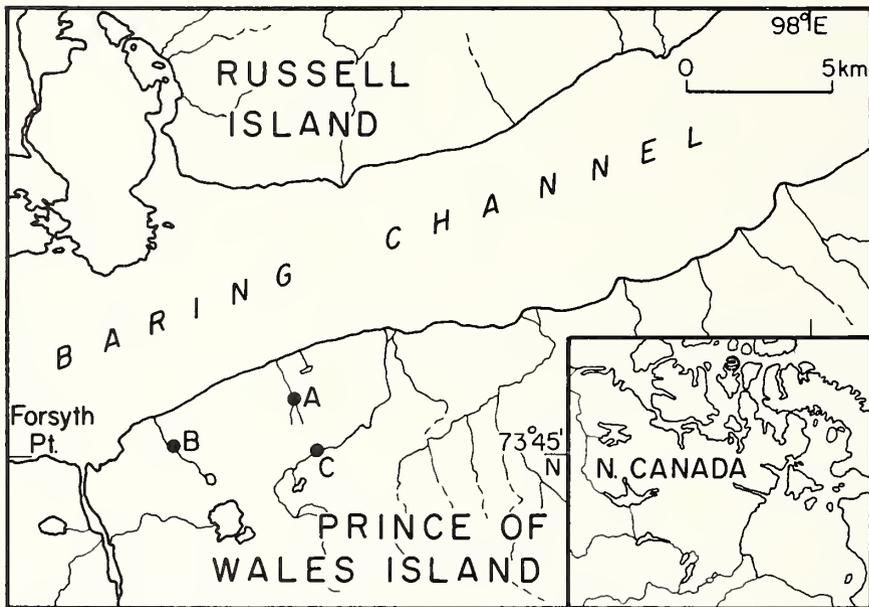
Diagnosis. An actinolepid arthrodire with narrow preorbital region, broad but short nuchal plate, wide paranuchals and broad anteriorly tapering straight-sided central plates, posterior dorsolateral plates deep, anterior lateral plates low, longer than high; ornamentation of scattered tubercles.

E. heintzi sp. nov.

Etymology. Species is named in honour of the late Professor A. Heintz.

Diagnosis. As for the genus.

Holotype. A nearly complete head shield with the counterpart, c. NMC 34101a and 34101b.



TEXT-FIG. 1. Southern coastal margin of Baring Channel, Prince of Wales Island, N.W.T., Canada, showing vertebrate-bearing localities in the Peel Sound Formation.

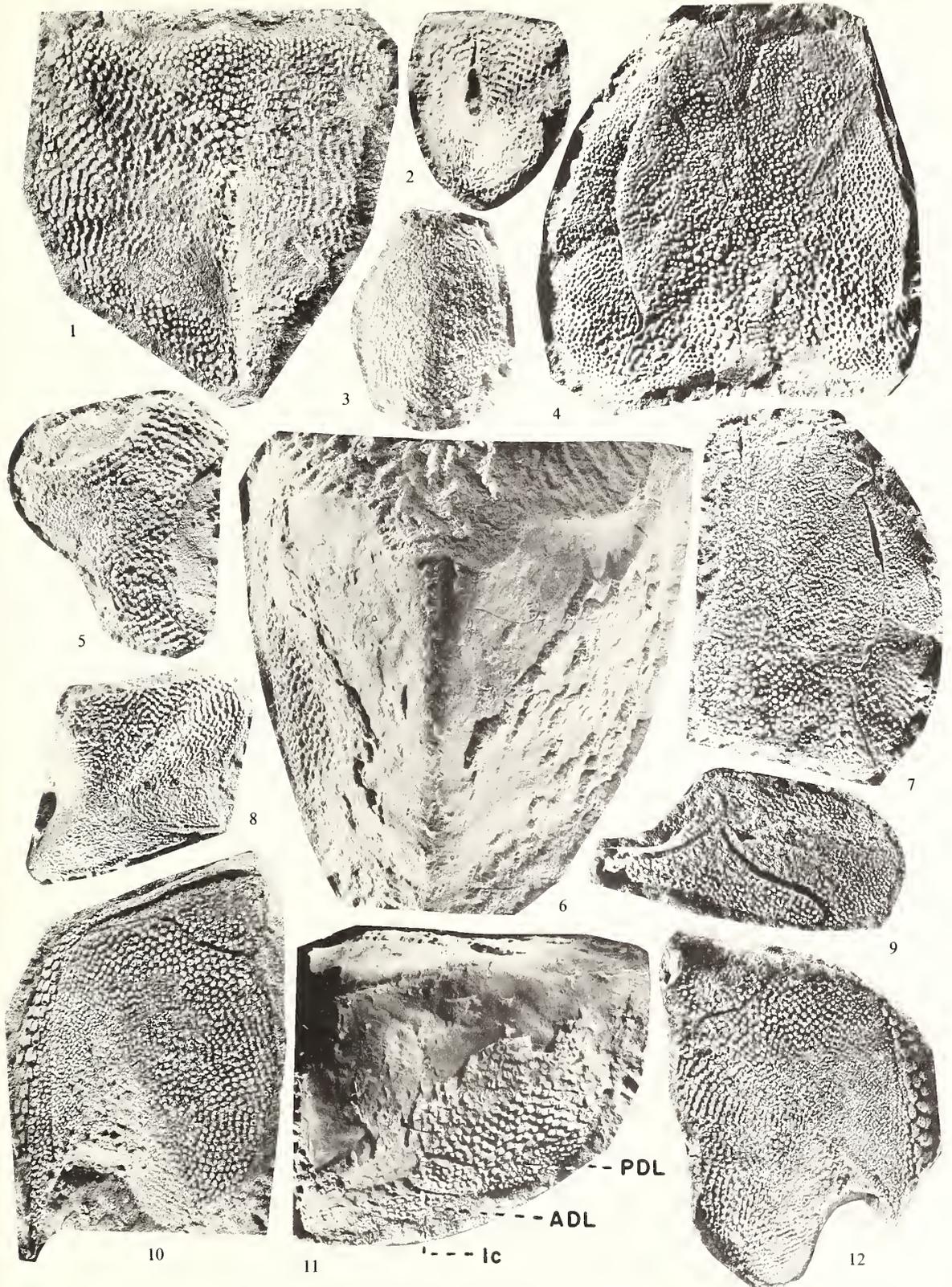
Locality. Early Devonian, Peel Sound Formation; Prince of Wales Island, Arctic Canada.

Description. Head shield (Pl. 79, figs. 4, 7; Pl. 80, fig. 5; text-figs. 2, 3A). At least six head shields are available. They are almost all the same in size, and the type is 43 mm in length excluding the rostral capsule. The roof is rather broad; despite the loss of the postmarginal plates its width is 52 mm crossing the antero-lateral corner of the paranuchal plate each side. The head shield has a typical outline of a dolichothoracan, with a moderate concavity for the reception of the separate rostral capsule, a quite narrow preorbital part in which the orbital notches are shallow but distinct. The lateral margins of the shield are smooth and regular, while the embayments for the postmarginal plates are shallow.

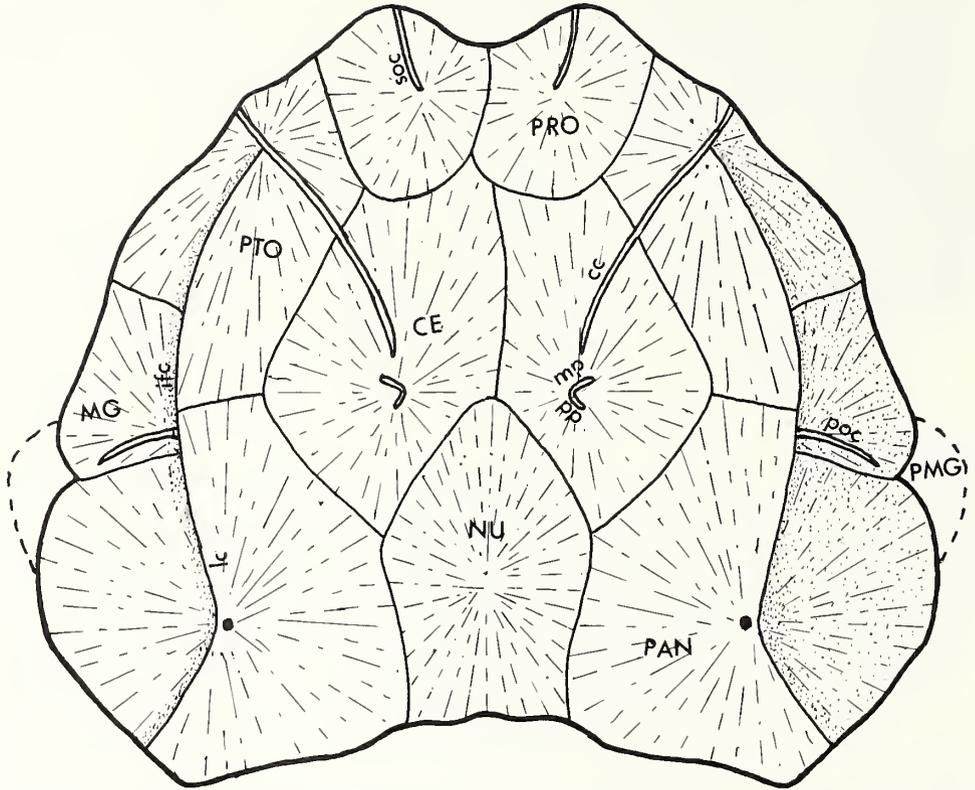
Owing to the complete fusion of the plates of the head shield, the sutures between them can be traced in only a few specimens. Closely comparing with *Kujdanowiaspis* and *Heightingtonaspis* (White 1969, figs. 29–32; text-figs. 3C, D this paper) the new form has a moderately long, five-sided nuchal plate which is with its pointed anterior end wedged between the posterior parts of the paired central plates. As that in *Kujdanowiaspis*, *Heightingtonaspis*, *Sigaspis* (Goujet 1973, fig. 3B) and *Baringaspis* (Miles 1973, fig. 2; text-fig. 3B this paper), the mesial margin of the marginal plate in *Eskimaspis* lies in the path of the main infraorbital sensory line. Nevertheless *Eskimaspis* is

EXPLANATION OF PLATE 79

Figs. 1–12. *Eskimaspis heintzi* gen. et sp. nov. 1, median dorsal plate, cast of 34120, locality A; $\times 1.5$. 2, posterior dorsal plate, type B, cast of 34119, locality A; $\times 2$. 3, posterior dorsal plate, type A, cast of 34118, locality A; $\times 2$. 4, head shield, cast of 34101, locality C; $\times 1.5$. 5, right posterior ventro-lateral plate, cast of 34116, locality A; $\times 1.5$. 6, median dorsal, anterior and posterior dorso-lateral plates, cast of 34117, locality A; $\times 1.5$. 7, head shield, cast of 34105, locality A; $\times 1.5$. 8, left anterior lateral plate, cast of 34113, locality C; $\times 1.5$. 9, left suborbital plate, cast of 34108, locality A; $\times 2$. 10, right intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34125, locality A; $\times 1.5$. 11, median dorsal, anterior and posterior dorso-lateral plates, cast of 34117, locality A; $\times 1.4$. ADL, anterior dorso-lateral plate; PDL, posterior dorso-lateral plate; Lc, main lateral line. 12, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34138, locality A; $\times 1.5$.



DINELEY and LIU, lower Devonian arthropod

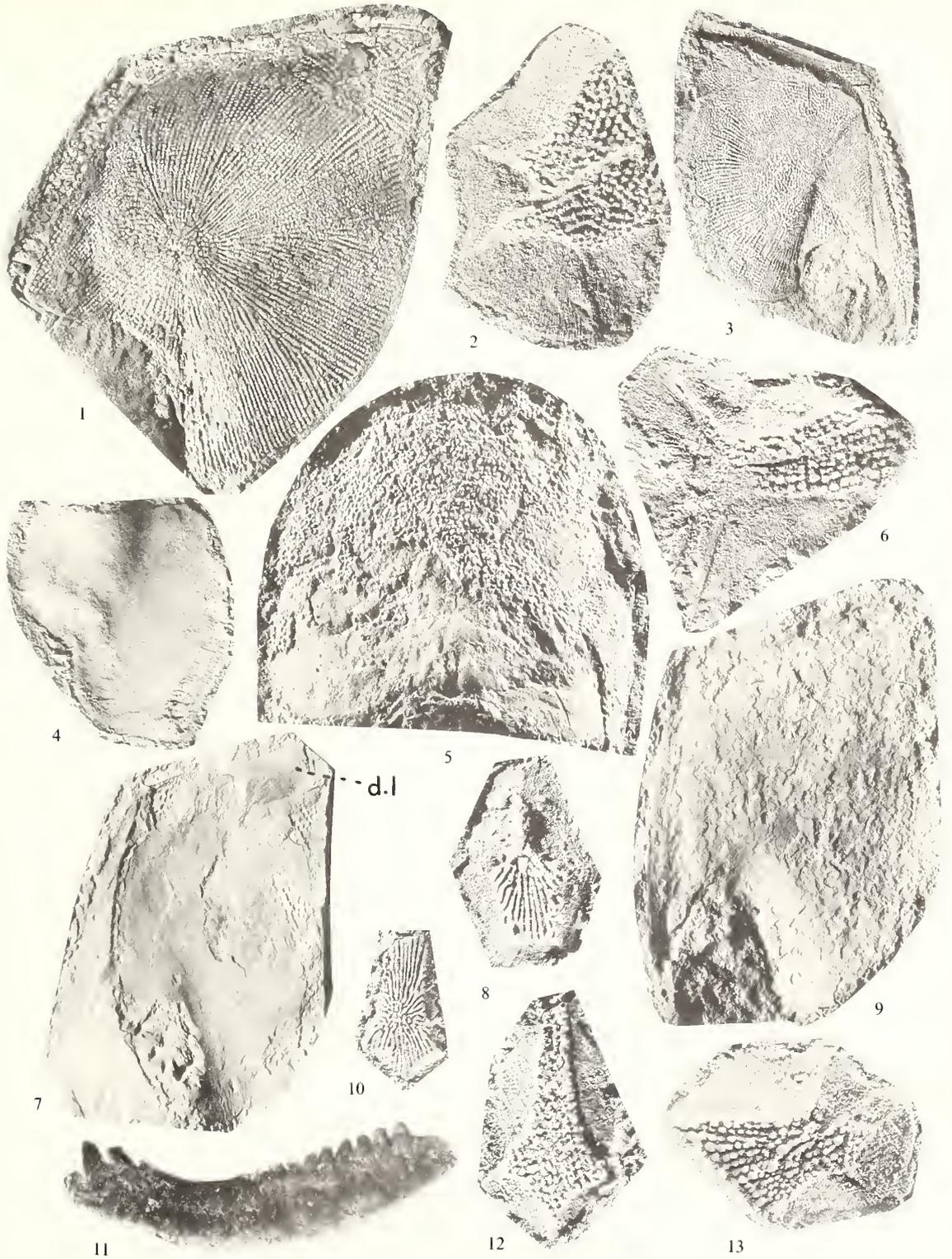


TEXT-FIG. 2. *Eskimaspis heintzi* gen. et sp. nov. Head shield in dorsal view, restored after holotype 34101, locality C; $\times 2$. CE, central; MG, marginal; NU, nuchal; PAN, paranuchal; PMG, postmarginal; PRO, preorbital; PTO, postorbital; cc, central canal; ifc, infraorbital canal; lc, main lateral line; mp, middle pit line; poc, preopercular canal; pp, posterior pit line; soc, supraorbital canal.

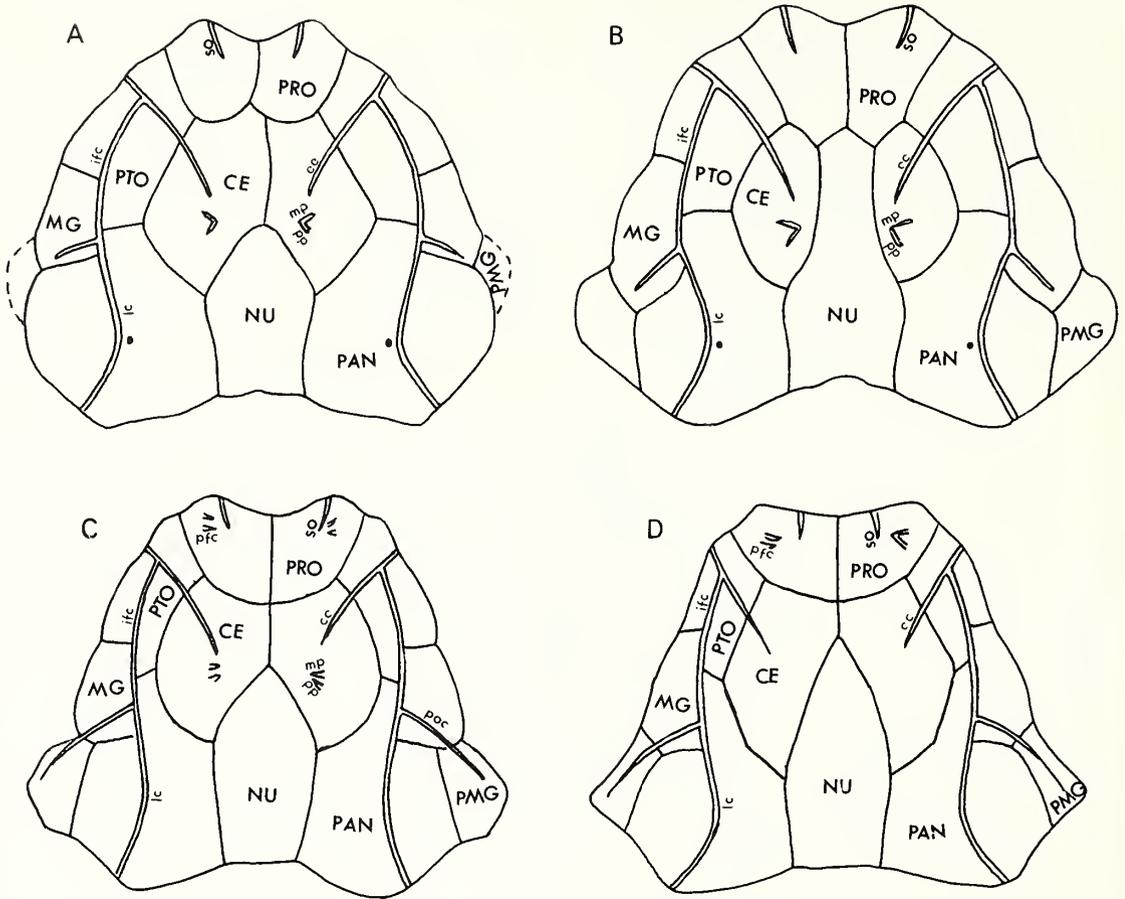
EXPLANATION OF PLATE 80

Figs. 2, 4-7, 9, 11-12. *Eskimaspis heintzi* gen. et sp. nov. 2, left posterior dorso-lateral plate, cast of 34110, locality A; $\times 2$. 4, left posterior ventro-lateral plate, 34111, locality C; $\times 1.5$. 5, head shield, cast of 34106, locality A; $\times 1.5$. 6, anterior dorso-lateral plate, cast of 34102, locality C; $\times 2$. 7, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34114, locality C; $\times 1.5$. d.l, dorsal lamina of intero-lateral plate. 9, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34126, locality B; $\times 1.5$. 11, arctolepida indet., right infragnathal, medial view, 34129, locality C; $\times 2$. 12, posterior medio-ventral plate, cast of 34139, locality A; $\times 1.5$.

Figs. 1, 3, 8, 10, 13. *Baringaspis dineleyi* Miles. 1, right intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34127, locality A; $\times 1.5$. 3, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34128, locality B; $\times 1.5$. 8, anterior medio-ventral plate, cast of 34143, locality A; $\times 1.6$. 10, posterior medio-ventral plate, cast of 34133, locality A; $\times 1.3$. 13, right posterior dorso-lateral plate, cast of 34135, locality A; $\times 2$.



DINELEY and LIU, lower Devonian arthropods



TEXT-FIG. 3. Head shields. A, *Eskimaspis heintzi* gen. et sp. nov., restored after 34101; $\times 1.2$. B, *Baringaspis dineleyi* Miles, after Miles 1973, fig. 2; $\times 1.2$. C, *Kujdanowiaspis* sp., modified from White 1969, fig. 30; $\times 0.9$. D, *Heightingtonaspis anglica* (Traquair), modified from White 1961, fig. 31; $\times 0.9$. CE, central; MG, marginal; NU, nuchal; PAN, paranuchal; PMG, postmarginal; PRO, preorbital; PTO, postorbital; cc, central canal; ifc, infraorbital canal; lc, main lateral line; mp, middle pit line; pfc, profundus canal; poc, preopercular canal; pp, posterior pit line; so, supraorbital canal.

distinguished from *Kujdanowiaspis* and *Heightingtonaspis* in detail, such as the proportionally larger width of the shield, the shorter nuchal, the broader paranuchals, and the finer tubercles.

The sensory lines of the head shield are arranged as in the other dolicho thoracans. However, the middle and posterior pit-lines, not usually seen in this group, display clearly at the termination of the supraorbital lines. Besides, the foramina of the endolymphatic ducts occurs at the top of the bend of the main infraorbital lines on the paranuchal plates in both specimens NMC 34104 and 34101.

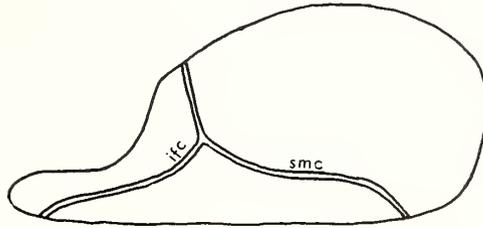
The ornamentation of the head shield consists of scattered tubercles, which in some parts, such as the paranuchal plates, have locally a linear arrangement or a tendency to concentric rows. The finer tubercles are crowded and lack regular distribution, while the larger ones are, on the whole, settled in the nuchal and mesial parts of the paranuchals as well as along some sutures.

As described above, *Eskimaspis* is distinguished from *Baringaspis* in the nuchal, paranuchal, and central plates. On the other hand, the tubercular ornamentation of *Eskimaspis* is different from the ridged one of

Baringaspis. This fact is important for our determination of the detached plates of both genera, which so far are always found together in Prince of Wales Island.

The visceral surface of the head shield is ill-disclosed in NMC 34016 (Pl. 80, fig. 5). The posterior margin of the shield is not thickened and is without the glenoid fossae for the articulation with the trochleae of the trunk armour. Of the endocranium only the occipital part is incompletely revealed. It emphasizes the similarity between the *Eskimaspis* and *Kujdanowiaspis*.

Cheek plate. The suborbital plates (Pl. 79, fig. 9; text-fig. 4), which are quite common in the collection, are the only cheek plates to be determined. They are as those described by Miles (Miles 1973, p. 112, pl. 13, fig. 2; pl. 14, fig. 5). On the basis of the tubercular ornamentation the suborbital plates both in the collection and as described by Miles, should belong to *Eskimaspis*, therefore, for the description of the plates readers are referred to Miles's paper. Surprisingly, in the great volume of the collections there has up to now been no suborbital plate determined as that of *Baringaspis*.



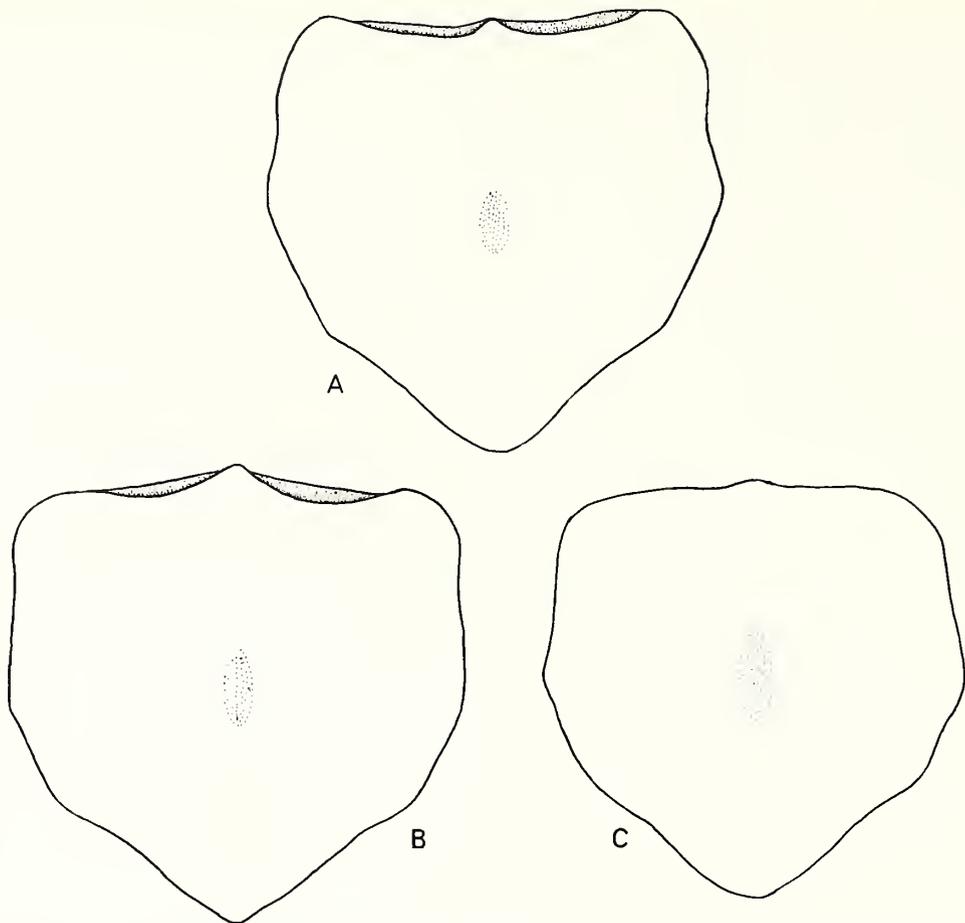
TEXT-FIG. 4. *Eskimaspis heintzi* gen. et sp. nov., left suborbital plate, after cast of 13226, unrecorded locality of Prince of Wales Island, in Miles 1973, Pl. 14, fig. 5; $\times 1.6$. ifc, infraorbital canal; smc, supra-maxillary canal.

Jaws. A lower jaw (Pl. 80, fig. 11) in the collection is for convenience described here; because of the lack of association it cannot be with certainty determined to belong to *Eskimaspis* or *Baringaspis*. It is exposed from medial side and bends towards the midline near its anterior end. The posterior end seems to be broken. On the dorsal face the bone curves slightly antero-posteriorly and in the posterior part nine small teeth can be seen, of which the anterior three have broken away. Further forward, the dorsal face is smooth without any teeth for about one-third of the length of the bone. At the very anterior end three large teeth are set. The transverse section of one broken tooth shows that the tooth is compact, without pulp cavity. Though the lower jaw cannot be examined in detail, comparing it with those of *Phlyctaenaspis* (Heintz 1935, pl. 11, figs. 3-4) and that of an actinolepid from the Water Canyon Formation of Utah (Denison 1958, fig. 101F) it is more similar to the latter.

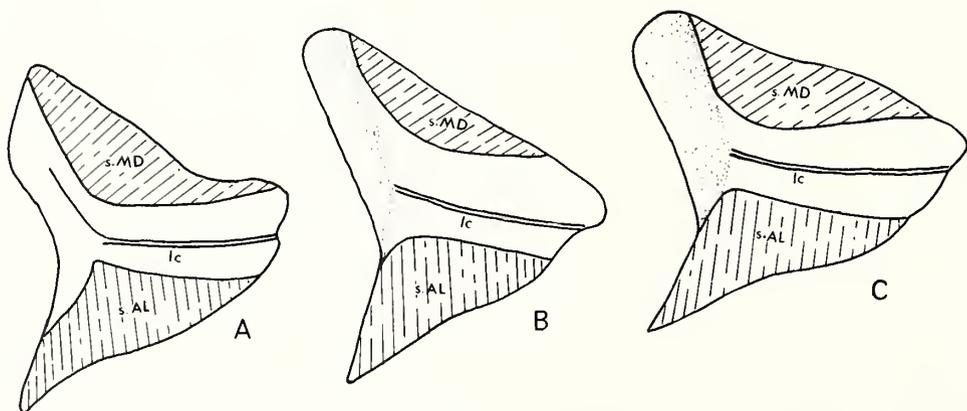
Trunk plates. Most plates of the trunk armour are detached, but some median dorsal plates are articulated with anterior dorsal-lateral plates, and with fragments of the posterior dorsal-lateral plates as well. As is the usual case in other dolichothoracans, the plates of the antero-lateral part of the ventral wall of the trunk armour are always associated as a unit.

The dorsal median plate (Pl. 79, figs. 1, 6, 11; text-fig. 5A) is typical actinolepid, short and broad (Denison 1958, pp. 515-518). In NMC 34120 it is 40 mm in length, 44 mm in width crossing the lateral angles. On the dorsal surface a median crest runs in the posterior half of the plate, while a pair of unornamented areas display along the anterior margin on both sides of the anterior median process of the plate. A posterior median lobe is developed as in most actinolepids. On the ventral surface a weak median crest has arisen (Pl. 79, fig. 11) which is interrupted to give two or three pieces in some specimens. The tubercles of the ornamentation are set in concentric rows except in the triangular area from the tip of the median crest to both anterior lateral angles of the plate where they are scattered and lack regular arrangement.

The anterior dorsal-lateral plate (Pl. 80, fig. 6; text-fig. 6A) has no trochlea for the articulation with the head shield. The ornamented surface is low, with a projection of the posterior margin dorsal to the lateral line. In this aspect the plate is similar to that of *Bryantolepis* (Denison 1958; text-fig. 108H) as well as *Baringaspis* (text-fig. 6B). The lateral line runs parallel to the edge of the overlap area for the median dorsal plate. The tubercles of the ornamentation are crowded and tend to rows parallel to the lateral line.



TEXT-FIG. 5. Median dorsal plates. A, *Eskinaspis heintzi* gen. et sp. nov., after 34120, locality A; $\times 1.5$. B, *Baringaspis dineleyi* Miles, restored after cast of 13264, in Miles 1973, pl. 15, fig. 4. C, *Kujdanowiaspis* sp., after Denison 1958, fig. 107I; $\times 1.6$.

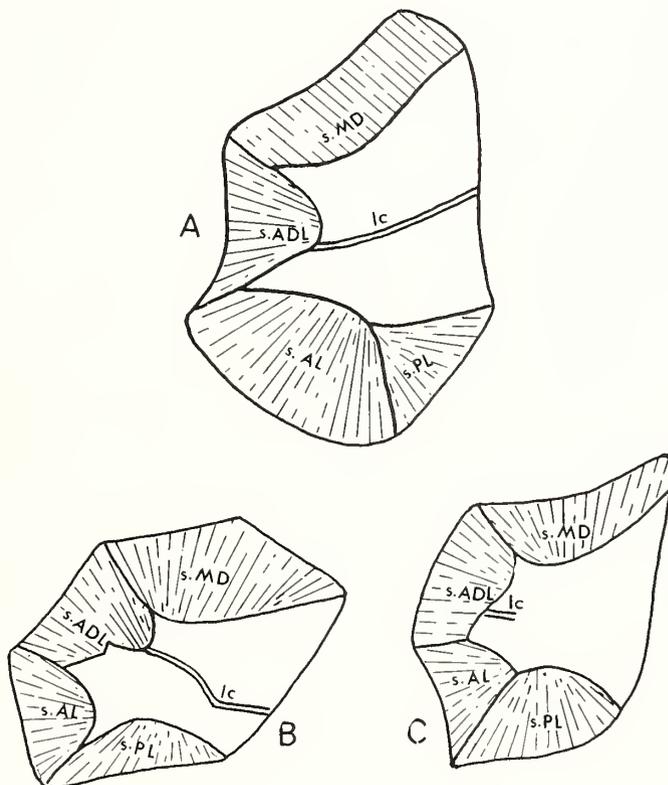


TEXT-FIG. 6. Left anterior dorso-lateral plates. A, *Kujdanowiaspis* sp. after Denison 1958, fig. 108I; $\times 1.7$. B, *Baringaspis dineleyi* Miles, restored after cast of 13263, in Miles 1973, pl. 4, fig. 1; $\times 2.4$. C, *Eskinaspis heintzi* gen. et sp. nov., restored after cast of 34102, locality C; $\times 2.2$. lc, main lateral line; s.AL, s.Md, overlap areas for anterior lateral and median dorsal.

The posterior dorsal-lateral plate (Pl. 80, fig. 9) is quite deep with wide overlap areas for the adjacent plates. The plate compares with that of *Bryantolepis* (Denison 1958, fig. 109H) and *Kujdanowiaspis* (Denison 1958, fig. 109I) in having an ornamented surface deep posteriorly and shallow anteriorly. It is unique in that the overlap area for the anterior lateral plate is strikingly large. To a great extent, therefore, the ornamented surface may be constricted ventrally by the overlap area of the anterior lateral plate, instead of the posterior lateral plate as in most actinolepids (Denison 1958, fig. 109). A longitudinal ridge divides the plate nearly equally. Part of the lateral line runs across the plate just under the ridge, and continues on the corresponding part of the anterior dorsal-lateral plate at an angle parallel to the lateral angle of the median dorsal plate (Pl. 80, fig. 11). The ornamentation consists partly of tubercles and partly of ridges.

A posterior dorsal-lateral plate of *Baringaspis dineleyi* occurring in this collection shows that it is shallower than that of *Eskimaspis* (both in overall proportion and in the ornamented surface alone), and like most actinolepids it has a moderate overlap area for the anterior lateral plate. The exposed surface is ornamented with lines of tubercles. The lateral sensory line crossing the plate is curved (Pl. 80, fig. 13; text-fig. 7B).

The anterior lateral plate (Pl. 79, fig. 8; text-fig. 8A), closely comparable with that of *Heightingtonaspis* (White 1969, fig. 22) and *Baringaspis* (Miles 1973, fig. 4), is little more than a parallelogram with the posterior dorsal corner rounded. But it differs from both genera in that the length is greater than the height. The focal-point from where the faint ridges dividing the plate into quadrants radiate is antero-ventral to the topographic centre of the plate. The anterior quadrant with very fine tubercles is inflected into an apron. A moderate embayment for the pectoral fenestra occurs in the posterior quadrant, which is roughly equal to the upper one in size. On the whole,



TEXT-FIG. 7. Left posterior dorso-lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34110, locality A; $\times 2.2$. B, *Baringaspis dineleyi* Miles, after cast of 34135, locality A; $\times 2$. C, *Kujdanowiaspis* sp., after Denison 1958, fig. 109I; $\times 1.5$. lc, main lateral line; s.ADL, s.AL, s.MD, s.PL, overlap areas for anterior dorso-lateral, anterior lateral, median dorsal, posterior lateral.

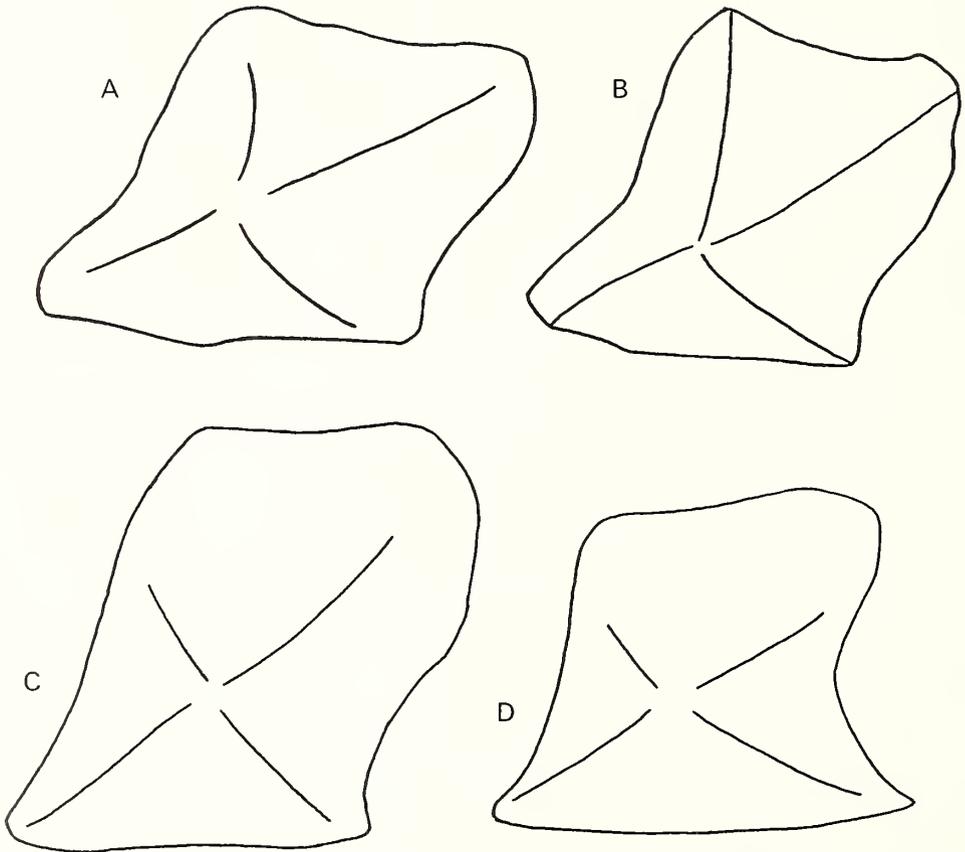
the nearer to the focal-point the tubercles of the ornamentation are, the finer they are. Meanwhile the tubercles are sometimes fused into disjointed rows.

The posterior lateral plate has not yet been determined.

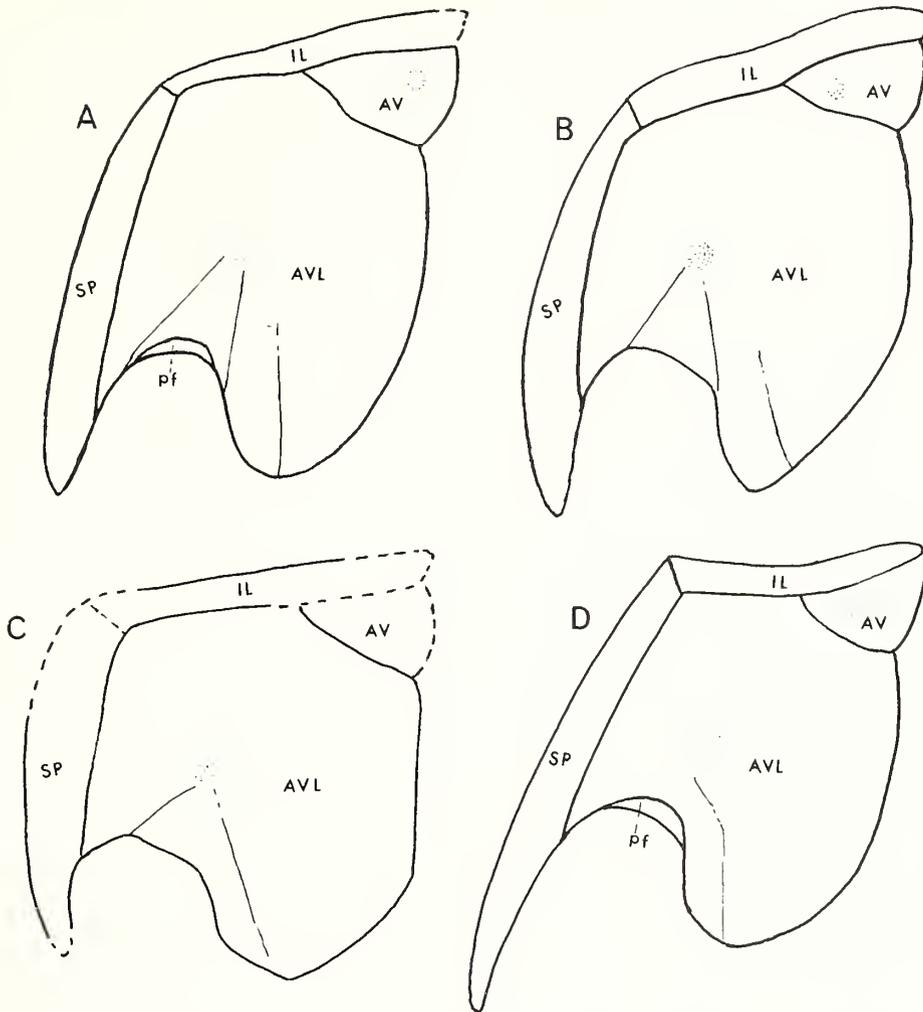
The ventral wall of the trunk armour with its pair of anterior ventral plates is of normal actinolepid type. On the whole, it is similar to that of *Baringaspis* disregarding the ornamentation.

The intero-lateral plate (Pl. 79, figs. 10, 12; Pl. 80, figs. 1, 3; text-fig. 9A) is identical to the pattern in most dolicho thoracans. Its ventral lamina is narrow, ornamented with scattered tubercles, which are as fine as those of the anterior quadrant of the anterior lateral plate. The dorsal lamina is not commonly preserved in the group but occurs in NMC 34114 d.1 (Pl. 80, fig. 7). It seems to be strongly infolded even allowing for distortion. The lamina is deeper and more uniform than in other genera. In contrast with that of the well-known genera of the group, it is remarkable for having a smooth surface without any ornamentation.

The anterior ventro-lateral plate and spinal plate are both similar to those of *Kujdanowiaspis* (Denison 1958, fig. 112H) and *Baringaspis* (Pl. 80, fig. 1; text-fig. 9B). The anterior ventro-lateral plate is relatively uniform owing to the less convex median margin and the moderate extension of the spinal margin in the posterolateral direction. A deep and narrow pectoral sinus occurs between the anterior ventro-lateral and spinal plates. The latter terminates level with, or over, the posterior margin of the anterior ventro-lateral plate. In some specimens the pectoral fenestra is displayed in counterpart. It is comparatively small, situated just at the top of the pectoral sinus and faces backward.



TEXT-FIG. 8. Left anterior lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34113, locality C; $\times 2.1$. B, *Baringaspis dineleyi* Miles, after Miles 1973, text-fig. 4; $\times 1.4$. C, *Heightingtonaspis anglica* (Traquair), after White 1969, text-fig. 33; $\times 1$. D, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 110H; $\times 2.1$.



TEXT-FIG. 9. Anterior paired plates of right side of venter. A, *Eskimaspis heintzi* gen. et sp. nov., restored after cast of 34123, locality A; $\times 1.4$. B, *Baringaspis dineleyi* Miles, restored after 34127, locality A; $\times 1.1$. C, *Heightingtonaspis anglica* (Traquair), modified from White 1969, text-fig. 35; $\times 1.1$. D, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 112H; $\times 1.3$. AV, antero-ventral; AVL, anterior ventro-lateral; IL, intero-lateral; SP, spinal; pf, pectoral fenestra.

The overlap areas on the anterior ventro-lateral plate (Pl. 80, fig. 10) suggest that the anterior medio-ventral plate is shorter than the posterior medio-ventral and the anterior ventro-lateral plate did not meet the posterior lateral plate.

The tubercles of the ornamentation in the anterior ventro-lateral plate tend to concentric arrangement, in the spinal plate they are enlarged, and flat-topped on the lateral margin.

The scapulocoracoid (Pl. 80, fig. 7) preserved on the visceral surface of the anterior ventral wall of the trunk armour is comparable with that of the *Kujdanowiaspis*. It consists of a coracoid and lateral process with grooves for cutaneous nerves and vessels.

The posterior ventro-lateral plate (Pl. 79, fig. 5; Pl. 80, fig. 4; text-fig. 10A) is closely similar to that of *Kujdanowiaspis* and *Baringaspis* in the subtriangular shape and proportional size.

The posterior medio-ventral plate (Pl. 80, fig. 12; text-fig. 11A) is remarkably long, with a narrow exposed surface ornamented with coarse tubercles. As in *Baringaspis* (Pl. 80, fig. 10; text-fig. 11C) the plate overlies the anterior medio-ventral.

The anterior medio-ventral plate has not yet been determined in the collection but, as said above, the adjacent plates suggest that it should be similar to that of *Baringaspis* (Pl. 80, fig. 8; text-fig. 11B), i.e. shorter than the posterior.

The overlap between the two medio-ventral plates is in a few instances known in dolichothoracans. Nevertheless, the genera well known in this aspect show that the longer of the two plates usually overlies the shorter. The present anterior plate is longer and overlies the posterior such as in *Bryantolepis* (Denison 1958, fig. 113C) and *Anarthraspis* (Denison 1958, fig. 113D), conversely the longer posterior overlies the anterior in *Eskimaspis*, *Baringaspis* as well as '*Phlyctaenaspis*' (Denison 1958, fig. 113A), and *Phlyctaenaspis* (Denison 1958, fig. 113B).

Posterior median plates. Three detached plates behind the trunk armour occur in the collection. They are symmetric, strongly arched, from 16 to 18 mm in length. Two of them are suboval in shape, with a blunt anterior end. The third differs in having a deep slot in its anterior half. Their ornamentation of scattered tubercles is similar to that of the armour of *Eskimaspis*. In his paper Miles described some disarticulated plates in the Peel Sound Formation as posterior medians of *Baringaspis*. Of them, the one figured (Miles 1973, pl. 13, fig. 2) shows ornamentation identical to that of *Eskimaspis* rather than to that of *Baringaspis*, but it is much larger and broader than the plates mentioned above. Though similar plates behind the trunk armour were found in both dorsal and ventral midlines of the body in the well-preserved *Sigaspis* (Goujet 1973), the three plates in the collection are assumed to be dorsals because of their great convexity.

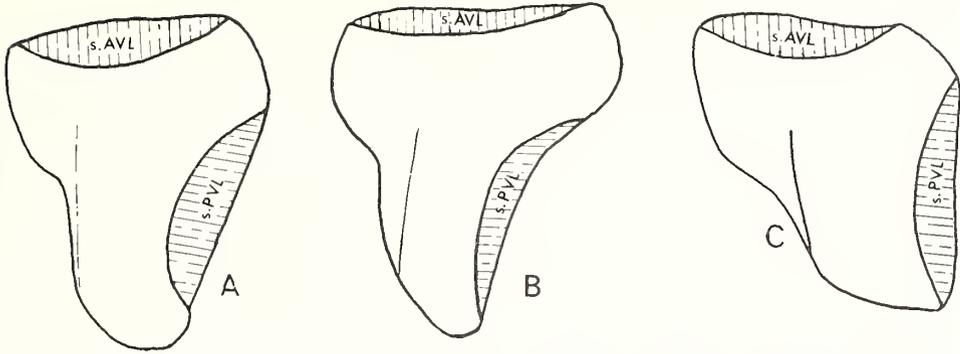
The age of the fish-bearing beds. The following vertebrates are associated with the arthrodires from the Peel Sound Formation south of Baring Channel.

	Location A	Location B	Location C
<i>Ctenaspis russelli</i> Dineley			X
<i>Escharaspis alata</i> Elliott			X
<i>Poraspis</i> sp.	X		
<i>Stegobrachiaspis baringensis</i> Elliott	X	X	X
<i>Weigeltaspis</i> sp.	X		
<i>Cephalaspis</i> sp.	X		
<i>Acanthodii</i> indet.	X	X	X
Poraspididae indet.	X	X	
Pteraspididae indet.	X		
<i>Crossopterygii</i> indet.	X	X	X

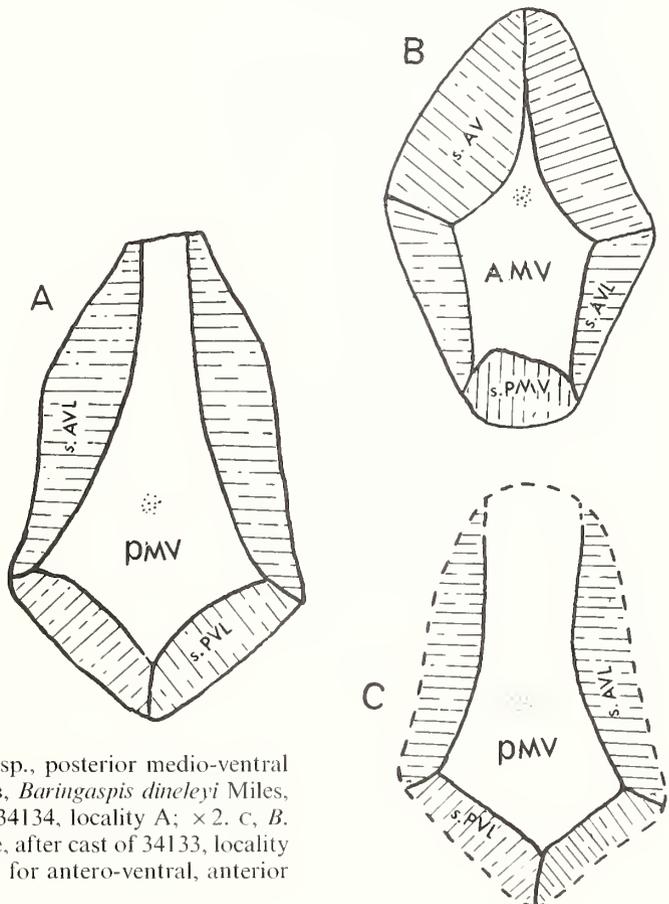
Elliott (1983) concluded that an age equivalent to the *crouchi* zone of the Anglo-Welsh succession (late Gedinnian) is probable on the basis of the fossils listed here.

As described above, *Eskimaspis* in many ways retains the primitive conditions proposed by Denison (Denison 1958, pp. 543-545) for dolichothoracans; in particular it approaches *Kujdanowiaspis* and *Heightingtonaspis* from the 'Old Red' Dnestrov Series of Podolia and the Dittonian of Britain respectively (Denison 1958, p. 500). Furthermore, together with *Baringaspis* and *Eskimaspis* occurs *Poraspis* sp. closely similar to *P. sericea* from the middle Dittonian of Britain. This tends to add weight to the opinion (Elliott 1983) that this part of the Peel Sound Formation is of middle Dittonian age which equates with the upper Gedinnian of the Rhenish facies.

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TEXT-FIG. 10. Right posterior ventro-lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34116, locality A; $\times 1.7$. B, *Baringaspis dineleyi* Miles, after cast of 13243, in Miles 1973, pl. 14, fig. 2; $\times 1.3$. C, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 114r; $\times 1.8$. s.AVL, s.PVL, overlap areas for anterior ventro-lateral, posterior ventro-lateral.



TEXT-FIG. 11. A, *Eskimaspis heintzi* gen. et sp., posterior medio-ventral plate, after cast of 34139, locality A; $\times 2$. B, *Baringaspis dineleyi* Miles, anterior medio-ventral plate, after cast of 34134, locality A; $\times 2$. C, *B. dineleyi* Miles, posterior medio-ventral plate, after cast of 34133, locality A; $\times 2$. s.AV, s.AVL, s.PMV, s.PVL, areas for antero-ventral, anterior ventro-lateral, posterior medio-ventral.

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THE PALAEOONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1983

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,413 on 31 December 1983, a decrease of 52 over the previous year. There were 910 Ordinary Members, a decrease of 32; 43 Retired Members, an increase of 8; 143 Student Members, a decrease of 15; and 317 Institutional Members, a decrease of 13. The number of institutions subscribing to *Palaeontology* through Marston's agency was 441, a decrease of 4. Subscriptions to *Special Papers in Palaeontology* number 122 individual, a decrease of 18, and 125 Institutional, a decrease of 5. Subscriptions to *Special Papers* through Marston's agency were 43 for *Special Paper 30*. Sales of back parts of *Palaeontology* via the Membership Treasurer totalled transactions realizing £608. There were no sales of back parts of *Palaeontology* to Institutional Members. Sales of *Special Papers* to individuals yielded £1,135. There were thirteen sales of *Special Papers* to Institutional Members. Sales of 77 copies of the *Atlas of the Burgess Shale* through the Marketing Manager yielded £775 plus U.S. \$1,550.

FINANCE. During 1983 the Association published Volume 26 of *Palaeontology* at an estimated cost of £54,252 (including postage and distribution). *Special Paper 30* was published at a cost of £14,729. In addition, *Fossil Plants of the London Clay* was published at an estimated cost of £4,850 and Cumulative Index (1970–82) at an estimated cost of £3,600. The Association is grateful to all who made donations.

PUBLICATIONS. Volume 26 of *Palaeontology*, published in four parts during 1983, contained 896 pages and 88 plates. The Cumulative Index to volumes 13–25 (1970–82) was published in November. *Special Paper 30: Trilobites and other early arthropods: papers in honour of Professor H. B. Whittington, F.R.S.* was also published in November 1983.

MEETINGS. Eight meetings were held in 1983. The Association is indebted to the organizers, hosts, and field leaders.

- a. *Review Seminar* on 'Cladistics and classification' held on 16 February at University of Birmingham. More than 200 attended the meeting. The local secretary was Professor A. Hallam.
- b. *Twenty-Sixth Annual General Meeting*, held in the Lecture Theatre of the Geological Society of London on 10 March. Professor A. Seilacher delivered the Annual Address on 'Evolutionary pathways in primary and secondary soft-bottom dwellers'. The Sylvester-Bradley Award was made to Mr. R. W. Hook.
- c. *Field Meeting*, organized by the Carboniferous Group, to the 'Carboniferous of north-west Ireland', led by Professor G. D. Sevastopulo, Mr. C. V. MacDermot, and Dr. M. E. Philcox. Sixty attended the excursion which was held on 15–18 April.
- d. *Review Seminar* on 'Palaeoceanography', held on 25 May at University College London. Twenty-five attended the meeting. The local secretary was Dr. A. R. Lord.
- e. *Field Meeting* on the 'Jurassic of North Yorkshire', held on 9–11 September, led by Dr. C. R. Hill. Seventeen attended. The organizing secretaries were Dr. C. R. Hill and Dr. P. D. Taylor.
- f. *Symposium on Autecology of Silurian Fossils*, held on 12–16 September at the University of Glasgow. This meeting was co-sponsored with IGCP Project Ecostratigraphy. Seventy-five attended. The local secretary was Dr. J. D. Lawson. Dr. E. N. K. Clarkson and Dr. G. Robertson led an excursion to the Pentland Hills.
- g. *Review Seminar* on 'Cephalopod palaeobiology', held on 16 November at Keele University. Ninety attended the meeting. The local secretary was Dr. H. S. Torrens.
- h. *The Annual Conference*, held at University College, Swansea, on 17–20 December, took the form of a one-day open meeting linked with a symposium on 'Evolutionary case histories from the fossil record'. One hundred and seventy attended. The President's Award was made jointly to Dr. P. R. Crane and A. T. Kearsley. Excursions were led to the Carboniferous and Jurassic of the Vale of Glamorgan by Professor D. V. Ager, and to the Precambrian–Llanvirn of south Dyfed by Dr. J. C. W. Cope and Dr. R. M. Owens. Dr. J. C. W. Cope and Dr. P. W. Skelton convened the symposium. The local secretary was Dr. J. C. W. Cope.

COUNCIL. The following members served on Council following the Annual General Meeting on 10 March 1983. *President*: Professor A. Hallam; *Vice-Presidents*: Dr. R. A. Fortey, Dr. J. C. W. Cope; *Treasurer*: Dr. M. Romano; *Membership Treasurer*: Dr. S. Kershaw; *Secretary*: Dr. R. Riding; *Marketing Manager*: Dr. R. J. Aldridge; *Editors*: Dr. D. E. G. Briggs, Dr. P. R. Crowther, Dr. L. B. Halstead, Dr. R. Harland, Dr. T. J. Palmer; *Other Members*: Dr. E. N. K. Clarkson, Dr. D. Edwards, Dr. P. D. Lane, Dr. A. R. Lord (Institutional Membership Treasurer), Dr. A. W. Owen, Dr. D. J. Siveter, Dr. P. W. Skelton (Circular Reporter), Dr. A. Smith, Dr. P. D. Taylor, Professor T. N. Taylor, Dr. A. T. Thomas, Dr. H. S. Torrens.

CIRCULARS. Four Circulars, numbers 111–114, were distributed to Ordinary, Student, and Retired Members, and on request to over 100 Institutional Members.

COUNCIL ACTIVITIES. During 1983 Council underwent major reorganization: the Executive Committee was dissolved and the total membership of Council was reduced to twenty. These changes have increased efficiency and reduced costs.

In addition to the regular field meetings and review seminars, the programme for the year was unusual in containing two international symposia. It is planned to publish the proceedings of both these as *Special Papers in Palaeontology*.

Publication of the new index of the last thirteen volumes of *Palaeontology* took place on schedule as part of the long-term planning for the journal. In addition, Volume 26, Part 3, incorporated the first of a series of specially commissioned review articles. The Association also published *Fossil Plants of the London Clay*, which it is hoped will mark the commencement of a series of handbooks.

Plans for future meetings include day-conferences sponsored in co-operation with the Geological Society of London.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING DECEMBER 1983

BALANCE SHEET AS AT 31 DECEMBER 1983

1982				
£	£		£	£
46,586		INVESTMENTS AT COST (see schedule)		46,586
		CURRENT ASSETS		
	3,824	Sundry Debtors	1,486	
	12,705	Cash at Bank	25,395	
	—	Sylvester Bradley Fund	1,912	
	<u>16,529</u>		<u>28,793</u>	
		CURRENT LIABILITIES		
	339	Subscriptions Received in Advance	2,215	
	13,250	Provision for cost of publication of <i>Palaeontology</i> 26/4	13,500	
	2,026	Sundry Creditors	9,631	
		Loan from Royal Society	2,000	
	<u>15,615</u>		<u>27,346</u>	
		Excess of current assets over current liabilities		1,447
<u>914</u>				<u>1,447</u>
<u>£47,500</u>				<u>£48,033</u>
		Represented by:		
		PUBLICATION RESERVE ACCOUNT		
	42,218	Balance Brought Forward	43,165	
		Excess of Income over Expenditure for the Year Transferred from		
	947	Income and Expenditure Account	970	
	<u>43,165</u>		<u>44,135</u>	
		SYLVESTER-BRADLEY FUND		
	2,010	Balance Brought Forward	2,021	
	211	Interest Received	91	
	(200)	Grant Awarded	(200)	
	2,021	Balance Carried Forward	<u>1,912</u>	
	<u>2,314</u>	MEETING RESERVE	<u>1,986</u>	
<u>£47,500</u>				<u>£48,033</u>

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1983

INCOME

1982		£	£
£			
	SUBSCRIPTIONS		
	1983	40,318	
	1982	275	
36,948		40,593	
	<i>PALAEONTOLOGY</i>		
	Sales	28,099	
	Donations	840	
26,063		28,939	
	<i>SPECIAL PAPERS</i>		
	Sales	6,080	
	Donations	1,200	
5,521		7,280	
44	PROFIT ON SALES OF INVESTMENTS		—
7,896	INVESTMENT INCOME (see schedule)		8,431
115	SUNDRY INCOME		330
	BURGESS SHALE PORTFOLIO		
	Sales	2,488	
	Postage/Stationery	(231)	
		2,257	
£76,587			£87,830

EXPENDITURE

	COST OF PUBLICATION OF <i>PALAEONTOLOGY</i>		
	Volume 26—Part 1	13,748	
	Part 2	13,524	
	Part 3	13,480	
	Part 4 (provisional)	13,500	
	Under Provision for Volume 25, Part 4	569	
50,648		54,821	
	COST OF PUBLICATION OF <i>SPECIAL PAPER</i>		
12,296	No. 30		14,729
	COST OF PUBLICATION OF CUMULATIVE INDEX (provisional)	3,600	
	COST OF PUBLICATION OF <i>FOSSIL PLANTS OF THE LONDON CLAY</i> (provisional)	2,425	
		6,025	
2,355	WAREHOUSING OF PUBLICATIONS		1,212
	COST OF CIRCULARS		
	Preparation	4,100	
	Postage	806	
	Credit	(875)	
4,932		4,041	
916	OFFPRINTS—LOSS		1,243
	GRANTS		650
	ADMINISTRATIVE EXPENSES		
	Postage and Stationery	1,639	
	Editorial Expenses	164	
	Meeting Expenses	2,076	
	Audit Fee	200	
	Membership of Societies	60	
3,217		4,139	
1,240	COST OF BURGESS SHALE PORTFOLIO		—
£75,640			£86,860
	EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO PUBLICATION RESERVE ACCOUNT		£970

SCHEDULE OF INVESTMENTS AND INVESTMENTS INCOME AS AT 31 DECEMBER 1983

		Cost	Gross Income
		£	£
£12,000	13¼% Exchequer Stock 1987	11,520	1,590
£1,000	9% Treasury Stock 1992/1996	992	90
£1,000	9% Treasury Stock 1994	955	90
£4,000	8% Treasury Stock 2002/2006	2,192	320
£5,357	13¼% Treasury Stock 1997	5,000	710
£3,280	13¼% Exchequer Stock 1996	3,000	435
£2,000	Agricultural Mortgage Corporation Ltd. 9¼% Debenture 1980/1985	1,938	185
5,270	M. & G. Charifund units	4,073	998
£2,425	Imperial Group p.l.c. 8% Convertible Unsecured Loan Stock 1985/1990	1,730	194
10,000	New Throgmorton Trust (1983) p.l.c. 25p Income Shares	1,706	314
1,600	Commercial Union Assurance Co. p.l.c. 25p Shares	2,157	270
700	Clarke, Nicholls & Coombs p.l.c. 25p Shares	668	52
5,000	Thorn EMI p.l.c. 7% Convertible Redeemable Second Cumulative Preference £1 Shares 1992/1999	5,009	500
6,180	M.E.P.C. p.l.c. 6½% Convertible Unsecured Loan Stock 1995/2000	4,943	402
374	M.E.P.C. p.l.c. 25p Shares	703	39
			6,189
	Bank Interest		2,242
		46,586	8,431
	MARKET VALUE at 31 December 1983 (1982—£57,589)	£68,428	

REPORT OF THE AUDITOR TO THE MEMBERS OF
THE PALAEOLOGICAL ASSOCIATION

In my opinion, the Accounts as set out on pages 891–893, give a true and fair view of the state of the affairs of the Association at 31 December 1983 and of its income and expenditure for the year ended on that date.

March 1984

Market Harborough, Leicestershire

G. R. POWELL
Chartered Accountant

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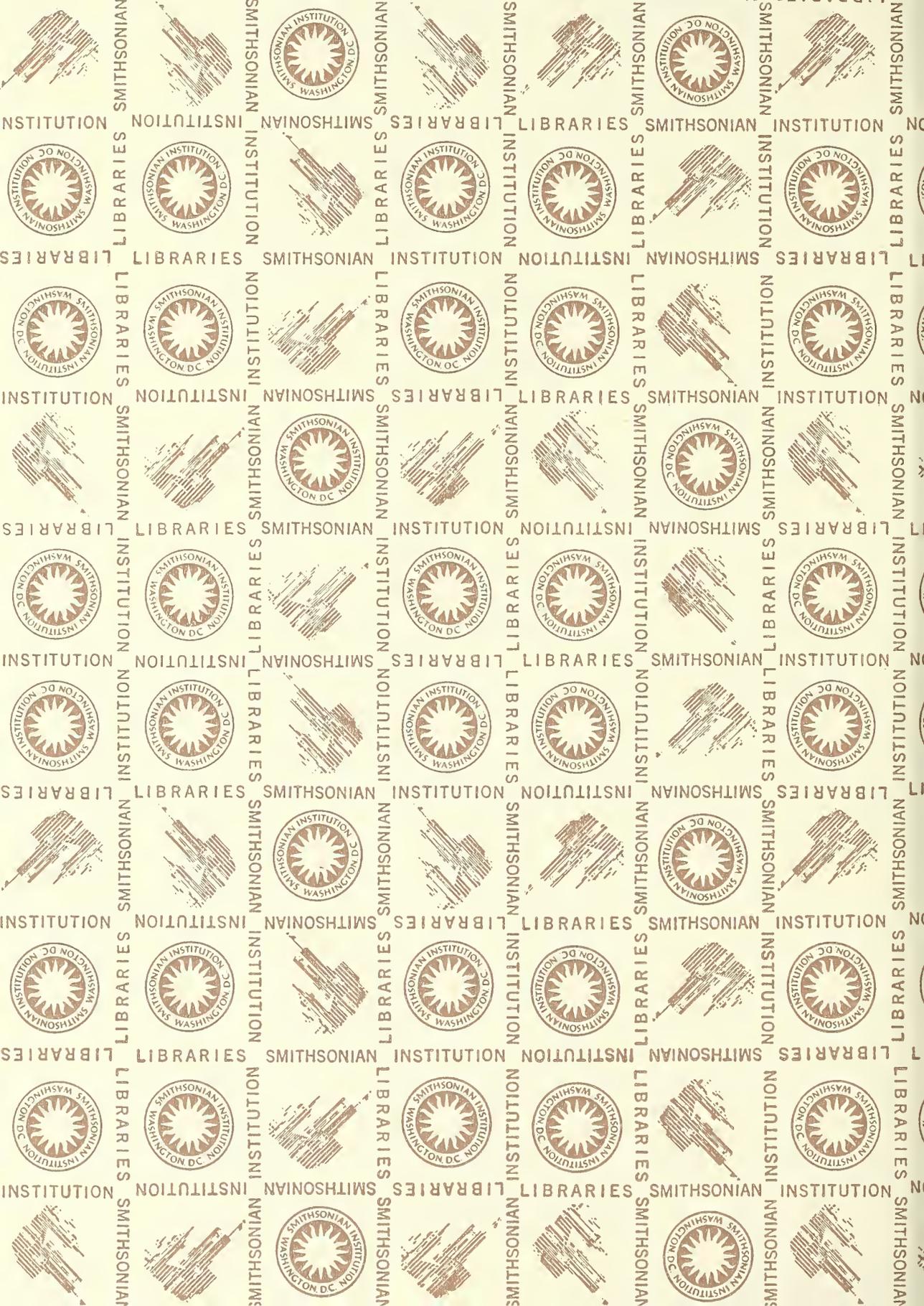
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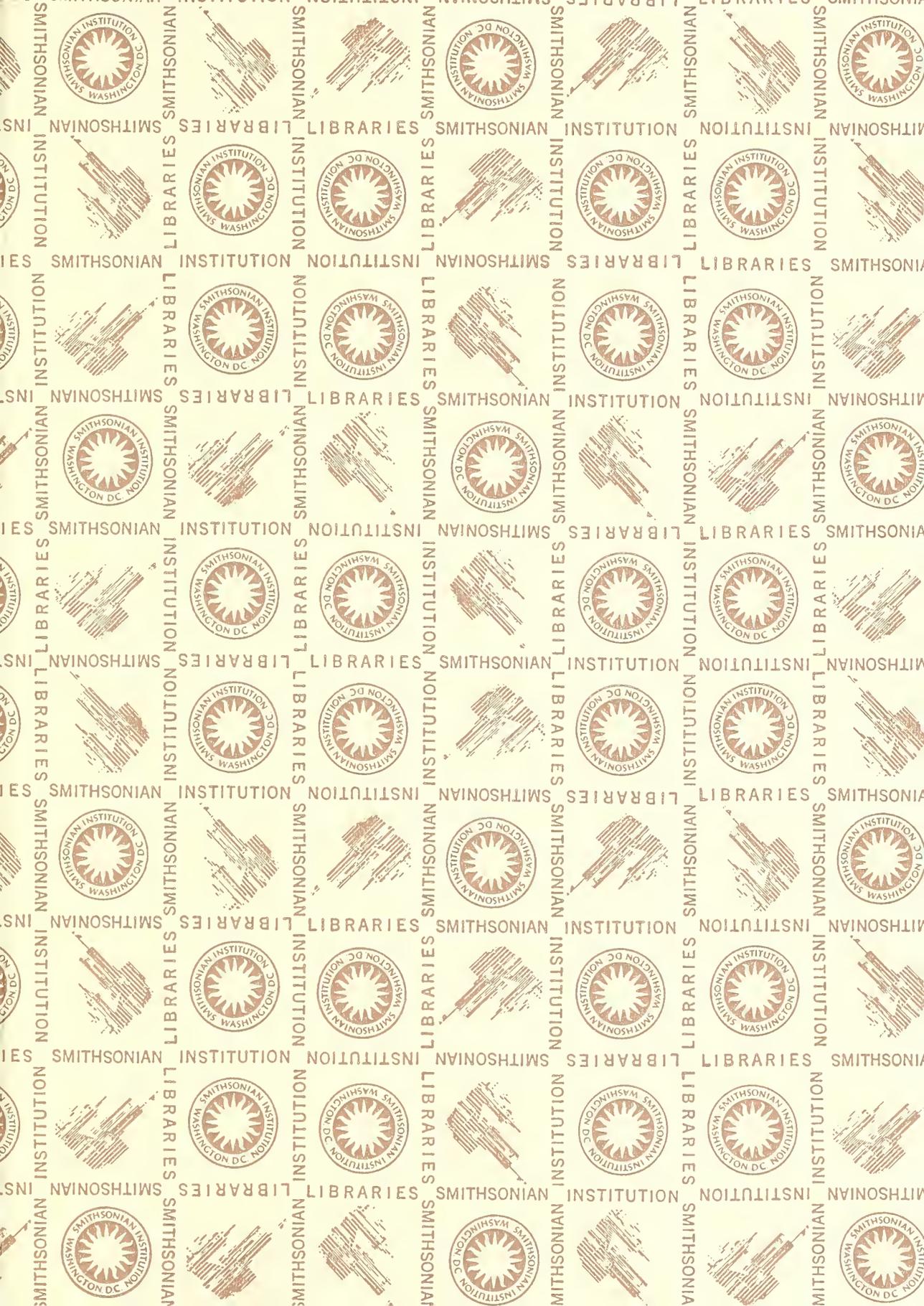
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